1 **Does initial spacing influence crown and hydraulic architecture of *Eucalyptus***

2 ***marginata*?**

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18 RUNNING TITLE: WATER USE ATTRIBUTES OF JARRAH IN RELATION TO

19 INITIAL SPACING

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21 **Summary**

22 In the face of long-term declines in rainfall in south-western Australia, the hydraulic

23 characteristics of jarrah (*Eucalyptus marginata* Donn Ex Smith) forest established in the

24 region's drinking water catchments have assumed greater importance. Much of this area is

25 also subject to bauxite mining. In this study we tested the following hypotheses for jarrah

26 forest established on rehabilitated mine sites: 1) Leaf area index (L) is independent of initial

27 tree spacing, 2) More densely planted trees will have less leaf area for the same leaf mass, less

28 leaf area for the same sapwood area and denser sapwood. Initial stand densities ranged from

29 approximately 600 to 9000 stems per hectare and trees were 16 to 18 years old at the time of

30 sampling. L was unaffected by initial stand density, except in the most sparsely stocked stands

31 that had L of 1.2 compared to 2.0 - 2.5 in the other spacing treatments. The ratio of leaf area

32 to sapwood area (A_l:A_s) was unaffected by tree spacing or tree size and was 0.2 at 1.3 m

33 height and 0.25 at the crown base. There were small increases in sapwood density and

34 decreases in A_l:A_s in more open stands. Tree diameter or basal area was a better predictor of

35 tree leaf area than sapwood area. At the stand scale, basal area was a very good predictor of L

36 ($R^2 = 0.98$, $n = 15$) except in very dense stands. We conclude that hydraulic attributes of this

37 forest type are largely independent of initial tree spacing, thus simplifying parameterisation of

38 stand and catchment water balance models.

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Introduction

The hydrologic function of jarrah (*Eucalyptus marginata* Donn Ex Smith) forest has recently assumed greater importance owing to long-term declines of rainfall in catchments close to Perth, Western Australia (IOCI (Indian Ocean Climate Initiative) 2002). The region has been mined for bauxite for over 40 years and, since 1988, an overstorey of native eucalpyt trees has been established on rehabilitated sites. Rehabilitation works aim to establish 500-2500 stems ha^{-1} (DOIR 2007). High densities at establishment can reduce rates of tree survival and growth (Stoneman et al. 1996, Koch and Ward 2005) but the impacts of tree spacing on the hydraulic characteristics of jarrah are less well known.

Growth of jarrah is principally limited by soil moisture and, unlike many other eucalypt species, jarrah is slow to self-thin (Stoneman et al., 1996). Hence, jarrah is an ideal species to test the effect of initial stand density on hydraulic characteristics such as leaf area index (*L*), leaf area to sapwood area ratio (A_l:A_s), sapwood permeability or density, and the ratio of leaf area to mass. *L* of rehabilitated stands of jarrah is often greater than that of the native forest, consistent with patterns recorded elsewhere in Australia for regrowth eucalypt forests following fire or logging (Cornish and Vertessy 2001, Vertessy et al. 2001). The response of *L* to initial tree spacing can be evaluated by changes in sapwood area and in A_l:A_s. There are few tests of the effect on A_l:A_s of either initial tree spacing or thinning in natural eucalypt forest. In eucalypt plantations, Medhurst and Beadle (2002) found that thinning influenced sapwood hydraulic conductivity of *E. nitens* (Deane & Maiden) Maiden trees but that A_l:A_s was unaffected. Pinkard and Neilsen (2003) also found that wider spaced *E. nitens* trees supported more leaf area, but that A_l:A_s was unaffected by initial spacing. In contrast A_l:A_s decreased after canopy closure in young stands of *E. globulus* Labill. and *E. nitens* (1998). A_l:A_s was smaller in suppressed trees in dense stands of *Pinus taeda* L. and *P. ponderosa* Dougl. ex P. Laws (Shelburne et al. 1993, Simonin et al. 2006) and is typically smaller in pine trees from dry versus wet environments (see Menucuccini and Grace 1995, Simonin et al. 2006 and references within). In *E. regnans* F. Muell., a species that is strongly

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70 self-thinning, sapwood permeability increases with age, but the relative increase in

71 permeability is less than the relative decrease in sapwood area of the forest. Thus there is an

72 overall decrease in hydraulic conductivity of sapwood at the stand scale (England and Attiwill

73 2007), which complements reductions in leaf area.

74   For a given rate of whole tree water use, variations in A_l:A_s imply either variations in

75 stem hydraulic conductance (k) or rates of leaf gas-exchange (Whitehead et al. 1984, Buckley

76 and Roberts 2005). Medhurst and Beadle (2002) found that k increased with increasing

77 growth rate in *E. nitens* plantations, hence, we might expect that slower growing jarrah trees

78 in denser stands might also have reduced k, compared to faster growing, more widely spaced

79 trees. The ratio of leaf area to leaf mass, specific leaf area (A_{sl}), also decreases as water

80 availability decreases such that more carbon and energy is needed to produce the same light

81 intercepting and gas exchanging leaf area (Eamus et al. 1999). There is evidence that A_{sl}

82 varies among genotypes across climatic gradients (Schulze et al. 1998, Cunningham et al.

83 1999, Fonseca et al. 2000, Lamont et al. 2002) but the evidence for within-genotype plasticity

84 of A_{sl} is less convincing. Anderson et al. (2000) and Macfarlane et al. (2004) found no

85 correlation between A_{sl} and rainfall within individual eucalypt species, but A_{sl} was about 20 %

86 larger for faster growing trees at a high rainfall site than for slower growing trees at a low

87 rainfall site in another study (Warren et al. 2006).

88   We took advantage of experimental plots planted in 1988 at four spacings in three

89 rehabilitated bauxite mine pits to test the hypotheses that L is independent of initial tree

90 spacing and that more densely planted trees will have smaller A_{sl} and A_l:A_s, and more

91 permeable sapwood. We used sapwood density as a proxy for its permeability (Barbour and

92 Whitehead 2003). We also tested Whitford's (1991) allometric relationships between leaf area

93 and a range of crown attributes, developed for trees in natural jarrah forest, on trees growing

94 in rehabilitated stands.

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Materials and Methods

Study sites

The study was conducted in 18-year old jarrah stands in rehabilitated bauxite mine pits at the Del Park and Willowdale mines, approximately 80km south-east of Perth, Western Australia. The stands had been established as part of a separate trial examining the effect of spacing, fertiliser application and understorey seed mix on subsequent tree growth and form (Ward and Koch 1995, Koch and Ward 2005). All pits were located in the high rainfall zone (1200 mm year^{-1}) of south-western Western Australia (Ward and Koch 1995, Koch and Ward 2005) and all had been rehabilitated using standard methods in the same year. As a consequence, and in conjunction with standardized treatment of topsoil and the generally similar nature of the ore bodies (e.g. depth below surface), all reconstructed soils were also similar (depth, texture).

In the present study, plots were selected to sample four tree spacings (1 x 1m, 2 x 2m, 2 x 4m and 4 x 4m) within a single fertiliser treatment (200g tablets of DAP fertiliser per tree at establishment) and understorey seeding mix (minor mix), at three replicate pits (Karri Rd, Scribbly and Scarp North). Plots consisted of 100 trees planted as tubestock in a 10 x 10 grid. Plot size therefore varied with spacing treatment, ranging from 0.001ha (1 x 1m spacing) up to 0.16ha (4 x 4m spacing). Further details of establishment are reported in Ward and Koch (1995) and Koch and Ward (2005).

Subjective tree assessments

The diameter at breast height (1.3 m) over bark (D) of all trees in the innermost eight rows of the twelve plots was measured in December 2005. In January-February 2006, four or five trees, representing the range of tree diameters in the plot, were selected in each of eight plots (two plots from each density treatment). At Scarp North, a further two trees were selected from the 2×4 treatment but none from the 4×4 m treatment because these stands were destroyed by wildfire in February 2006, before destructive sampling was completed. No trees were selected from the 1×1 and 2×2 m treatments at Karri Rd because of poor site access for

124   harvesting. *D*, bark depth and crown dimensions (tree height, crown depth and crown width)

125   of each selected tree were measured as described by Whitford (1991). The main crown was

126   defined by Whitford (1991) as the outline of the crown that is made up of contiguous leaf

127   clumps, i.e., "the crown width is an average crown diameter that excludes leaf clumps outside

128   of the main crown". To measure crown width, opposite edges of the crown were sighted from

129   below and using a plumb line, the distance between the edges was measured to ± 5 cm. We

130   measured height to the top of each tree and to the crown base, ignoring leaf clumps that were

131   more than a clump diameter below the main crown. Crown depth was calculated by

132   subtracting the height to the crown base from the tree top height. Subjective, visual crown

133   assessments of Grimes crown density, objective crown density and crown size (Grimes 1978,

134   Whitford 1991) were also made prior to felling. Interpretation of these standards relies on text

135   and diagrams that can be found in Whitford (1991) and Grimes (1978). Crown assessment

136   data were used to calculate leaf areas for each individual tree using equations derived by

137   Whitford (1991) for jarrah from unmined forest.

138

139   *Tree harvesting for measurement of sapwood area and density and leaf area*

140   Once the trees were felled, all limbs were removed and 10 cm thick wood discs from each of

141   the individual stems were cut at 1.3 m above ground level (which had been marked prior

142   felling) and at the crown base. If there were multiple stems at 1.3 m or at the crown base, then

143   discs were collected from each stem. Wood discs were sealed in labelled plastic bags and

144   stored in a fridge prior to measuring sapwood area. Branches were then removed and any

145   branches with a diameter larger than 15 mm were stripped of smaller branches so that all

146   leaved-branches had a diameter less than 15 mm. On the basis of a visual assessment of their

147   diameter, the branches were separated into three groups (large, medium and small) and

148   weighed. A subsample of branches from each group (more than 30 % of the total mass) was

149   immediately reweighed and stripped of leaves. The area of leaves from each subsample was

150   measured with a calibrated leaf area meter. The leaf samples were dried at 70˚C and weighed

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151   to calculate specific leaf area. The ratio of leaf area to fresh branch mass of the sample

152   branches was used to calculate the leaf area of all the branches in that size class. These were

153   summed for each sample tree to estimate its total leaf area. The ratio method of estimating

154   individual tree leaf areas has the advantage that the estimate of tree leaf area is constrained by

155   the known total canopy mass (Snowdon 1986), and the error in the estimation of the ratio of

156   leaf area to total branch mass is small if at least 30 % of branches are sampled (Snowdon

157   1986).

158   On each fresh wood disc, the under-bark diameter and heartwood diameter were

159   measured to the nearest 0.5 mm in two directions using a ruler; if one axis of the disc was

160   longer than the other then the long and short axes were measured. The natural colour change

161   between heartwood and sapwood in *E. marginata* was accentuated by staining with dimethyl

162   yellow to identify the sapwood-heartwood boundary. Sapwood area was calculated as the

163   difference between the total under-bark area and the heartwood area, which were calculated

164   from the averaged diameter measurements.

165   Using a hammer and chisel, sections of sapwood were removed from four sides of

166   each wood disc to determine sapwood basic density (ratio of wood dry mass to its swollen

167   volume). After soaking overnight, the sections were blotted dry and their volume measured by

168   mass of water displacement. The wood sections were then oven dried (70°C) and their basic

169   density calculated.

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171   *Photographic estimation of cover*

172   Cover images were collected during the afternoon on a grid in each plot using a Nikon

173   Coolpix 4500 camera. Nine images were collected from the 1×1 and 2×2 m plots, twelve

174   images from the 2×4 m plots and 16 from the 4×4 m plots. All digital photographs were

175   collected as FINE JPEG images with maximum resolution (3,871,488 pixels total). The

176   camera, without fisheye converter, was set to F2 lens, automatic exposure, Aperture-Priority

177   mode and minimum aperture (*f*/9.6). The lens was pointed directly upwards and the camera

178 lens was levelled using a bubble level fixed to an aluminium plate fitted between the camera

179 tripod mount and tripod.

180 The blue channel of the sharpened (medium) RGB images was analysed using

181 WinSCANOPY Pro 2006a (Regent Instruments, Ste-Foy, Quebec) as described by

182 Macfarlane et al. (2007). Sky pixels were separated from canopy pixels using a threshold

183 brightness value that was automatically determined by algorithms within the software.

184 WinSCANOPY separated large gaps from small gaps based on their area; gaps larger than

185 50,000 pixels (1.3 % of the total image area) were arbitrarily classified as large gaps and

186 foliage cover (f_f) and crown cover (f_c) were calculated after Macfarlane et al. (2007). Note that

187 the term "crown cover" describes the fractional ground cover of the vertical projection of

188 solid crowns that may or may not overlap, and which cannot exceed one. All calculations

189 were performed automatically by WinSCANOPY.

190

191 *Calculation of leaf area index and other statistical analyses*

192 Leaf areas and Ds were natural logarithm transformed and allometric regressions of leaf area

193 versus D were constructed for both individual stems and whole trees. Stronger correlations

194 were obtained using the leaf areas calculated for whole trees and all further analysis were

195 conducted on that basis. Analysis of covariance was used to test whether the slope and

196 intercept of regressions differed between different treatments (tree spacings), and was

197 calculated using the ordinary least squares method. All regressions of leaf area versus D were

198 corrected for bias using Snowdon's (1991) bias correction factor then applied to all trees in

199 each stand and their leaf areas summed to obtain leaf area index of each stand.

200 All statistical analyses were performed using Minitab released 13.1 (Minitab Inc.State

201 College, PA USA) except for the linear regression using the reduced major axis method

202 (McArdle 1988) for which PAST version 1.04 was used (Hammer et al. 2001). Forwards and

203 backwards stepwise regression was used to identify crown variables that were good predictors

204 of tree leaf area; the alpha value to enter and remove was set to 0.05.

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206   **Results**

207   *Effect of initial stocking rate on tree and stand attributes*

208   Slopes and intercepts of regressions of tree leaf area versus D did not differ between pits or

209   tree spacings (ANCOVA), hence, we used Equation 1 ($n = 49$, $R^2 = 0.70$, $P < 0.001$, BCF =

210   1.10) to calculate tree leaf areas and stand leaf area index (L):

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212    $\ln A_1 = 2.32 \ln D - 4.22$ (1)

213

214   L ranged from 0.85 to 2.83 and basal area ranged from 17 to 67 m^2 ha^{-1} (Table 1). Tree

215   height ranged from 7 to 14 m in the 2×2, 2×4 and 4×4 spaced stands, but was only 3 to 10 m

216   in the 1×1 m stands. One-way ANOVA and Tukey's test indicated that the stands with the

217   widest spaced trees had a smaller L than the other three treatments ($P < 0.05$), which did not

218   differ. L did not differ statistically between pits (one-way ANOVA). In contrast, cover

219   decreased with decreasing stocking rate (Table 1).

220   Sapwood area at 1.3m height was strongly correlated with basal area under bark

221   (Figure 1). Likewise, sapwood area at crown base was moderately well correlated with

222   sapwood area and basal area at 1.3m (Table 2). With few exceptions there was no heartwood

223   present at crown base. Leaf area was only moderately well correlated with sapwood area

224   (Figure 2; Table 2). A_1:A_s was unaffected by tree spacing (ANCOVA) and A_s at crown base

225   was roughly three-quarters that at 1.3m. As a result A_1:A_s was greater at crown base (0.25)

226   than at 1.3m (0.21).

227   Leaf specific area (A_{ls}) ranged from 49 to 51 cm^2 g^{-1}, did not differ between tree

228   spacings (ANCOVA) and was not correlated with tree height; there was a non-significant

229   trend for A_{ls} to decrease in wider spaced trees (Table 1). Basic density of sapwood, sampled

230   from either 1.3m or crown base, was not correlated with either D or tree height (ANCOVA).

231   At crown base, sapwood was less dense in 1×1 m spaced trees than in 2×4 m or 4×4 m spaced

232 trees, which did not differ from each other (Tukey's test, Table 1). Sapwood density of 2×2 m

233 spaced trees did not differ from that in the other spaced trees. A similar but non-significant

234 trend was observed at 1.3m. Sapwood density at the crown base was correlated with that at

235 1.3m (RMA slope = 1.00, R^2= 0.35, P<0.001). The increase in density between 1.3m and the

236 crown base was, on average, 0.025 g cm^{-3} (one-way ANOVA, P = 0.001).

237 Tree height, crown depth and crown width were all strongly correlated with D (Table

238 3); Grimes density and objective density were weakly correlated with D. Slopes and intercepts

239 of the regressions did not differ between spacing treatments (ANCOVA) except for height, for

240 which the largest and smallest intercepts were barely different (P = 0.04). Overall, trees with

241 larger diameters were taller and had wider, deeper crowns that, to a lesser extent, were also

242 denser. Hence, more widely spaced trees, which on average had larger diameters (Table 1),

243 had taller, wider and denser crowns. Despite this, basal area and cover decreased as trees were

244 wider spaced (Table 1) owing to the fewer trees per hectare.

245

246 *Prediction of tree leaf area from crown attributes*

247 Many of the crown dimensions and crown assessments were well correlated with tree leaf

248 area but, based on stepwise regression, crown area (CA) and Grimes density (GD) were the

249 best combined estimators of leaf area, while crown width (CW), crown depth (CD) and GD

250 were the best combined estimators of the square root of leaf area. Objective density was

251 highly correlated with GD but GD was always a better predictor of leaf area. Whitford (1991)

252 also found that crown width, CD and GD were good predictors of jarrah tree leaf area, hence,

253 we tested equations (ii), (iii), (iv), (vii), (viii) and (ix) from Whitford (1991) against our

254 dataset of tree leaf area (Table 4). Plots of all data were noticeably heteroscedascic. Equation

255 (ii), which contained only diameter under bark at 1.3 m height, performed the best based on

256 its small intercept, slope of nearly one, good correlation coefficient and small root mean-

257 squared error (RMSE); indeed it appeared to be as good a predictor of leaf area as equation 1

258 and a better predictor than sapwood area (Table 2). Including crown dimensions or crown

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259   assessments in the regressions actually appeared to make the estimates of tree leaf area worse

260   (Table 4). Of the regressions that did not include DUB, leaf area from equation (vii) provided

261   the best estimates of actual tree leaf area. Leaf area estimated from equation (viii) was most

262   highly correlated with actual tree leaf area, but this equation significantly overestimated leaf

263   area.

264   Given the lack of effect of tree spacing on ratios of basal area, sapwood area and leaf

265   area to each other, we decided to test how robust a simple relationship of L to basal area might

266   be across several recent studies in jarrah grown on rehabilitated mine pits, which ranged in

267   age from 12 to 18 years old. L was very highly correlated with basal area except for the very

268   dense (1×1 m) spaced stands (Figure 3). The OLS regression equation ($n = 15$, $R^2 = 0.98$, $P <$

269   0.001), excluding the dense stands, was:

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271    $L = 0.0464A_b + 0.213$ (2).

272

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Discussion

This is only the second study of the effect of initial tree spacing on hydrological characteristics of eucalypt trees and the most thorough test of the effect of tree spacing on L, A_l:A_s and sapwood density in eucalypts to date. Initial tree spacing had little effect on stand leaf area index (L) except in the stand with the most widely spaced trees. We judged that this stand was understocked based on its much smaller accumulation of basal area (Table 1). Whereas L was largely unaffected by tree spacing, cover increased with decreasing tree spacing. Specht's (1972) theory that canopies will be in equilibrium with the hydric environment, that is, rainfall, potential evaporation and soil moisture holding capacity, have been couched in terms of both foliage cover and L (see Specht and Specht 1999). Eagleson's (1982) hypothesis similarly suggested that canopy density will equilibrate with climate and soil to a value that maximises equilibrium soil moisture and Hatton et al. (1997) cited numerous studies supporting Eagleson's hypothesis. Ellis et al. (2005) used L in preference to cover to develop an "ecological optimality" model to predict deep drainage beneath tree belts. Assuming that the similar climate and soil type of our sites is indicative of a similar site water balance, our results also suggest that L is a better indicator of equilibrium site water balance than cover.

The hypothesis that trees in more densely planted stands would have smaller leaf area to sapwood area ratios (A_l:A_s), smaller leaf specific area (A_{sl}) and more dense sapwood was not supported. The overall weak trend was for trees in sparser stands to have denser sapwood and a smaller A_{sl}, and no statistically significant effect of tree spacing on A_l:A_s was detected. Unlike the study of Medhurst and Beadle (2002) in *E. nitens*, we found a linear relationship between leaf area and sapwood area at both 1.3 m and at the crown base, hence, A_l:A_s was affected by neither tree size nor stand density. Thus, it appears that this ratio could be used to extrapolate from sapwood area to leaf area at the stand scale. The ratio of A_l:A_s in jarrah was 20 % larger at crown base than at 1.3m; similar results were obtained for *E. nitens* (Medhurst

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300   and Beadle 2002). However, unlike that study, we found that sapwood area at crown base was
301   not a better predictor of leaf area, based on the smaller R^2 (Table 2).

302   Although sapwood area is generally preferred to basal area for leaf area estimation we
303   found that regressions of tree leaf area versus sapwood area in jarrah explained less of the
304   variation in leaf area (56-65 %) than that explained by tree basal area (70 %, Equation 1). At
305   the stand scale the relationship was even stronger ($R^2 = 98$ %) and, for the range of tree ages
306   studied, stand basal area appeared to be the best predictor of L in stands of jarrah grown on
307   rehabilitated mine sites (Equation 2), provided that the stands were not comprised mainly of
308   small trees. The 1×1 m spaced trees were in small 10×10 m plots and were much smaller trees
309   than in the other plots (Table 1); at the time of sampling they were surrounded by much taller
310   trees that had been established in wider spaced plots where there was presumably less
311   competition for light, water and nutrients between trees during the earlier stages of growth. At
312   the stand scale, plots of smaller trees had a smaller ratio of leaf area to basal area (Figure 3),
313   which is consistent with the smaller ratio of leaf area to sapwood area observed in suppressed
314   *Pinus* trees (Shelburne et al. 1993, Simonin et al. 2006). However, this finding contradicts the
315   results obtained at the tree scale; linear plots of basal area versus sapwood area (Figure 1) and
316   sapwood area versus leaf area (Figure 2) together suggest that the ratio of leaf area to basal
317   area should, if anything, be greater in smaller trees. Thus, the dense stands comprised mainly
318   of small trees would be expected to have larger ratios of leaf area to basal area than the
319   sparser stands. Instead the stand scale ratios derived from the allometric regression of
320   logarithmically transformed data for individual trees (Equation 1) yielded the opposite result
321   (Figure 3). Analysis of covariance failed to detect differences between treatments for
322   regressions describing any of the above relationships, and it may be that contradictory results
323   from the linear and logarithmic regressions simply reflect a lack of statistical power in the
324   analysis to detect that very densely spaced trees were different from the others.

325   Sapwood was denser at the crown base than at 1.3 m, which is consistent with many
326   other observations that hydraulic conductivity of stems declines with height (see Buckley and

327 Roberts 2005 for discussion and references), but is inconsistent with the increase of $A_l:A_s$

328 higher in the stem. It was expected that $A_l:A_s$ would be positively correlated with sapwood

329 hydraulic conductivity (Whitehead et al. 1984, Medhurst and Beadle 2002) and, thus,

330 negatively correlated with sapwood density, if xylem water potential is to be maintained near

331 constant in the stem (Buckley and Roberts 2005). This inconsistency may result from the

332 methods used in this study; the colour change and stain based method used to estimate

333 sapwood area in this study may be inaccurate or sapwood density in jarrah may not be a

334 suitable proxy for its hydraulic conductance. Bleby (2003) found that the colour change in

335 jarrah wood corresponded closely with the sapwood-heartwood boundary based on

336 microscopic examination of whether or not vessels were occluded, but this was only tested at

337 1.3 m height and not at crown base. We observed no colour change in wood at crown base in

338 most samples and, thus, concluded that in most cases all wood at the crown base was

339 sapwood. Microscopic examination of the vessels may have revealed that inner wood was, in

340 fact, non-conducting, although our finding of a decrease in sapwood area higher in the stem

341 was very similar to that found in *E. nitens* (Medhurst and Beadle 2002), which, together with

342 the work of Bleby (2003), gives us confidence in the sapwood areas measured. An alternative

343 explanation is that sapwood density is a poor proxy for hydraulic conductivity in jarrah; based

344 on a theoretical analysis, Roderick and Berry (2001) concluded that sapwood density would

345 be less sensitive to water balance in hardwood species than in conifers owing to their

346 fundamentally different wood anatomy, and it is possible that the sapwood density of jarrah

347 does not reflect its hydraulic conductivity. However, the density of sapwood was negatively

348 correlated with its hydraulic conductivity in *E. camaldulensis* (Dehn.) seedlings (Thomas et

349 al. 2004).

350   An explanation for the unexpected trends of sapwood density and A_{sl} with stand

351 density may lie in the different structures of the canopies. Cover generally decreased as tree

352 spacing increased, hence, the canopies of trees in the sparser stands more resembled those of

353 open-grown trees. Trees in more open stands may have had a larger fraction of their leaf area

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354 directly sunlit than trees in denser stands. More open stands would experience other

355 microclimatic differences such as faster wind speeds, which would tend to increase the

356 conductance of boundary layers and increase leaf transpiration rates. A_{sl} is sensitive to light

357 intensity in addition to water availability (Pearcy 1987, Ellsworth and Reich 1992, King

358 1994). Given the apparently constant ratio of A_l:A_s across all treatments, this might have

359 resulted in lower xylem water potentials in the stems of trees in the more open stands. It has

360 been suggested that xylem water potential is the critical signal for physiological changes with

361 height (Ryan et al. 2006), therefore it is reasonable to think that sapwood density is also

362 sensitive to water potential variations that might result from tree spacing, in this case, via

363 changes in canopy microclimate that might increase water use.

364 Whitford's (1991) equations based on canopy dimensions did not predict tree leaf area

365 as well as tree diameter. We had expected that estimates of leaf area based on crown

366 dimensions would be largely site or age independent, but this was not supported be our study.

367 Instead Whitford's (1991) equation (ii) yielded estimates of tree leaf area from diameter under

368 bark that were unexpectedly accurate given that the trees sampled by Whitford (1991) were

369 taken from natural forest and were up to three times taller than the trees sampled in this study.

370 That this study appears to support the use of equation (ii) to indirectly estimate leaf area of

371 jarrah trees, regardless of the age, size or growth rate of the trees, is surprising given that

372 allometric equations are expected to be climate, age and stand density specific (Menucuccini

373 and Grace 1995, Le Dantec et al. 2000). It is probable that crown assessments are more

374 important for predicting leaf area of larger, older trees that may vary in vigour; less vigorous

375 trees might have a diameter that does not reflect the size of the crown..

376

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503   Table 1. Mean (standard error in brackets) structural attributes of trees, stands and leaves for four

504   different tree spacings in three rehabilitated bauxite mine pits. Measured attributes include stocking rate

505   (SR, trees ha^{-1}), height range (m), leaf area index (L), basal area (A_b, m^2 ha^{-1}), median tree diameter (D,

506   cm), crown cover (f_c), foliage cover (f_f), sapwood density (ρ, g cm^{-3}) at 1.3m and the crown base, and

507   specific leaf area (A_{ls}, cm^2 g^{-1}).

Spacing	SR	Height	D	A_b	L	f_c	f_f	$\rho_{1.3}$	$\rho_{\text{crown base}}$	A_{ls}
1×1	8981	3.3-10.6	6.4 (0.37)	53 (7.2)	2.0 (0.36)	0.75 (0.060)	0.63 (0.048)	0.464 (0.0075)	0.475 (0.0053)	50.9 (1.30)
2×2	2292	9.0-14.7	13.8 (0.61)	51 (5.4)	2.5 (0.30)	0.61 (0.067)	0.53 (0.062)	0.481 (0.0110)	0.499 (0.0113)	50.2 (1.03)
2×4	1181	8.1-14.7	19.3 (0.64)	45 (3.3)	2.3 (0.19)	0.48 (0.072)	0.43 (0.064)	0.476 (0.0086)	0.515 (0.0079)	49.9 (1.82)
4×4	579	6.9-14.3	18.4 (0.77)	23 (4.3)	1.2 (0.27)	0.28 0.095	0.24 0.079	0.497 (0.0101)	0.525 (0.0069)	48.8 (1.48)

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510 Table 2. Relationships among tree leaf area (A_l, m^2), sapwood area at 1.3m ($A_{s,1.3}$, cm^2), sapwood area at the

511 crown base ($A_{s,cb}$, cm^2), and basal area under bark at 1.3m (A_b, cm^2). All regressions were significant to $P <$

512 0.001 ($n = 48$). Only intercepts that differed from zero ($P < 0.05$, t-test) are shown. Otherwise, no constant is

513 given (nc) and the slope was calculated forcing the regression through zero. All regressions were linear and no

514 data were transformed.

Y variable	X variable	Slope	Intercept	R^2
$A_{s,1.3}$	A_B	0.429	12.1	0.85
$A_{s,cb}$	A_B	0.388	nc	0.59
$A_{s,cb}$	$A_{S,1.3}$	0.746	nc	0.58
A_l	$A_{S,1.3}$	0.206	nc	0.64
A_l	$A_{S,cb}$	0.247	nc	0.56

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518   Table 3. Regressions of tree height, crown depth and crown width (all in metres), and Grimes density and

519   objective density, versus diameter at breast height over bark (D, cm). All regressions were significant to P <

520   0.001, except for Grimes density ($P = 0.003$). Asterisks indicate intercepts that differed from zero ($P < 0.05$, t-

521   test).

Crown attribute	n	Slope	Intercept	R^2
tree height	41	0.298	4.72*	0.71
crown depth	41	0.119	0.888	0.41
crown width	43	0.114	-0.0637	0.74
Grimes density	43	0.0529	3.26*	0.20
Obj. density	43	0.00941	0.472*	0.27

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525 Table 4. Ordinary least squares regressions ($n = 35$) of tree leaf area (A_l) estimated from destructive sampling

526 versus tree leaf area (LA) obtained from diameter at 1.3 m height under bark (DUB), crown width (CW), crown

527 depth (CD) or Grimes density (GD) using selected equations from Whitford (1991). The correlation coefficient

528 (R^2), significance of the regression (P), the significance of the t-test for slope $\neq 1$, and root mean-squared error

529 (RMSE) are also given. The 95 % confidence interval for all intercepts included zero except eq. iii. Canopy

530 attributes could not be measured for individual stems of forked trees, hence, the single-stemmed equivalent DUB

531 was used for forked trees.

Equation	Slope	Intercept	R^2	P	P (slope $\neq 1$)	RMSE
(ii) $A_l = 0.19 \times DUB^{1.73}$	0.95	-0.27	0.75	<0.001	0.62	5.6
(iii) $A_l = 0.238 \times CW^{1.47} \times GD^{1.95}$	0.79	3.57	0.58	<0.001	0.08	7.6
(iv) $A_l = 0.033 \times DUB^{1.45} \times GD^{1.71}$	0.92	-0.92	0.71	<0.001	0.34	6.9
(vii) $A_l = 0.199 \times CD^{1.56} \times GD^{1.43}$	1.08	2.94	0.67	<0.001	0.54	7.4
(viii) $A_l = 0.159 \times CD^{0.82} \times GD^{1.61} \times CW^{0.94}$	1.43	1.17	0.81	<0.001	0.001	7.5
(ix) $A_l = 0.052 \times DUB^{1.02} \times GD^{1.76} \times CW^{0.55}$	0.86	1.80	0.71	<0.001	0.15	6.1

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Figure captions

Figure 1. Relationship of tree sapwood area to basal area under bark at 1.3 m. See Table 2 for details of regressions. Open circles represent 1×1 m spaced trees.

Figure 2. Relationship of tree leaf area to sapwood area at 1.3 m. See Table 2 for details of regressions. Open circles represent 1×1 m spaced trees.

Figure 3. Leaf area index is tightly correlated with basal area over bark in 12-18 year old stands of *E. marginata* grown in rehabilitated mine pits. Data from 18 year old trees in this study (circles) were combined with data from 16 year old trees (squares) from the study of Macfarlane et al. (2007) and 12 year old trees (triangles) from the study of Grant and Norman (2006). The regression line was calculated excluding the 1×1 m spaced trees (open circles).

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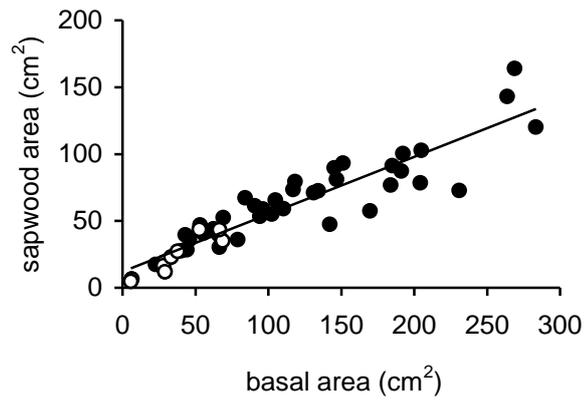
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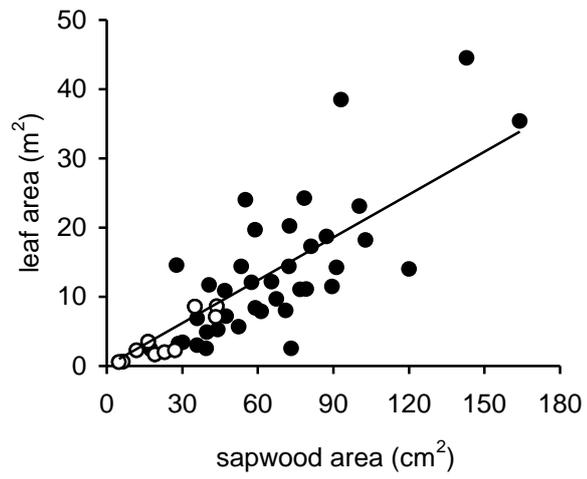564

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572   Grigg et al. Figure 1

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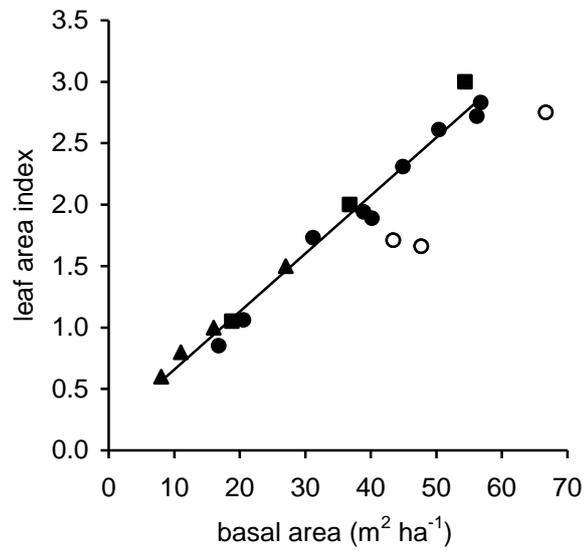583

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