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1 **Factors controlling *Eucalyptus* productivity: How resource**
2 **availability and stand structure alter production and carbon**
3 **allocation**

4

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29

30 **Abstract**

31 Wood production varies substantially with water availability and stand structure
32 or evenness. Variation in wood production can result from differences in canopy
33 photosynthesis or differences in partitioning, the annual fraction of photosynthesis used
34 by different sinks. Wood production is only a small fraction (20- 30%) of the carbon
35 fixed annually in photosynthesis, and changes in wood production can result from a
36 variety mechanisms that need to be examined with a complete carbon budget. We
37 measured annual carbon flows to wood production, foliage production and total
38 belowground carbon allocation (the sum of root production, root respiration, and
39 mycorrhizal production and respiration) over a six-year rotation for four *Eucalyptus* sites
40 with different productivities and climates (Aracruz, Suzano Celulose, International Paper
41 do Brasil and Veracel) with treatments designed to change fertility, water availability and
42 stand structure.

43 Wood biomass at age six varied from 5.6 kg C m⁻² (Suzano, traditional
44 fertilization, unirrigated, uniform stand structure) to 11.1 kg C m⁻² (Veracel, non-limiting
45 fertilization, irrigated, uniform stand structure) and wood net primary production
46 averaged over age three to five ranged from 0.84 kg C m⁻² (Aracruz, traditional
47 fertilization, unirrigated, uniform stand structure) to 2.09 kg C m⁻² (International Paper,
48 Brazil, non-limiting fertilization, unirrigated, uniform stand structure). Increased water
49 through irrigation increased light use and growth efficiency, gross primary productivity
50 and wood net primary productivity, decreased partitioning belowground and increased
51 partitioning to wood (all averaged over age three to five). Annual flux belowground
52 varied among sites (with a different clone for each site), but varied little with resource

53 availability. For all sites, heterogeneous stand structure reduced light-use efficiency,
54 gross primary productivity, and wood net primary productivity compared to uniform
55 stands, but had little effect on total belowground carbon flux.

56

57 **1. Introduction**

58

59 Predicting how forest growth and ecosystem carbon storage will respond to
60 changes in resources remains a challenge, particularly because the controls over carbon
61 allocation are poorly understood (Landsberg, 2003; Trumbore, 2006). Considerable
62 progress has been made for modeling the effects of climate and resources on wood
63 production, and in some cases, other ecosystem carbon fluxes. However, lack of
64 understanding of carbon allocation currently limits the capacity to model the forest
65 carbon cycle, accurately predict the effects of global change on carbon cycling, and
66 accurately predict forest productivity for new climates, sites and genotypes (Gower et al.,
67 1997; Ryan et al., 1997; Friedlingstein et al., 1999; Landsberg, 2003; Litton et al., 2007)

68 Two indices have been developed to allow simple, rapid assessment of changes in
69 productivity and carbon allocation: annual production per unit photosynthetically active
70 light absorbed by the canopy (light-use efficiency, Monteith, 1972, 1977) and annual
71 wood production per unit leaf area (growth efficiency, Waring, 1983). The ‘production’
72 in light use efficiency has been defined as crop or dry matter yield (Monteith, 1977),
73 gross primary production or photosynthesis (for example, Drolet et al., 2005), and wood
74 production (Linder, 1985), but we will use wood production in this paper. Differences in
75 light-use or growth efficiency indicate differences in canopy photosynthesis, partitioning
76 of the annual photosynthesis to different sinks or respiration, or both. Additionally, for
77 dense canopies, growth efficiency may also indicate changes in light absorbed per unit of
78 leaf area.

79 Light-use and growth efficiency have been shown to change with stand
80 development, fertility, and water availability. To uncover the changes in canopy
81 photosynthesis and partitioning responsible for changing efficiency requires measurement
82 of all of the components of a forest carbon balance.

83 Measuring canopy photosynthesis is very challenging, and all three methods have
84 limitations. Photosynthesis can be estimated by measuring the photosynthetic capacity of
85 and the response of photosynthesis and stomatal conductance to the environment, and
86 using simple (for example, Landsberg and Waring, 1997) or complex models (for
87 example, Williams et al., 2001; Medlyn, 2004) to extrapolate to the canopy. The more
88 often photosynthetic capacity and environmental response are measured for more
89 portions of the canopy, the more accurate canopy estimates are likely to be. The
90 limitations of this approach are the difficulty in obtaining the measurements in a tree
91 canopy, spatial and temporal variability, and the accuracy of any model used. A second
92 way to estimate photosynthesis is to use net ecosystem exchange measurements from
93 eddy covariance (Curtis et al., 2005; Sacks et al., 2007). Respiration at night is adjusted
94 to temperatures during the day using a temperature response function, and added to the
95 net ecosystem carbon exchange in the day. The strength of this approach is that it is
96 derived from whole-canopy measurements. The limitations are that eddy covariance
97 often underestimates ecosystem respiration because of advective flow and lack of
98 turbulence (Lavigne et al., 1997), temperatures at night are rarely encountered during the
99 day (at least in the same season), foliar respiration during the day is likely less than at
100 night (Kirschbaum and Farquhar, 1984), and eddy covariance requires a large area with
101 uniform vegetation (~0.5 km²), which makes assessing treatments and replication

102 difficult. A third way to estimate photosynthesis is to measure the sinks and fluxes
103 resulting from photosynthesis and sum them to get photosynthesis (Möller et al., 1954;
104 Ryan, 1991). Estimation of total belowground carbon flux using soil respiration,
105 litterfall, and carbon pool changes (Giardina and Ryan, 2002) has greatly aided this
106 approach. The strengths of this approach are that it can be applied to small plots to assess
107 treatment effects and that variability in respiration is lower than that in photosynthesis.
108 The limitations are that much work is required to sample temporal and spatial variability
109 and the accuracy of the models used to extrapolate measurements to the stand.

110 For this study, we used the third method of estimating photosynthesis, which also
111 estimates other important components of the carbon budget (Giardina et al., 2003; Litton
112 et al., 2004; Maier et al., 2004; Ryan et al., 2004; Forrester et al., 2006; Bown et al.,
113 2009). We considered carbon flux for five major components: foliage respiration, foliage
114 net primary production, wood respiration, wood net primary production, and total
115 belowground carbon flux (carbon flux to root growth and respiration, exudates and
116 mycorrhizae). We also manipulated resources (Linder, 1981; Raison and Myers, 1992)
117 and assess how efficiency, and the three components of carbon allocation (biomass, flux,
118 partitioning, Litton et al., 2004) change when resources and structure change. These
119 manipulations were done over a six year rotation (tree height ~ 60% of maximum) for
120 four locations with different climates for fast growth *Eucalyptus* in Brazil. Our
121 objectives were to compare across sites and treatments (1) how well light-use or growth
122 efficiency indices varied with site productivity and if they predicted changes in flux and
123 partitioning; (2) if water availability changed flux and partitioning in a similar manner to

124 the changes observed for fertility for a wet site in Hawaii (Ryan et al., 2004); and (3) if
125 stand structure (uniform or heterogeneous) changed flux or partitioning.

126

127 **2. Methods**

128

129 *2.1 Site descriptions*

130 This paper reports data from four Brazil Eucalyptus Productivity Project (BEPP)
131 sites, and these are described in detail in Stape et al. (2010). The Aracruz site was
132 located at 19° 49'S, 40° 05' W near Aracruz City in Espirito Santo, Brazil on an Ultisol
133 with a clay content of 37%. Mean annual temperature was 23.6 °C, with 1360 mm/yr
134 precipitation. Trees from the same clone were planted in March 2001 at a 3 m x 3 m
135 spacing. The International Paper, Brazil site was located 22° 21'S, 46 ° 58'W near Mogi
136 Guaçu in São Paulo, Brazil on an Oxisol with 45% clay content. Mean annual
137 temperature through the rotation was 21.6 °C with 1320 mm/yr precipitation. Trees were
138 planted in October, 2000 at a spacing of 3.0 m x 2.8 m. The Suzano site was located at
139 18° 02'S, 39° 52' W near Teixeiras de Freitas in Bahia, Brazil on an Ultisol with 21%
140 clay. Annual mean temperature was 23.1 °C, with 1350 mm/ yr precipitation. Trees were
141 planted beginning in December 2001 at 3 m x 3 m spacing. The Veracel site was located
142 at 16° 21'S, 39° 34'W near Eunapolis in Bahia, Brazil on an Ultisol soil with about 37%
143 clay content in the upper meter. Mean annual temperature during this rotation was 23.0
144 °C with an average of 1430 mm/yr precipitation. Trees were planted beginning March
145 2001, at 3 m x 3 m spacing.

146

147 *2.2 Experimental Design*

148 The Aracruz, Suzano, International Paper do Brasil, and Veracel sites
149 implemented two fertilization regimes, traditional (T) and non-limiting (F); irrigation to
150 remove any soil water deficit (I) and unirrigated (N); and a uniform (U) or heterogeneous
151 (H) stand structure. The traditional fertilizer regime represented current operational best
152 practices for *Eucalyptus* and varied by site, based on current operations of each
153 Company. The non-limiting fertilization regime was applied quarterly throughout the
154 study. For nutrients and amounts of fertilizer added, see Stape et al. (2010). For the
155 irrigation treatment, water from a well or nearby stream was added weekly if needed to
156 maintain soil water near field capacity. For the uniform treatment, trees from the same
157 clone (but different clones among sites) were planted on the same day for each plot. For
158 the heterogeneous treatment, one-third of the trees (again clonal) for a plot were planted,
159 then one-third were planted 20 days after the first third, then the final third were planted
160 40 days after the first third. This scheme allowed the trees in the first third to establish
161 dominance and led to a much more heterogeneous stand structure than the uniform
162 treatment (Binkley et al., 2010). Aracruz, Suzano, International Paper do Brasil, and
163 Veracel each implemented four replicates of the FIU, FIH, FNU, and TNU treatments,
164 but Aracruz measured the carbon budget only on one FIH and one FNU plot and two
165 FNU and two TNU plots. The carbon budget was measured on all four replicate plots for
166 the other three sites. Plots were ~40 m x 40 m, with a measurement plot of 36 trees (440
167 m²). Trenches were cut to 1 m deep around the irrigation plots to isolate them from
168 adjacent plots. The carbon budget measurements were taken from ages two-five at the
169 Aracruz and International Paper do Brasil sites, and from ages three-five at the Suzano and
170 Veracel sites.

171

172 *2.3 Biomass and Aboveground Net Primary Production*

173 We used a similar approach to estimating carbon fluxes and pools as outlined in
 174 Ryan et al. (2004) and Stape et al. (2008). Biomass of stem, bark, branches, and roots < 5
 175 mm were estimated using allometric equations (Table 1). Equations were developed
 176 using trees harvested from all treatments over the life of the stand. Biomass by
 177 component was estimated using quarterly measurements of stem diameter at 1.3 m and
 178 tree height. We estimated net production of stems, branches, bark and roots > 5 mm as
 179 the difference in biomass between two measurement periods. We estimated foliage net
 180 production as the difference in biomass between two measurement periods plus any
 181 litterfall over the period. We assumed dry mass was 50% carbon. Leaf area was
 182 estimated from leaf biomass and periodic samples of leaf mass per area.

183

184 *2.4 Total Belowground Carbon Flux*

185 Total belowground carbon flux was estimated using techniques described in
 186 Giardina and Ryan (2002) and Ryan et al. as

187

$$188 \text{ TBCF} = F_S - F_A + \Delta(C_R + C_L + C_S + C_T) \quad [1]$$

189

190 where F_S is soil respiration, F_A is aboveground leaf and twig litterfall, C_R is root biomass,
 191 C_L is soil organic layer (forest floor) biomass, C_S is carbon in 0-0.45 m mineral soil, and
 192 C_T is the biomass in stumps and roots from the prior plantation (Aracruz and Suzano sites
 193 only). All stocks and fluxes were converted to carbon units.

194 Soil respiration was measured approximately monthly from ages three-five at all
195 four sites and also at age two at the Aracruz and International Paper do Brasil sites.
196 Equipment breakdowns precluded monthly measurements for some months. At the
197 Aracruz site, soil respiration was measured at nine locations per plot with a LI-COR
198 6400-09 soil efflux chamber (0.1 m diameter) using collars inserted into the soil 24 hours
199 prior to measurement. At the International Paper do Brasil, Suzano, and Veracel sites,
200 soil respiration was measured at nine locations per plot using a PP Systems EGM-4 gas
201 analyzer with a PP Systems soil respiration chamber (0.1 m diameter). The PP Systems
202 chamber was directly inserted into the soil without a collar for the measurements. The
203 nine locations per plot were stratified into three strata: three samples were located in the
204 planting rows, three in the rows of the prior plantation and three approximately halfway
205 in between the prior and new rows.

206 Because the PP Systems chamber can give higher efflux measurements when
207 compared with the LI-COR 6400-09 chamber (Janssens et al., 2000; Butnor et al., 2005),
208 we compared them once for each site where the PP Systems equipment was used. At the
209 Aracruz site, we compared the Aracruz LI-6400-09 with the LI-6400-09 instrument used
210 for the comparison with the other sites' PP Systems equipment at four plots. At the
211 International Paper do Brasil, Suzano, and Veracel sites, we measured soil CO₂ efflux
212 with the LI-COR LI6400-09 and the PP Systems equipment used on site. Measurements
213 were made 0.2 m apart in all plots with ongoing soil CO₂ efflux measurements. For the
214 Aracruz site, the instruments gave a flux that differed overall by 0.14 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and a
215 regression of the sample points gave $R^2 = 0.92$. At the International Paper do Brasil site,
216 a regression of the plot means gave LI-COR soil respiration = 0.83 * PP Systems soil

217 respiration ($R^2 = 0.44$). For the Suzano site, a regression of the plot means for each
218 instrument was not significant, but the mean difference of $1.68 \mu\text{mol m}^{-2} \text{s}^{-1}$ was. At the
219 Veracel site, LI-COR soil respiration = $0.70 + 0.235 \cdot \text{PP Systems soil respiration}$ ($R^2 = 0.28$).
220 Because the LI-COR soil respiration instrument is likely to be more accurate, we used
221 these equations or means to adjust the PP Systems measurements to that given by the LI-COR.

222 Previous studies had shown little or no diurnal variability in soil respiration for
223 *Eucalyptus* in tropical locations (Giardina and Ryan, 2002; Stape et al., 2008), so we
224 assumed no diurnal variability for these locations. Annual estimates of soil respiration
225 were estimated using linear interpolation between sampling periods.

226 Litterfall was collected monthly, corrected for decomposition prior to collection,
227 dried at 70°C , and the branches $> 2 \text{ mm}$ removed before weighing. Litter was collected
228 in six 0.25 m^2 traps per plot.

229 The organic soil layer (forest floor) was sampled annually at four 1 m^2 locations
230 within each plot and a subsample was ashed in a muffle furnace to correct for any mineral
231 soil in the samples. The annual change in forest floor was calculated from the mean
232 difference per plot between these samples.

233 The 0-0.45 m mineral soil and soil bulk density was sampled at nine locations per
234 plot prior to plantation establishment and at harvest (age six to 6.5 years) at the same
235 locations. The annual change in soil carbon was estimated as the per plot difference
236 between these two samples divided by the time in years between the samples. The C
237 content on the top 0.45 m of the soil profile represented 60% of the total C down to
238 2 m depth in a prior study (Stape et al., 2008). We expected the rate of change in soil C
239 would be very small below 0.45 m depth relative to the upper soil, based on results from

240 Bashkin and Binkley (1998). Soil C contents were converted to an area basis by plot by
241 multiplying concentrations by average bulk density.

242 Stumps from the previous rotation comprised a substantial portion of soil carbon
243 at the Aracruz and Suzano sites. We surveyed the old stumps in each plot after planting,
244 measuring the diameter on the top of the stump. We used a regression from a prior study
245 (Stape et al., 2008) to estimate initial stump and root biomass carbon. We estimated
246 decomposition of the stumps and roots from the previous rotation assuming an
247 exponential decay measured in a previous study ($k = 0.190 \text{ year}^{-1}$, Stape et al., 2008) and
248 the stump and root biomass estimated above.

249 We estimated the change in root biomass ($> 5 \text{ mm}$) from site-specific allometric
250 equations and diameter measurements. We assumed no difference in fine root biomass
251 important enough to impact the belowground carbon budget (fine root turnover was
252 captured in soil respiration).

253

254 *2.4 Light measurements*

255 At the International Paper do Brasil, Suzano, and Veracel sites, we measured light
256 interception (photosynthetically active radiation) every two months with a Decagon
257 AccuPAR LP-80 Ceptometer (Decagon Devices, Pullman, WA, USA 99163) on three
258 transects per plot with eight measurement locations each. Measurements were taken
259 between 1030 and 1430 local time and compared with periodic clear sky readings to
260 measure the light absorbed by the canopy. At the Aracruz site, we estimated light
261 absorption from leaf area index measured with a LI-COR LAI-2000 (LI-COR
262 Biosciences, Lincoln, NE, USA 68504) and an extinction coefficient for the exponential

263 decay of light with leaf area estimated from coupled destructive harvest measurements of
 264 leaf area and LAI-2000 measurements. We used linear interpolation to estimate light
 265 interception by the canopy for a year and calculated light-use efficiency from wood net
 266 primary production and canopy light absorption.

267

268 *2.5 Aboveground Tree Respiration*

269 Foliage respiration and wood CO₂ efflux were measured only for a two-week
 270 campaign at the Aracruz site (Ryan et al., 2009). At the Aracruz site, foliage dark
 271 respiration was identical to that found in fast-growth *Eucalyptus* in Hawaii (4.2 μmol C
 272 mol N⁻¹ s⁻¹ at 20 °C (Ryan et al., 2004)). We estimated foliar dark respiration for all sites
 273 using monthly estimates of leaf area and the mean flux per unit leaf area measured at the
 274 Aracruz site for three- and four-and-a-half-year-old trees (0.66 μmol C m⁻² s⁻¹ at 20 °C).
 275 Rates were adjusted to the actual monthly mean temperature at night using an exponential
 276 relationship with temperature and a Q₁₀ of 2. We applied the equation of Ågren and
 277 Axelsson (1980) to correct for the effect of temperature amplitude.

278 Wood CO₂ efflux at the Aracruz site (Ryan et al., 2009) was 8-10 times lower
 279 than that for similar sized trees for *Eucalyptus* in Hawaii (Ryan et al., 2004). Therefore,
 280 we estimated wood CO₂ efflux for all sites using the decline in CO₂ efflux with tree age
 281 and size in the Hawaii study (Ryan et al., 2009), with the average rates for wood CO₂
 282 efflux measured for the three- and four-and-a-half-year-old trees (0.034 and 0.020 μmol
 283 (kg C)⁻¹ s⁻¹ at 20 °C, respectively). Wood CO₂ efflux was estimated as:

284

285 Wood CO₂ efflux (μmol (kg C)⁻¹ s⁻¹ at 20 °C = 0.25 * exp(-0.4949*age(yr)) [2]

286

287 Rates were adjusted to the actual monthly mean temperature using an exponential
288 relationship with temperature and a Q_{10} of 2. We applied the equation of Ågren and
289 Axelsson (1980) to correct for the effect of temperature amplitude.

290

291 *2.6 Statistical Analysis*

292 Because the sample design was unbalanced (for example, the heterogeneous
293 treatment was only applied to the non-limiting, irrigation treatments), differences in
294 fluxes and partitioning within a site were assessed using two-sample t -tests for the
295 fertility, irrigation and stand structure treatments and the appropriate treatment pairs
296 (FNU *versus* TNU for fertilization, FIU *versus* FIH for structure and FIU *versus* FNU for
297 irrigation). Because rainfall and growth are highly variable among years, tests were
298 applied to the means for ages three to five. The effect of operational fertilization versus
299 non-limiting fertilization was also evaluated for aboveground wood biomass and
300 aboveground wood net primary production using the mean of ages two through six.
301 Differences in flux and partitioning with stand structure and irrigation across all sites
302 were assessed using a paired samples t -test, with each site as a pair. Trends in flux,
303 partitioning and light-use efficiency with gross primary productivity were assessed with
304 linear regression. The type 1 error level was $\alpha = 0.05$, and SPSS Version 17.0 (SPSS
305 Inc., Chicago, IL, USA 60606) was the statistical package used.

306

307 **3. Results**

308

309 *3.1 Site Productivity and Light Use and Growth Efficiency*

310 Our four sites spanned a wide range in productivity and biomass at age six (Table
311 2). Wood biomass at age six varied from 5.6 kg C m⁻² (Suzano, TNU) to 11.1 kg C m⁻²
312 (Veracel, FIU), wood net primary production at age three ranged from 0.83 kg C m⁻²
313 (Aracruz, FNU) to 2.4 kg C m⁻² (Veracel, FIU), and gross primary productivity varied
314 from 3.2 kg C m⁻² (Aracruz, FNU) to 5.5 kg C m⁻² (Veracel, FIU).

315 More productive sites showed higher efficiency. Light use efficiency for age
316 three to five three increased as gross primary productivity increased (Fig. 1, $R^2 = 0.92$).
317 Growth efficiency for age three to five was not related to gross primary productivity ($P =$
318 0.21). Across sites, both wood net primary production (NPP) and gross primary
319 productivity (GPP) increased with leaf area index ($R^2 = 0.84$ and 0.81 , respectively).
320 Wood NPP at age three was positively correlated with harvestable wood biomass at age
321 six ($r=0.89$) as was growth efficiency at age three ($r = 0.68$). Light-use efficiency and
322 growth efficiency were correlated ($r = 0.76$).

323

324 *3.2 Resource Availability*

325 Non-limiting fertilization increased wood production for only one of the four sites
326 (Suzano, an 8% increase) compared to operational fertilization. The fertilization
327 treatment had little or no effect on other fluxes or partitioning for the Suzano or for the
328 other sites.

329 Across all sites, irrigation increased light-use efficiency by 20%, growth
330 efficiency by 15%, wood NPP by 27%, GPP by 18%, foliage production by 14% (Fig. 2),
331 and GPP per unit of light absorbed by 10%. Total belowground carbon flux did not vary
332 with water availability within or among sites (Fig. 2D). Fluxes to foliage production,

333 wood CO₂ efflux, and foliage respiration all increased linearly as GPP increased across
334 the site × irrigation gradient ($r^2 = 0.46, 0.84, 0.91$, respectively).

335 Within a site, irrigation increased wood net production and GPP for all sites (Fig.
336 2), but the differences at the Veracel site were not significant ($P = 0.08$ and 0.09 ,
337 respectively). Irrigation increased light-use efficiency at the Aracruz and International
338 Paper do Brasil sites, but not at the Suzano or Veracel sites ($P = 0.06$ and 0.22 ,
339 respectively).

340 Flux to wood production increased through two mechanisms as water availability
341 increased. First, greater photosynthesis provided more carbon for wood production (Fig.
342 3A). Second, the fraction of annual photosynthesis used for wood production also
343 increased as productivity increased (Fig. 3C). Irrigation did not affect the flux of carbon
344 belowground for any of the sites, and belowground carbon flux was not related to annual
345 photosynthesis (Fig. 3B). Increased productivity shifted partitioning between wood
346 production and belowground, but only because of changes in the flux and partitioning of
347 wood.

348

349 *3.3 Stand Structure*

350 Across all four sites, uniform stand structure for ages three to five increased light-
351 use efficiency by 9% ($P = 0.12$), wood NPP by 9% ($P = 0.11$) and GPP by 7% ($P = 0.17$,
352 Fig. 4). These increases were not significant, but we report them because the cross-site
353 difference in wood biomass at the end of the six year rotation (14%) was. Total
354 belowground carbon flux did not vary with stand structure across sites ($P = 0.33$).

355 Stands with uniform structure had higher GPP for ages three to five for the
356 Suzano and International Paper sites, higher light-use efficiency and wood NPP at the
357 Veracel site, and higher total belowground carbon flux at the International Paper do
358 Brasil site (Fig. 4). Partitioning of annual photosynthesis at age five to wood production
359 and belowground did not change with stand structure.

360

361 **4. Discussion**

362 Light-use efficiency and growth efficiency were good indicators of changes in the
363 carbon balance. When fluxes or partitioning changed, these measures of efficiency did so
364 as well, and the magnitude of the changes in efficiency, flux, and partitioning was
365 similar. Light-use efficiency appeared to be a better metric for indicating changes in flux
366 and partitioning for this study because it varied with gross primary productivity, while
367 growth efficiency did not. However, both indices differed with irrigation.

368 In our study, increased resources (water) increased both the carbohydrate
369 available for wood growth (through increased photosynthesis), and the fraction of
370 photosynthesis used for wood production. Both flux and partitioning appeared to be
371 equally important. Across our site \times irrigation productivity gradient, GPP increased 62%
372 while wood NPP increased 114%. The greater percentage increase in wood NPP than
373 GPP resulted from partitioning changing from 35% to 45% of GPP across the gradient in
374 GPP. Fluxes to foliar respiration, wood CO₂ efflux, and foliage production efflux also
375 increased as productivity increased, but partitioning changed less than 2% of
376 photosynthesis.

377 With the exception of belowground flux, the patterns for flux and partitioning
378 across the site \times irrigation productivity gradient matched those found in Litton et al

379 (2007) in a cross-site study. Flux to wood NPP, respiration, and leaf production all
380 increased as photosynthesis increased. Partitioning to wood production increased with
381 GPP, while partitioning belowground decreased. Partitioning to wood CO₂ efflux,
382 foliage respiration, and foliage production was constant over the BEPP productivity
383 gradient, as also found in the Litton et al. (2007) study. The annual fraction of GPP used
384 belowground and for wood production differed substantially between the BEPP study and
385 the Litton et al. (2007) cross-site analysis. In the BEPP study, 42% of gross primary
386 productivity went to wood production, compared to 30% for the cross site analysis. And,
387 in the BEPP study 19% of gross primary productivity went belowground, compared to
388 36% for the cross site analysis. We suspect that tree-breeding efforts have changed
389 partitioning to favor wood production relative to belowground flux for these fast-growth
390 forests.

391 A remarkable result from these four studies is that belowground carbon flux did
392 not change with increased resources, because we expected that it would (Litton et al.,
393 2007). The lack of change in belowground carbon flux is consistent with a fertility study
394 in Hawaii (Ryan et al., 2004) that showed no difference in belowground flux with fertility
395 treatments that doubled aboveground wood production. It is somewhat consistent with
396 another *Eucalyptus* study (Stape et al., 2008) in Brazil that found increased flux to
397 irrigated plots in both a wet and normal year. However, in the Stape et al. (2008) study,
398 irrigation increased flux to wood production 140% in the normal precipitation year, while
399 only increasing total belowground carbon flux 24%. Forrester et al. (2006) found that
400 belowground carbon flux in a *Eucalyptus* – *Acacia* mixture was similar to that for pure-
401 species stands, while aboveground primary productivity was greater in the mixed stand.

402 The BEPP results suggest that belowground flux is constant for a given site and
403 clone combination, and does not change with irrigation. The pattern of constant
404 belowground flux with resource availability in *Eucalyptus* studies is not supported by
405 other studies in temperate ecosystems. Belowground carbon flux was unchanged in an
406 irrigation treatment, but decreased substantially in the irrigated plus fertilizer treatment in
407 a study with radiata pine (Ryan et al., 1996). In that study, aboveground wood
408 production increased by > 100% for the irrigation plus fertilizer treatment compared to
409 the control, while belowground flux decreased 28%. Our results are also not consistent
410 with an irrigation and fertilization study in loblolly pine (Maier et al., 2004), where
411 belowground carbon flux increased 77% with fertilization and aboveground wood
412 production increased 102%. The *Eucalyptus* results are also not consistent with a within
413 and cross-site elevated CO₂ experiment (Palmroth et al., 2006), where belowground flux
414 decreased substantially as productivity increased (three angiosperm sites, one conifer
415 site).

416 Belowground flux for this study varied two-fold among site-clone combinations,
417 from 0.43 kg C m⁻² yr⁻¹ at the International Paper do Brasil site to 0.99 kg C m⁻² yr⁻¹ at
418 the Suzano site. These fluxes are substantially lower than the ~1.8 kg C m⁻² yr⁻¹
419 measured for *Eucalyptus* in Hawaii (Ryan et al., 2004), and the 1.4 kg C m⁻² yr⁻¹
420 measured for *Eucalyptus* elsewhere in Brazil (Stape et al., 2008). We do not know the
421 cause of the site or clone differences. Two potential candidates are differences among
422 clones, or differences among sites in climate or soils. Climate for these four sites was
423 similar for the study years (Stape et al., 2010), and belowground flux did not respond to
424 irrigation, so we suspect climate is not the cause. Belowground flux did decrease as site

425 clay content increased, suggesting a potential role for soil ($r^2 = 0.79$, $P = 0.11$, $n=4$). We
426 have no information on genetic differences in belowground flux.

427

428

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436

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556 **Tables.**

557 **Table 1.** Coefficients of the allometric equations by site and compartment. Equations
 558 are: $W=aDBH^bH^c$, where W is the bole dry weight (kg), DBH is the diameter at breast
 559 height (cm), and H is the total height (m); $B=AGE^a DBH^{b(b.AGE+c)}$, where B is the
 560 branch or leaf dry weight (kg), AGE is the forest age (months) and DBH is the diameter
 561 at breast height (cm); $R = aW^b$, where R is the coarse root (> 5 mm diameter) dry weight
 562 (kg) and W is the bole biomass (kg). Trees were sampled at 12, 24 and 75 months of age
 563 for ARA, at 24 and 72 months of age for SUZ, at 12, 30, and 84 months of age for IPB,
 564 and at 12, 24, 64, 76 months of age for VER; n is sample size for each component.

Site	Bole	Branches	Leaves	Coarse Roots (> 5 mm)
Aracruz - ARA				
<i>a</i>	0.004	-0.466	-1.807	0.3565
<i>b</i>	1.959	0.003	0.004	0.7773
<i>c</i>	1.512	1.349	2.713	
<i>n</i>	128	128	128	55
Suzano - SUZ				
<i>a</i>	0.009	-1.24	0.6278	2.3026
<i>b</i>	1.622	-0.008	3.0632	1.4988
<i>c</i>	1.515	3.002	-2.0283	
<i>n</i>	92	92	92	50
International Paper do Brasil - IPB				
<i>a</i>	0.005	-1.445	-1.531	1.2279
<i>b</i>	1.751	0.00007	0.003	0.475
<i>c</i>	1.542	2.509	2.47	
<i>n</i>	169	169	169	61
Veracel – VER				
<i>a</i>	0.027	-1.163	-1.084	0.6691
<i>b</i>	2.221	0.004	-0.002	0.7858
<i>c</i>	0.625	2.063	2.084	
<i>n</i>	264	264	264	138

Table 2. Stocks, fluxes, partitioning, and efficiency for unirrigated and irrigated treatments for *Eucalyptus* in Brazil.

	Aracruz Site				Suzano Site				International Paper do Brasil Site				Veracel Site			
	Un-Irrigated		Irrigated		Un-Irrigated		Irrigated		Un-Irrigated		Irrigated		Un-Irrigated		Irrigated	
	----- kg C m⁻² yr⁻¹ -----															
Stocks	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Wood	3.01	0.45	5.00	0.75	3.80	0.48	4.66	0.60	3.91	0.46	4.78	0.59	5.56	0.65	6.76	0.62
Bole	2.60	0.43	4.50	0.73	3.26	0.55	4.00	0.69	3.69	0.47	4.51	0.60	5.21	0.64	6.34	0.61
Branch	0.41	0.01	0.50	0.03	0.54	0.07	0.67	0.10	0.22	0.01	0.27	0.01	0.35	0.02	0.42	0.01
Foliage	0.11	0.01	0.17	0.02	0.15	0.02	0.20	0.02	0.20	0.01	0.25	0.01	0.25	0.02	0.29	0.02
Roots > 5 mm	0.38	0.05	0.57	0.07	0.93	0.08	0.99	0.09	0.48	0.03	0.53	0.03	1.28	0.12	1.49	0.12
Fluxes	----- g C m⁻² yr⁻¹ -----															
Wood	983	110	1,600	177	1,310	116	1,610	125	1,700	117	2,090	141	1,790	167	2,060	142
Bole	839	93	1,430	184	1,270	101	1,580	125	1,540	103	1,920	133	1,710	165	1,970	142
Branch	145	23	179	14	38	24	24	12	160	23	175	23	83	5	93	5
Foliage	176	26	218	33	205	39	240	71	254	9	278	6	216	24	232	20
ANPP	1,160	120	1,820	152	1,510	106	1,850	172	1,960	113	2,370	140	2,010	163	2,290	126
Foliage Respiration	330	24	416	41	429	25	491	31	491	20	544	15	584	52	588	49
Wood Respiration	493	34	829	133	678	82	821	61	859	38	1,060	51	925	98	1,070	105
Soil Respiration	1,240	282	1,250	288	1,280	124	1,340	109	768	46	811	54	705	35	665	34
Litterfall	318	41	377	50	292	22	345	48	402	27	434	33	294	20	317	18
Stump Biomass Change	-128	13	-128	13	-34	3	-34	3	0		0		0		0	
Root Biomass Change	88	7	133	23	183	32	191	20	91	7	101	7	311	30	347	32
Mineral Soil C Change	13	22	-70	34	-24	0	-24	0	-62	23	-50	35	-27	46	-3	32
Organic Soil C Change	99	85	124	85	28	3	13	6	28	25	29	23	32	15	32	19
Total Belowground C Flux	903	272	812	248	1,000	232	989	188	421	84	449	100	727	60	724	58
GPP	2,890	238	3,880	524	3,620	349	4,150	185	3,730	153	4,420	175	4,240	318	4,680	314
Partitioning																
Foliage NPP:GPP	0.06	0.01	0.06	0.01	0.06	0.02	0.06	0.02	0.07	0.00	0.06	0.00	0.05	0.01	0.05	0.01
Wood NPP:GPP	0.35	0.05	0.42	0.02	0.36	0.03	0.39	0.03	0.46	0.02	0.47	0.02	0.42	0.01	0.44	0.01
Foliage Respiration:GPP	0.12	0.01	0.11	0.01	0.12	0.01	0.12	0.01	0.13	0.00	0.12	0.01	0.14	0.01	0.12	0.00
Wood Respiration:GPP	0.17	0.02	0.21	0.01	0.19	0.01	0.20	0.01	0.23	0.00	0.24	0.00	0.21	0.01	0.23	0.01

Carbon Flux and Partitioning - 29

Respiration:GPP

TBCF:GPP 0.30 0.07 0.20 0.04 0.27 0.05 0.24 0.04 0.11 0.02 0.10 0.02 0.17 0.01 0.16 0.01

Other

LAI 2.64 0.19 3.33 0.33 3.44 0.20 3.93 0.25 3.93 0.16 4.36 0.12 4.67 0.42 4.70 0.39

Leaf Mass per Area
(kg/m²) 0.101 0.001 0.101 0.001 0.116 0.004 0.116 0.004 0.108 0.001 0.108 0.001 0.110 0.001 0.110 0.001

Light-Use Efficiency
(g C wood NPP
MJ⁻¹) 0.55 0.08 0.78 0.07 0.54 0.05 0.59 0.04 0.69 0.05 0.81 0.06 0.75 0.06 0.85 0.03

Growth Efficiency
(g C wood NPP
LAI⁻¹) 383 64 485 40 380 28 415 44 438 33 483 36 392 30 445 16

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569 **Figures**

570

571 Figure 1. Light-use efficiency (annual wood production per unit of photosynthetically
572 active radiation absorbed) is positively correlated with mean gross primary productivity
573 (GPP) for age 3-5.

574

575 Figure 2. The effect of irrigation on (A) light-use efficiency (wood net primary
576 productivity (NPP)/ photosynthetically active radiation absorbed), (B) gross primary
577 productivity (GPP), (C) wood net primary productivity, and (D) total belowground
578 carbon flux (TBCF). Values are means for age 3 to 5. Light-use efficiency, GPP, and
579 Wood NPP were greater for the irrigated treatments. Annual flux to TBCF varies little
580 with resources.

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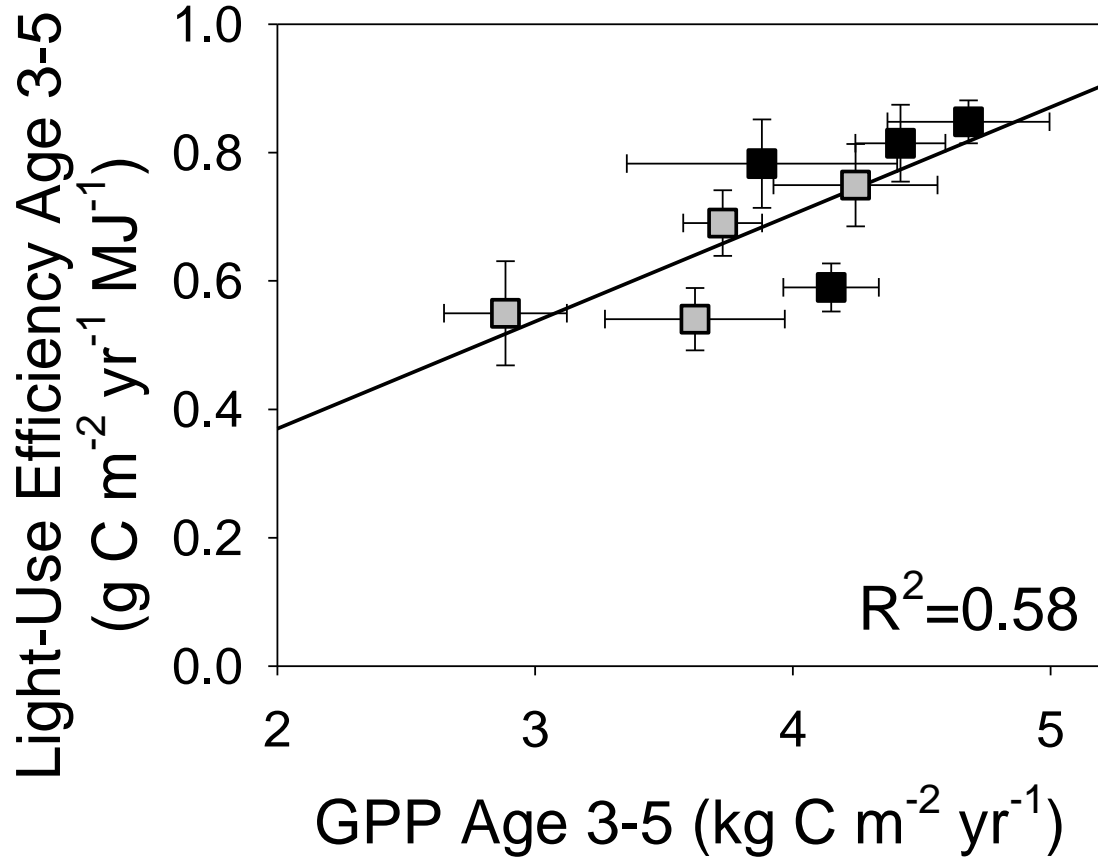
582 Figure 3. Wood net primary productivity (NPP) increases with annual photosynthesis
583 (GPP) (A) via two mechanisms: higher carbohydrate supply (GPP) and (C) increased
584 partitioning to wood NPP. Partitioning to TBCF (B) does not vary with GPP for these
585 sites and treatments.

586

587 Figure 4. The effect of stand structure (uniform – clonal individuals planted at the same
588 time, heterogeneous, clonal individuals planted in three tranches separated by 20 days) on
589 (A) light-use efficiency (wood net primary productivity (NPP)/ photosynthetically active
590 radiation absorbed), (B) gross primary productivity (GPP), (C) wood net primary
591 productivity, and (D) total belowground carbon flux (TBCF). Differences for all sites
592 combined were not significant ($P \sim 0.12$ for LUE, GPP, Wood NPP). However, averaged

593 over all four sites, wood biomass at age six was 14% lower for the heterogeneous
594 treatment.

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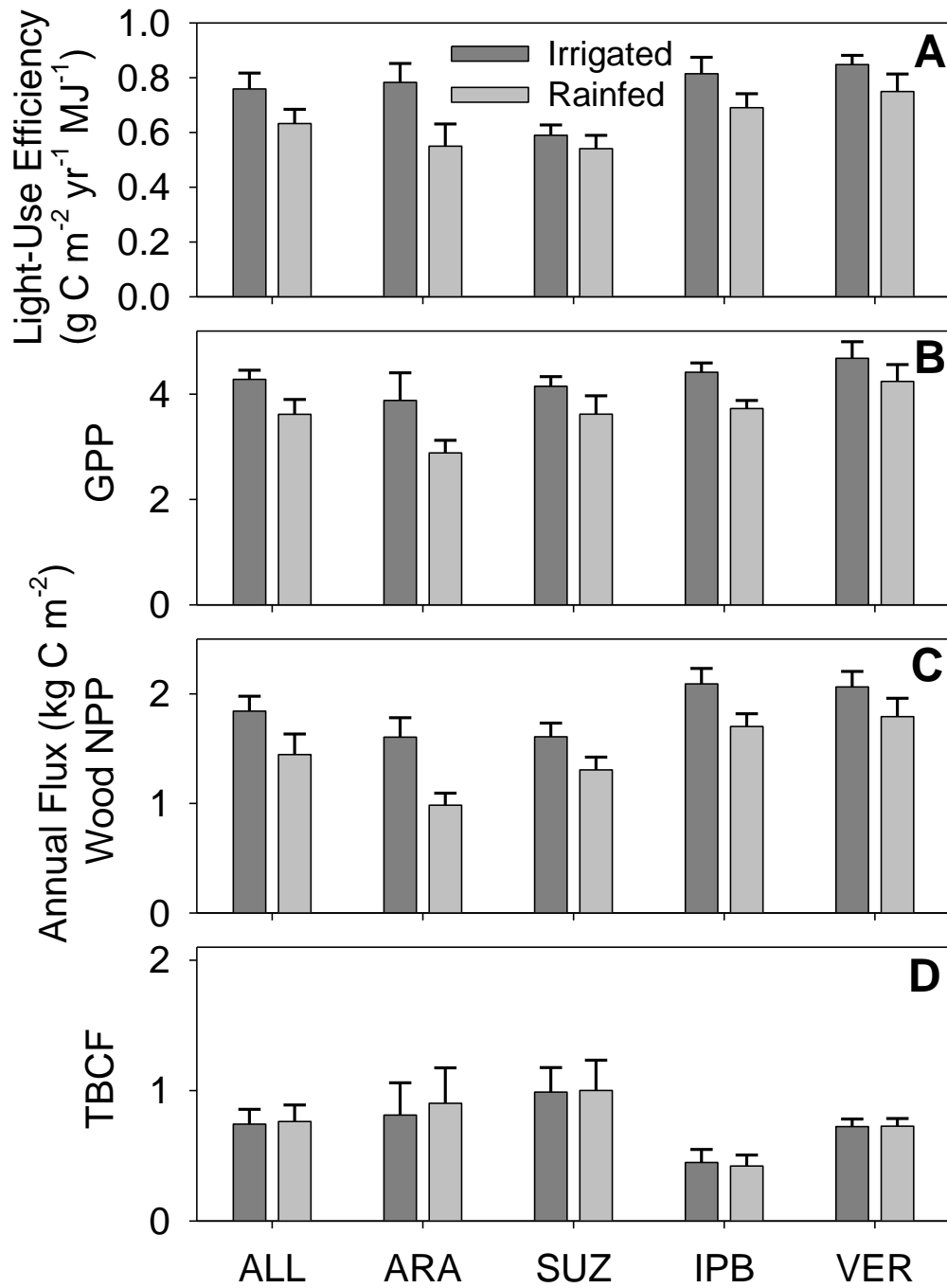


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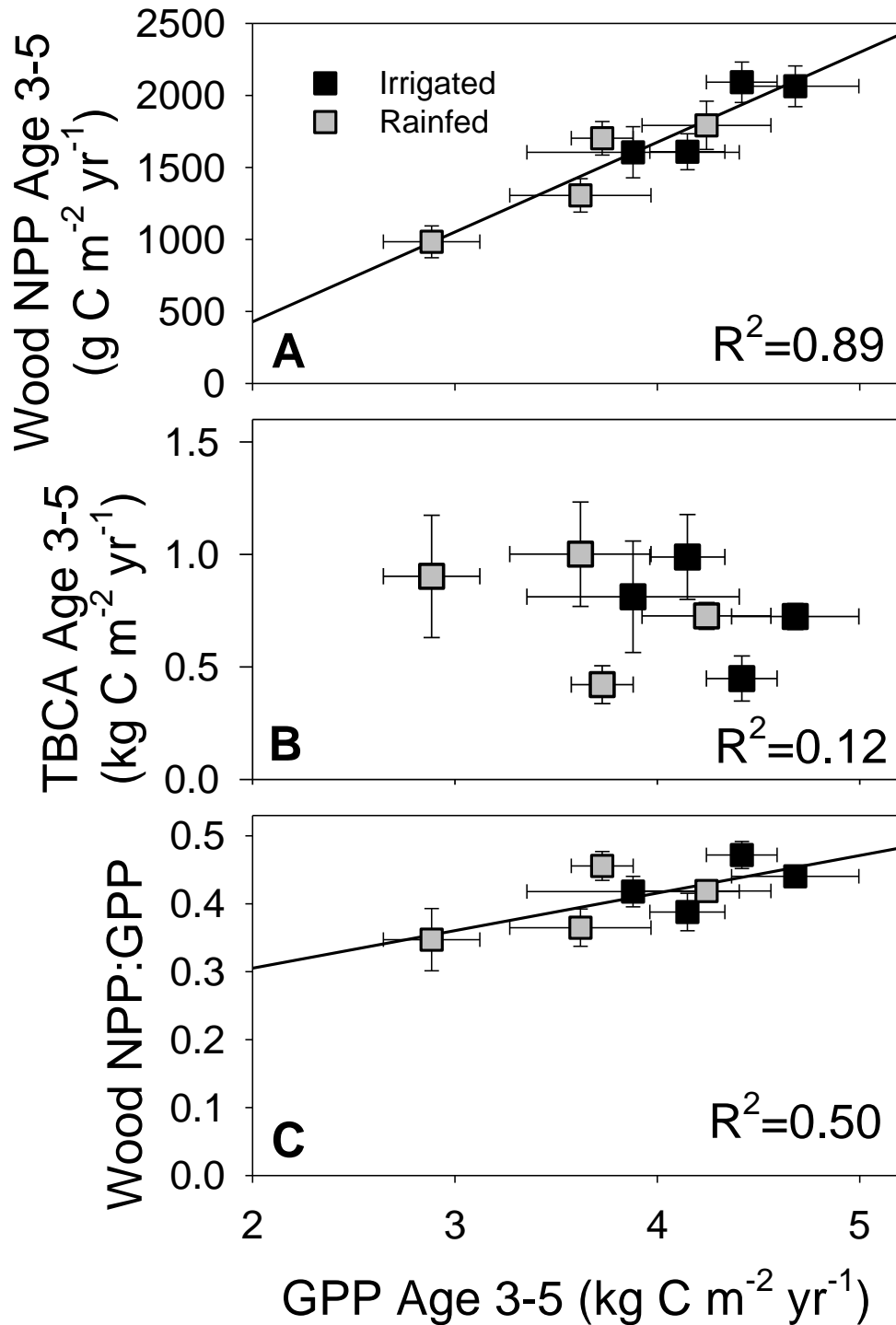
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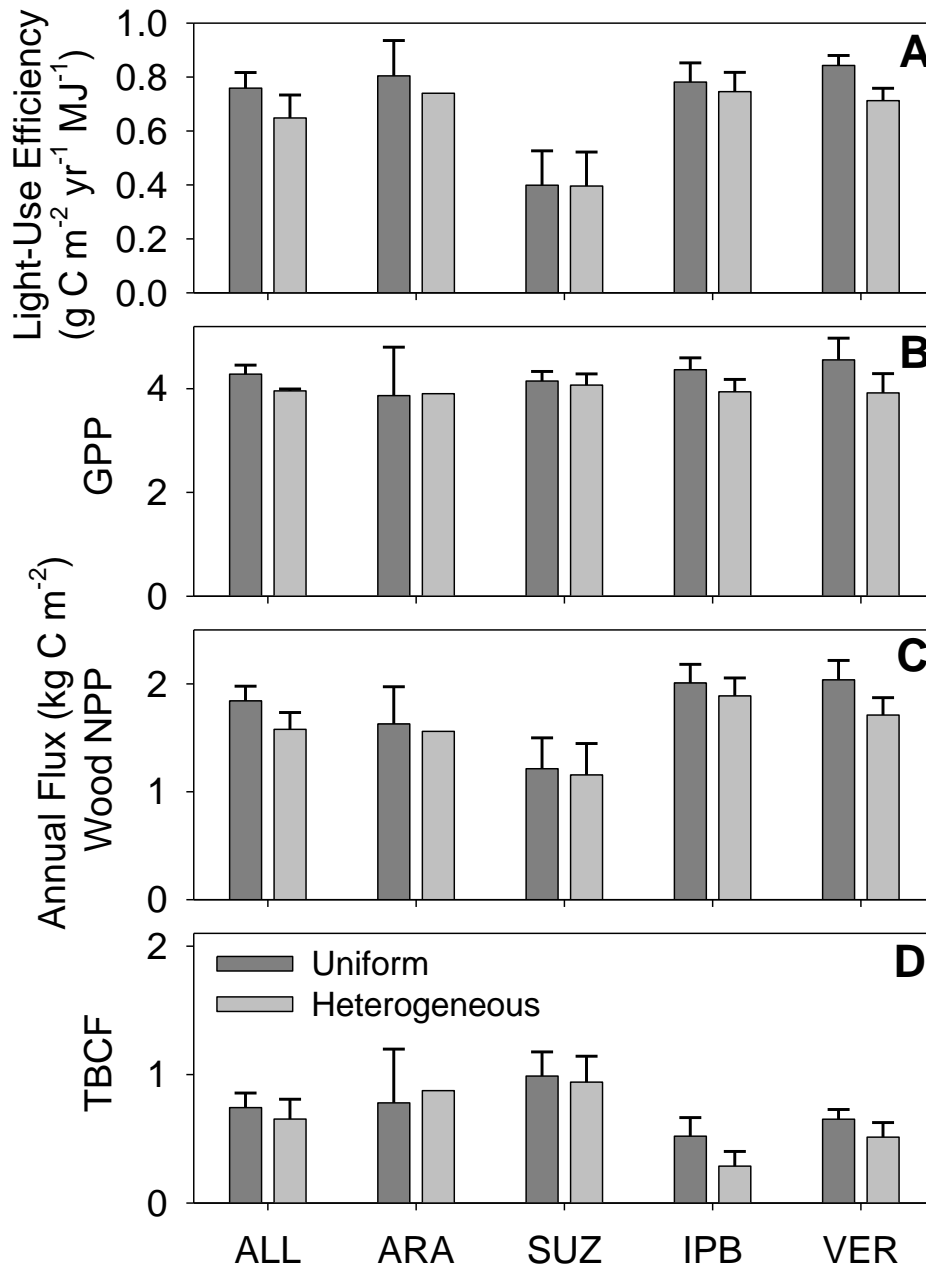
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Figure 3. Wood net primary productivity (NPP) increases with annual photosynthesis (GPP) (A) via two mechanisms: higher carbohydrate supply (GPP) and (C) increased partitioning to wood NPP. Partitioning to TBCF (B) does not vary with GPP for these sites and treatments.



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