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3 Species-specific water use by forest tree species: from the tree to the stand

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24   Abstract

25

26   Forests play a critical role in the hydrological cycle making the study of water use by

27   trees and forest stands of prime importance in the global change context .Very negative

28   effects of increasing and more intense droughts on forest vegetation have been

29   described over the last decades. Symptoms of disease and decline have been associated

30   with changed precipitation patterns in many forests particularly in European temperate

31   and Mediterranean regions. Intra- and inter-specific differences in both physiology and

32   morphology exert a large but not well understood influence on the water balance of

33   forest ecosystems, further affecting their vulnerability to drought. Stand structure and

34   composition influences rainfall interception, runoff and water fluxes of the whole

35   ecosystem. Both expanding plantations of renovated interest for biofuel industry and

36   natural and semi-natural forests must be managed in a sustainable way on the basis of

37   their water consumption. We review the role of key drivers on forest water use such as

38   species composition, tree canopy status of each of them and species specific sensitivity

39   to soil water scarcity. Specifically we discuss the role of these factors for natural forest,

40   but with references also to forest plantations.Water scarcity is expected to be one of the

41   largest societal problems worldwide in the near future, so water use by natural and

42   planted forest ecosystems has become a central subject in current research agendas.

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46 *1 Introduction*

47

48   Forest lands cover wide areas in the world, being one of the main actors in the

49 global hydrological cycle. Trees, the key individual component of forests, have distinct

50 characteristics, such as secondary growth and long lifespan, that differentiate them from

51 other kinds of plants such as annual weeds or crops in terms of water use and must be

52 considered for management purposes. The idiosyncratic characteristics of forest trees

53 impact upon the water economy at the ecosystem level depending on the composition

54 and structure of the particular forest community (Asbjornsen et al., 2011; Dierick and

55 Holscher, 2009).

56   Water use by trees is controlled basically at the interphase leaf-atmosphere by a

57 strict regulation of leaf stomatal conductance to water vapour. This role of stomatal

58 performance in regulating the flux of water through the soil-plant-continuum is common

59 to most plants. Unlike herbaceous species, however, forest tree species must attain not

60 only hydration of aboveground organs, but also functionality of the hydraulic system

61 assuring the continuity of the water column from soil to leaves (Meinzer et al., 2009;

62 Salleo et al., 2000; Tyree and Sperry, 1988). The interplay between stomatal control of

63 water losses and maintenance of function in the hydraulic pathway has important

64 consequences for the development of different strategies. Tree species range in its

65 performance from isohydric to anysohidric strategies depending on whether they

66 prioritize under dry conditions hydraulic safety or gas exchange respectively (Franks et

67 al., 2007; Tardieu and Simonneau, 1998; Kumagai and Porporato, 2012).

68   However, water use by forest tree species goes beyond the specific

69   differentiation in terms of sensitivity to environmental factors. Forest communities

70   attain a functional and structural complexity that contributes to emergent properties at

71   different scales. Thus, water is not only managed according to the species-specific

72   response to factors such as water in soil and atmosphere or radiation inputs into the

73   forest ecosystem. Dominance and hierarchical position of individual trees in the stand

74   (Martin et al. 1997; Granier et al., 2000), and other elements such as the coupling to

75   atmospheric conditions of the different tree crowns within the functional unity of the

76   canopy, play important roles in the final water budget of the ecosystem (Jarvis and

77   McNaughton, 1986). The proper structure of the stand in terms of stratification on

78   different size and age classes (Martin et al., 1997; Delzon and Loustau, 2005) and the

79   origin of individuals (e,g, seed-origin vs. resprouts from coppice), are elements that

80   modulate the amount and type of water used by forests (Asbjornsen et al., 2011).

81   Forest vegetation has been seen to be quite vulnerable to the negative effects of

82   climate change, particularly in terms of increasing intensity and recurrence of dry

83   periods (IPCC 2007). The negative effect of increasing dry periods will be reinforced by

84   a parallel increase in temperature, further magnifying the effects of drought.

85   Consequences of water stress are especially relevant for broad-leaved temperate species

86   not well adapted to droughts, as was notorious after the heat wave of 2003 that affected

87   wide forest areas in Central Europe (Leuzinger et al., 2005; Breda et al., 2006; Geßler et

88   al., 2007). The presence of extreme dry periods might be common worldwide in the

89   future, impacting very negatively the sustainability and productivity of forests already

90   threat by drought such as those at the rear edge of their geographical distribution; this

91   has been well documented for some areas of the Mediterranean Basin (Jump et al.,

92   2006; Linares et al., 2010). The capacity of forest trees to cope with dry periods is

93   conditioned by the many factors linked to the species specific use of water (Oren et al.,

94   1999; Martínez-Vilalta et al., 2003; Leuzinger et al., 2005), and to the structure of the

95   forests in terms of size and age classes, and tree density (Granier and Breda, 1996;

96   Granier et al., 2000; Moreno and Cuvera, 2008). All these factors can be controlled and

97   considered in the adaptive forest management since they have a direct effect on the

98   water budget of trees remaining after intervention in forest stands (Breda et al., 1995;

99   Bladon et al., 2006; Gyenge et al., 2011). Water use has not been considered a target in

100   many afforestation programs, which are typically more centred in either increasing

101   productivity or optimizing forests as carbon sinks. The expected increase in the

102   importance of water as a limiting factor for the future of many forests supports its

103   inclusion as a priority in the planning of new forest systems. However, gaps in

104   knowledge may prevent an effective inclusion of water as a management priority in

105   many cases.

106   We carry out an overview of some of the main factors influencing water use by

107   forest ecosystems, from basic functional mechanisms involved in the regulation of the

108   water use by trees to changes in the land use. Though, we acknowledge previous

109   reviews that have dealt with specific key issues in relation to water use by trees (i.e. see

110   Breda et al., (2006)) to build upon them, and to identify important gaps and challenges

111   for future research.

112

113   *2 Importance of species specific physiological mechanisms*

114   *2.1 Physiological control of water use by forest tree species*

115

116   The need of controlling water losses by a fine tuning of leaf stomatal regulation

117   has been, as in other kind of plants, one of the most important selective forces of

118   evolution of forest tree species (Franks and Beerling, 2009; Lawson et al., 2011).

119   Probably, stomatal conductance is one the most relevant and complex plant

120   physiological processes, acting during plant evolution as a crossroad in the interplay

121   between carbon fixation and water loss. Daily and seasonal response of leaf stomatal

122   conductance to water vapour (g_{wv}) establishes clear differences between forest tree

123   species coexisting at a given site (figure 1). The response is highly variable according to

124   the differential species sensitivity to climatic events such as drought (Aranda et al.,

125   2000; Mediavilla and Escudero, 2003; Tenhunen et al., 1990), or atmospheric factors

126   such as evaporative demand (Bladon et al., 2006).

127   The need to maintain functionality of hydraulic system through long living

128   periods is probably one of the most singular and particular characteristics of forest tree

129   species with regard to other plant groups. In this respect, the relationship between the

130   response of leaf stomatal conductance, and the functionality of the hydraulic pathway

131   through water movements within the tree, has emerged in the last decades as one of the

132   most important points in the understanding of water use by trees (Johnson et al., 2011;

133   Meinzer et al., 2009). Like other plants, stomatal regulation in trees must allow

134   conservation of hydration of aboveground tissues. Stomatal performance also operates,

135   in the specific case of forest tree species, maintaining the hydraulic system functionality

136   within margins of security from catastrophic dysfunction (Brodribb and Cochard, 2009;

137 Tyree and Sperrry, 1989). There are numerous examples where the stomata closure, as

138 drought intensify, runs in parallel with a decrease of the hydraulic efficiency into the

139 water pathway of trees. Thus, it is common to observe a decrease in the leaf stomatal

140 conductance to water vapour coupled to the loss of efficiency in the hydraulic system at

141 different points in the continuum soil-tree-atmosphere. For instances, Aranda et al.

142 (2005) observed a seasonal decrease in g_{wv} of beech leaves at the top of the canopy as

143 dry intensified at the end of summer (figure 1). It was followed by a parallel drop of

144 hydraulic efficiency in the continuum soil-plant-atmosphere, arriving almost to a 50 %

145 when comparing the beginning of summer with the peak of drought. Similar results are

146 frequently signed for most forest tree species, and points out to the complex interplay

147 between maintenance of the water supply to leaves and the risk of hydraulic failure from

148 tensions developed within the xylem (Meinzer et al., 2009; Salleo et al., 2000; Tyree

149 and Sperry, 1988). Under extreme droughts, the hydraulic failure can make trees to

150 sacrifice branches and show symptoms of crown die-back (Rood et al., 2000; Sperry,

151 1998). This particular characteristic of the water conducting system has fostered the

152 development of very different hydraulic designs in the evolution of woody plants,

153 rendering not only very different xylem anatomies , but also different leaf hydraulic

154 designs (Sack and Holbrook, 2006). Furthermore, hydraulic function has been

155 underscored and is now claimed, together with the maintenance of a positive carbon

156 balance, as the basis to understand the success of woody plants during acute water stress

157 periods (Breshears et al., 2009; McDowell, 2011). In this respect, functioning of the

158 hydraulic system is directly connected to the capacity of maintaining a positive carbon

159 balance (Mc Dowell et al., 2008; Woodruff and Meinzer, 2011). However, the matter is

160   under debate, at least with regard to the role played by starvation of stored non-

161   structural C compounds for tree survival (Breda et al., 2006; Sala et al., 2010). The

162   expected depletion of carbon balance with water stress is not always in accordance with

163   empirical data (Körner 2003; Villar-Salvador et al., 2004; William et al., 2012).

164   Endogenous tree factors such as age (Genet et al., 2010), height (Woodruff et al., 2011),

165   sensitivity of species to water stress (Tissue and Wright 1995; Latt et al., 2001; Piper

166   2011) and seasonal coupling between supply and demand of carbon for growth (Walter

167   et al., 2005; Smith and Stitt 2007), are all factors modulating the final carbon balance of

168   tree and their capacity to cope with extreme dry events in the long term (see Sala et al.

169   2012 for a recent review on the matter). Finally, whichever the direct physiological

170   mechanisms implied in the weakening and final death of trees, either maintenance of the

171   functionality of tree hydraulic system or starvation by depletion of carbon reserves, they

172   represent the mechanistic basis underpinning the recently observed decline of forest tree

173   species under water stress conditions worldwide (Mc Dowell et al., 2008, though see

174   Sala and Hoch, 2009; Sala et al., 2010). This issue is of great relevance as forest die-

175   back in same cases (Carnicer et al., 2011), or even important phenomena of mortality

176   (Linares et al., 2010) seem to have accelerated and aggravated in the last decades

177   (Breshears et al., 2009; Allen et al., 2010; Linares et al., 2011). Whichever the ultimate

178   mechanistic basis, it seems clear for trees hydraulic failure and impairment of an

179   optimum carbon balance are both elements impacting the capacity to cope with acute

180   drought events in the long term.

181

182   *2.2 Integration of water use mechanisms at the tree and canopy levels*

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184   It should be noted that despite the large amount of information available, there is

185   no current, successful mechanistic model accounting for the physiological basis and

186   integrating the complex stomatal conductance performance in response to a multiplicity

187   of endogenous and exogenous factors (Franks et al., 2007; Mott and Peak, 2010, 2011).

188   Nonetheless, main environmental drivers, namely, soil moisture, air humidity and

189   radiation, have been recognized historically as key factors eliciting different daily and

190   seasonal patterns observed for g_{wv} within tree crowns and canopies (Jarvis and

191   McNaughton, 1986).

192   The physiological functioning of leaves in the regulation of water losses is

193   coupled to the physical control imposed by leaf size and form. Morphology of leaves

194   conditions the leaf boundary layer resistance to water diffusion (Gates, 1968). Smaller

195   leaves of trees would be adaptive under warmer environments preventing leaf heating

196   over harmful temperatures. Thus, recent reports highlight also its impact on the

197   transpiration consumption at the individual tree level (Bauerle and Bowden, 2011).

198   Thought importance of the leaf boundary layer at the ecosystem level relies in the

199   consideration of canopies as aggregate of leaves (Jarvis and McNaughton, 1986). In this

200   respect, the aggregation of the performance of different leaves into the crown in a

201   unique functional unit, the canopy, results in the highest level of integration for

202   transpiration, and where forest stand is viewed on the perspective of a big leaf

203   (McNaughton and Jarvis 1984). Although the overall flux of water through the

204   continuum soil-tree-atmosphere is a very complex process, there are two main physical

205   drivers exerting a control on the rates of water losses at the canopy scale under wet

206   conditions, the physiological control and the boundary layer control over the canopy.

207   Both impact the degree of coupling of tree canopy to the atmosphere (Wullschleger et

208   al. 2000; Gyenge et al. 2011), and in particular to the two principal factors influencing

209   evapotranspiration, the vapour pressure deficit surrounding vegetation and the incoming

210   net radiation. After the inversion of the Penman-Monteith equation, and considering the

211   flux of water into trees as water transpired, it is possible to estimate a physiological and

212   aerodynamic canopy conductance to water vapour. Canopies integrate different

213   structural and functional properties of individual leaves, but they do not result from the

214   summing of those from individual leaves. The coupling to environmental factors of the

215   aerodynamic and physiological conductance of canopy as a functional unity follows

216   similar biophysical rules to those emerging from individual leaves (Jarvis and

217   McNaughton, 1986). The coupling to the atmosphere is modulated daily from wind

218   velocity, incoming radiation and VPD (Wullschleger et al., 2000), and seasonally from

219   a high influence of the water deficit endured by trees (Granier et al. 2000; Kumagai et

220   al. 2004). In this regard, the increase of canopy physiological conductance sensitivity to

221   air water vapour deficit, as drought progresses, would be an effective manner to avoid

222   the hydraulic failure in the soil-leaf-air pathway. Surface roughness of most forest

223   canopies increase the degree of coupling to atmospheric conditions, and decrease the

224   importance that aerodynamic conductance may play in controlling the overall water flux

225   from vegetation to atmosphere (Jarvis and McNaughton, 1986). This is a fundamental

226   difference of forest tree covers, mostly in temperate and Mediterranean areas, when

227   compared to the smoothness of plant surfaces in grasslands or crops cultivars. However,

228   even considering forest tree species as a group, there are important differences between

229 conifers and temperate broad-leaved or tropical species (Meinzer et al., 1993; Meinzer

230 et al., 1997; Kumagai et al. 2004; Wullschleger et al., 2000), and even between

231 different species within the same functional group (Leuzinger and Körner, 2007).

232 Temperate broad-leaved forest tree species seems to be slightly decoupled from

233 atmosphere (table 1, and see table 2 in Wullschleger et al., (1998)), though this degree

234 of decoupling is not as large as in tropical rainforest species. It translates in the later,

235 into a higher importance of the control exerted by the physiological conductance to

236 water vapour of the canopy for some forest tree species, transpiration becoming more

237 dependent on the sensitivity of leaf stomata to changes in water vapour deficit of

238 atmosphere.

239   Water use by forests has been ascertained mainly from the use of techniques

240 such as leaf porometry (Goulden and Field 1994), tree sap-flow (Oishi et al. 2008), eddy

241 covariance (Baldocchi and Ryu, 2011) and catchment water balance (Zhang et al. 2001;

242 Noseto et al. 2011). The overview of all these methods is beyond the scope of this work,

243 and good reviews have been already published (see Goulden and Field, 1994;

244 Baldocchi, 2011; Wilson et al. 2001; Wullschleger et al., 1998). We are going to outline

245 only briefly one of them: the sap flow record. This measurement is an intermediate

246 methodological approach to dissect the use of water by forest tree species from the

247 micro-scale at the leaf level (e.g. porometry), to the macro-scale represented by the

248 whole ecosystem (e.g. eddy covariance or catchment water balance). The response in

249 terms of control of water use at the leaf level, and integrated through the full tree crown,

250 result in different patterns in the water use at the integrative scale represented by a

251 whole individual tree. Individual trees at the same place make use of water in different

252   ways according to species (Martínez-Villalta et al. 2003; Aranda et al. 2005; Poyatos et

253   al. 2005, 2007), and hierarchical status of tree into the stand (Ryan et al., 2000).

254   Measurement of sap flow density is one of the most extensively employed methods that

255   allow discriminating water use by individual trees. The method has different technical

256   approaches and methodological shortcomings (Köstner et al., 1998). Some of them

257   related with the different patterns of sap flow profiling across sapwood depending on

258   species, daily time lag between canopy transpiration and sap flow, or adjustment of the

259   zero base line during nocturnal periods when sap flow is considered null. However, the

260   technique allows resolving water consumption at the individual tree scale reasonably

261   well, allowing to extrapolate to the overall forest stand after an affordable scaling

262   exercise (Kaufmann and Kelliher, 1991; Schwärzel et al. 2009; Oishi et al. 2010). The

263   approach has shortcomings as already mentioned, with some emerging ones as the

264   nocturnal water fluxes, which have to be included in the water balance calculations

265   (Oishi et al. 2008).

266   Once water is captured it moves through trees inhabiting the same forest in a

267   very species-specific manner. This is linked in some cases to specific morphological

268   traits such as leaf and rooting habits, namely deciduous versus evergreen leafing, and

269   shallow vs deep rooting patterns.The sensitivity of different species to environmental

270   factors, specifically to soil water availability, evaporative demand or radiation, explain

271   the different strategies in the sap flow on daily and seasonal temporal scales. An

272   example is found when comparing the daily sap flow of two evergreen species, *Quercus*

273   *ilex* and *Pinus nigra*, growing together in mixed stands at the mid-mountains of the

274   Iberian Peninsula. Both species showed a decline in the daily sap flow from the

275   beginning to the middle of summer (figure 2). However, *P. nigra* maintained a much

276   more conservative performance with regard to the water transpired, showing an acute

277   depression in daily sap flow, making transpiration almost null around midday, which

278   was not observed in *Q. ilex*. Similar segregation and differential performance among

279   species inhabiting the same place has been frequently explored in many kinds of forest

280   tree species, from temperate to tropical biomes.

281   Therefore water consumption by forest trees varies daily and seasonal among

282   species according to seasonal changes in the relative extractable water, radiation and

283   vapour pressure deficit (Oren et al., 1999). Despite the well-known differentiation

284   among forest tree species to climate and atmospheric factors, there has been a debate if

285   the final water budget of forest stands is controlled purely by biophysical rules (West et

286   al., 1999; Enquist et al., 2002; Meinzer et al., 2001; Meinzer, 2003). In this case, the

287   proper application of general transformation scaling rules (e.i. relationship between

288   sapwood and total leaf area) would result in the adjustment of the water use by different

289   tree species to a similar pattern (Meinzer et al., 2001). Another example of confluence

290   in the whole water used by different kind of species, was recently presented by

291   Baldocchi et al. (2010). They observed a similar pattern in the overall annual water

292   budget and carbon fixed when comparing evergreen vs. deciduous species in

293   Mediterranean oak woodlands. It was concluded most important factor controlling, as

294   much water use or carbon uptake, was leaf area index. Inter-annual modulation in the

295   maximum interchange of water and carbon fluxes with the atmosphere according to leaf

296   habit was given by the changes in leaf area index. Thus, and besides leaf habit could be

297   considered to exert an important role on the fluxes of water and carbon in forest

298   ecosystems, it seems that the species-specific response was blurred when the overall

299   water used through the full growing season was considered. In this respect, deciduous

300   species would compensate their shorter vegetative period by maximizing the

301   consumption of water during the wet spring months. However, as shown worldwide and

302   from many studies, the sensitivity of each species to evaporative demand (Hinckley et

303   al., 1978; Oren et al., 1999), perturbations such as intense droughts (Leuzinger et al.,

304   2005) and modification of tree physiological performance in the subsequent years to the

305   perturbation (Breda et al., 2006), are issues to consider at least in environments where

306   water is one of the main limiting environmental factors at some times during the

307   growing season, and different adaptive strategies may have evolved. In this regard, there

308   are numerous examples showing how sensitivity to drought explain differential species-

309   specific decreases in the water use by trees as dry period advances (Aranda et al., 2005;

310   Davis et al. 2007; Kunert et al. 2010; Leuzinger et al., 2005; Oren and Pataki, 2001).

311

312   *2.3 Other functional species-specific processes involved in the water use: capacitance,*

313   *nocturnal water flux and hydraulic lift*

314

315   Not only use, but also control and management of soil water differ from trees to

316   other plant life styles. Unlike other plants, forest trees represent important aboveground

317   reservoirs of water themselves (Scholz et al. 2007). Sapwood and elastic tissues of trees

318   are the two main internal water storages. The relative importance of both compartments

319   varies according to species (Kravka et al., 1999), tree size (Phillips et al., 2010), and soil

320   water availability (Hernández-Santana et al., 2008; Betsch et al., 2011). Although,

321 sapwood seems to be more relevant by conditioning daily tree water budget (Čermak et

322 al., 2007). The impact of dry years on the amount of water withdrawn from both

323 internal water storages has been assessed recently for *Fagus sylvatica* considering the

324 exceptional drought of 2003 in Central Europe (Betsch et al., 2011). The contribution of

325 water accumulated within trees to the overall daily water balance, and specifically to the

326 transpiration stream, increased with the intensity of drought reaching almost a 70 % at

327 the peak of the dry period (Betsch et al., 2011). However, its relevance as mechanism to

328 avoid dry periods should be considered moderate, as most water depleted during diurnal

329 hours must be replaced during the night in order to maintain hydration of aboveground

330 tissues. Otherwise, a fast death of plant tissues would be expected from a fast

331 dehydration. In fact, this recharge is lowered as water in soil gets scarcer (Giovanelli et

332 al., 2007), showing the progressive difficulty to collect and replace internal water

333 reservoirs as drought intensifies.

334   Until recently, water use by trees was considered to operate mainly during the

335 daylight period. In the last years, this view is beginning to change, and nocturnal water

336 flux has been described already for numerous forest tree species (Daley and Phillips,

337 2006; Fisher et al., 2007; Sellin and Lubenets, 2010). It can be a mere consequence of

338 the recharge of internal water reservoirs on the first night hours, but also a consequence

339 of incomplete stomatal closure during night (Caird et al. 2007; Fisher et al. 2007). After

340 replacement of the internal reservoirs, the reason why trees assume costs of night-time

341 water loss without simultaneous photosynthetic carbon gain remains unclear (Phillips et

342 al., 2010). However, there are some possible benefits derived from this, such as the

343 increase of nutrient availability to the plant (Caird et al., 2007), or provide oxygen to the

344 respiring cells of the deep sapwood (Daley and Phillips, 2006). The nocturnal water

345 transport has been quantified as a significant fraction of total daily water use although it

346 depends on several factors including the particular species studied (Dawson et al.,

347 2007). The value ranges from 4.9 % to 7.3 % in *Eucalyptus* species (Phillips et al.,

348 2010) and it is established as 2.4 %, 6.6 % and 13 % in *Acer rubrum*, *Quercus rubra*

349 and *Betula papyrifera,* respectively (Daley and Phillips, 2006) and 6-8 % in *Eucalyptus*

350 *parramattensis* and *Angophora bakeri* (Zeppel et al., 2010). According to these values,

351 the inter-specific variation in nocturnal water transport has been described to be lower

352 than the intra-specific variation in some studies (Phillips et al., 2010; Zeppel et al.,

353 2010). Another important factor that affects significantly to nocturnal sap flow is tree

354 height (Pfautsch et al., 2011). Nevertheless, the factors that present higher correlations

355 with nocturnal sap flow are the environmental ones. For example, it depends on the

356 season, being higher when the soil water availability is not limited: up to almost 50 %

357 (commonly 35 %) and 20-25 % in *Eucalyptus victrix* in wet and dry season, respectively

358 (Pfautsch et al., 2011). Thus, nocturnal transpiration is highest in sites with higher soil

359 water content and less prone to atmospheric or soil water deficits (Dawson et al., 2007).

360 The night-time water transport is highly correlated with vapour pressure deficit

361 (Pfautsch et al., 2011; Zeppel et al., 2010), although there is some study where the

362 product between the vapour pressure deficit and the wind speed are both the principal

363 drivers (Phillips et al., 2010). Specifically, some studies indicate nocturnal transpiration

364 is less than 10 % of the daily sap flow (Daley and Phillips, 2006; Novick et al., 2009).

365 This supports the idea nocturnal refilling is more important than night-time

366 transpiration, which disagree with the study carried out by Zeppel et al. (2010) and

367 where nocturnal sap flow depended mainly on transpiration.

368   The deep rooting patter of trees, unlike other plants, makes possible the

369 movement of water from deep to shallow soil horizons. This specific water pumping

370 property of trees, known as hydraulic lifting (Caldwell and Richards, 1989; Dawson,

371 1993), can have an important ecological role in terms of water redistribution in soils

372 (Horton and Hart, 1998). Not only the water balance may be modulated by this process

373 in some forest trees, but also hydraulic lift is affecting important ecological processes

374 such as the facilitation of water use by individuals of different species and by juveniles

375 of the same species (Brooks et al., 2006). Hydraulic lift was first observed in plants

376 from dry sites such as deserts (Caldwell and Richards, 1989). Afterwards, there have

377 been numerous reports describing this phenomenon for forest tree species from tropical

378 rainforest to typical Mediterranean and temperate forests (Meinzer et al., 2004;

379 Nadezhdina et al., 2008; Scholz et al., 2002). Yet the process seems to be species-

380 specific as recently reported in a mixed beech-oak stand (Zapater et al., 2011).

381

382   *3 The interacting influence of species identity, age, size, stand structure and*

383 *management in the forest water use*

384

385   Segregation of many forest tree species across ranges of soil and atmospheric

386 moisture availability is linked to the control exercised over the water use, on the other

387 hand related to the own sensitivity of different species to water scarcity (Baquedano and

388 Castillo 2006; David et al. 2007; Chirino et al. 2011). From Mediterranean to temperate

389 and tropical areas, there is a plethora of strategies ranging from a characteristic

390 isohydric performance to other fully anysohydric ones (Chirino et al. 2011; Kumagai

391 and Porporato, 2012; Tardieu and Simonneau, 1998). In the first case a water saver

392 performance is expected as soil moisture availability decreases, in the second one, a

393 more water spender use of water is sustained by trees. A typical example is given by

394 *Fagus sylvatica* and *Quercus petraea* under sub-Mediterranean conditions. The former

395 has a very high sensitivity to the depletion of soil water supply, suffering higher

396 decreases in sap flow density rates than *Quercus petraea* as drought advances in

397 summer months (Aranda et al. 2005; Jonard et al. 2011). However, most species would

398 represent a point in what should be more considered a range of variation in the water

399 economy management, than a strict double categorical classification (Franks et al.,

400 2007).

401   Along with the species-specific strategy followed in the water use, other factors

402 are fundamental to understand the water balance of forests. In this respect, two

403 important structural drivers influence water consumption. Height of tree and its

404 hierarchical position in the stand determine total volume of water transpired (figure 3).

405 Frequently, dominant trees maintain higher sap flow densities in the sapwood, together

406 a higher spending of total water as consequence of higher inputs of radiation into tree

407 crowns (Martin et al., 1997; Meinzer et al., 1999; Granier et al., 2000). Different

408 sensitivity of leaf stomatal response to evaporative demand with tree height brings

409 about also differences in the sap flow of tree (Woodruff et al., 2010). Even more,

410 whether forest tree species grow in pure or mixed stands, it is also a factor that modifies

411   the species-specific response and performance in terms of individual tree sap flow,

412   conditioning the overall water use of stand in the last (Jonard et al., 2011).

413   Beyond the size of the tree and its dominance of the forest stand, its own age

414   profoundly modulates its water use (Delzon and Loustau, 2005). As trees age, there is a

415   progressive decrease in the movement of water per sapwood unit, explained by what has

416   been termed "the hydraulic limitation hypothesis" (Ryan and Yoder, 1997; Ryan et al.,

417   2006). The lost of efficiency through the hydraulic path as tree ages, in terms of lower

418   leaf-specific hydraulic conductance, would explain a more water conservative

419   performance at the leaf stomatal control level at the top of the tree crown. This has

420   practical consequences on the water used by natural or artificial forests. If stands are

421   structured according to young or old age tree classes impacts directly in the forest water

422   budget. For a similar sapwood area, young trees tend to maintain higher rates of

423   transpiration than old ones. In this respect, silviculture practices focuses to maintain

424   short rotation systems might promote a more water spending use by outstanding trees

425   (Lagergren and Lindroth, 2004; Forrester et al., 2010). In the same way, some

426   perturbations as wildfires or intensive logging prompt transformation of old to re-

427   growth forests or coppice, the direct impact being an increase in the water consumption

428   by forest in subsequent years (Buckley et al., 2012; Macfarlane et al., 2010).

429   Therefore, modification in the structure of stand as a consequence of different

430   management practices, impacts directly in the water used by the remaining trees (Breda

431   et al., 1995; Jiménez et al., 2008). Coppice or seedling re-establishment are two

432   different forest management practices for regeneration of natural forests or plantations,

433   both also influencing forest water economy in the following years after the silvicultural

434   practice (Drake et al., 2012). The former involves a higher development of root system

435   which translate into a better access to deep water resources from groundwater, together

436   with larger water interception and stand-scale transpiration rate (Drake et al., 2012).

437   This would result in a more wasteful water use in stands maintained in a permanent re-

438   growth state as coppice, at least on the first years after logging and re-sprouting of

439   stumps.

440   The need of a precise knowledge of the water consumption of forest tree species

441   or specific stand structure, it is also extensible to the impact of some management

442   practices such as forest thinning (Bréda et al., 1995; Gyenge et al., 2011; Moreno and

443   Cubera, 2008). Silvicultural treatments where forest stand stocking is reduced bring

444   about direct structural changes making more open the stand. This has an impact not only

445   in the interrelationships among residual trees (Jiménez et al., 2008), and species in the

446   case of mixed stands (Bladon et al., 2006), but also on the surrounding microclimate

447   conditions (Zheng et al., 2000). It's well established that a decrease in tree density

448   prompt an immediate positive effect on remnant trees, increasing on many cases the use

449   of resources such as water (table 2), and improving growth in the subsequent years after

450   stand stocking decrease (Bréda et al., 1995; Gracia et al., 1999; Lagergren et al., 2008).

451   Amelioration of growth is clearly related with an increase in the water and radiation

452   availability. However, it has been also observed on some cases, an abrupt change in the

453   evaporative demand around remaining trees after cutting. This increases the xylem

454   tension drop below the hydraulic margins of security for the hydraulic system of

455   standing trees (Bladon et al., 2006). In the last, this could translate in a negative impact

456   on the tree hydraulic system, provoking an increase of xylem dysfunction. The response

457   is highly species-specific as shown by Bladon et al. (2006) from a variable retention

458   partial harvesting stand experiment. Forest tree species making up the mixed stand

459   responded in a very different way. There was an improved in the water use of residual

460   trees in *Picea glauca* at the clear cutting plot, a moderate and slight increase in *Betula*

461   *papyrifera* and the maintenance of the same water consumption between control and

462   cleared plots for *Populus balsamifera*. In the case of Populus there was an increase in

463   the risk of hydraulic failure after the thinning.

464   One the most important needs of information to assure management of new

465   planted and natural forest in a sustainable way in the future is related to the water

466   requirements of forests. The specific composition, along with structure, will be both the

467   main drivers in the forest water use. This issue is especially relevant for areas of the

468   world as tropical zones where basic information in the water use at the specific level is

469   scarce (Kunert et al., 2009). Water is already a problem in wide areas of the world as the

470   Mediterranean Basin. This obligates to have a good knowledge on the specie-specific

471   water use at the tree level for plant materials used in reforestation programs, given the

472   aforementioned different strategies followed by forest tree species. In order to assure

473   sustainability of planted forest stands in the future, it is needed to ascertain how much

474   water will be used by these new forest systems (Petzold et al., 2010), paying attention to

475   the impact of natural hazards such as intensification of droughts in the water use by

476   forest tree species in general (Martínez-Vilalta et al., 2003; Gartner et al., 2009). For

477   instance, new plantations aimed to produce biomass as source for bioenergetic use,

478   might increase the water consumed with regard traditional agricultural crops or natural

479   forests (Gyenge et al., 2008; Petzold et al., 2010). Tricker et al. (2009) reported an

480   increase in the annual water use by *Populus* trees in bioenergy plantation under the

481   future higher air CO_2 levels expected in the next decades. This was despite the response,

482   in terms of lower leaf stomatal conductance, followed the general pattern of decrease in

483   the CO_2 enriched air treatment regarding ambient conditions. Increases in other factors

484   such as total leaf biomass would compensate the lowering in the water use at the leaf

485   level. If these data are confirmed, the result could be the establishment of new plant

486   production systems that would not be sustainable in relation to available water resources

487   at some places in the world (Delucchi, 2010). The picture could be worse considering

488   the forecasted more extreme dry period that forests will have to withstand in areas as the

489   Mediterranean (IPCC 2007), or even ample tropical zones.

490

491   *4 Water use by forests and impact at the landscape scale*

492

493   Trees exert a strong control over the terrestrial ecosystem water cycle through

494   their effect on forest water use. As a consequence, changes in land cover may lead to

495   profound hydrological changes, affecting the water balance and the quantity and quality

496   of water resources (Kume et al., 2007). During the last decade, afforestations have been

497   proposed as a promising tool for carbon sequestration, but their full environmental

498   consequences have not been considered. Regarding water budgets, current evidence

499   suggests that tree plantations usually reduce stream flow and groundwater recharge

500   (Farley et al., 2005; Nosetto et al., 2011), since tree covers present greater

501   evapotranspiratory capacity than croplands and herbaceous covers (Farley et al., 2005;

502   Huxman et al., 2005). The combination of deeper root systems extended growing

503 seasons, higher transpiration rates, greater interception of precipitation and higher inputs

504 of radiant energy because of lower albedos explain the higher evapotranspiration and

505 lower deep drainage in forest compared to herbaceous covers or croplands (Kelliher et

506 al., 1993; Canadell et al., 1996; Nosetto et al., 2011). Due to these hydrological impacts

507 reforestations programs are considered as a land use activity that may threaten water

508 resources security, particularly in some drought prone areas (Pacala and Socolow, 2004;

509 Jackson et al., 2005). In a global synthesis study, Farley et al. (2005) showed that

510 afforestation of grass and shrublands reduced annual runoff on average by 44% and by

511 31%, respectively. Similarly, stream flow reductions of up to 50% have been reported in

512 the Ecuadorian Andes (Buytaert et al., 2007) after afforestation with *Pinus* plantations

513 while a water budget study in Brazil demonstrated that 95% of the precipitation is

514 evapotranspirated by *Eucalypt* plantations (Almeida et al., 2007). However, positive

515 effects related to the control of flooding or the improvement of the quality of water

516 resources are also claimed as main arguments for reforestation programs. In some cases,

517 due to higher root density, microfaunal activity and/or content of soil organic matter and

518 litter, tree plantations may improve the porosity and capacity of water transport of soils,

519 improving water infiltration and deep drainage, and reducing erosion and the volume of

520 sediment, nutrients and salt volumes transported into river systems (Nosetto et al., 2007;

521 Van Dijk and Keenan, 2007; Nosetto et al 2011).

522   Replacement of native woody vegetation by tree plantations has also strong

523 effect on the water cycle. Reforestation programs usually used fast-growing species

524 which are characterized by higher productivity and biomass, but also by higher annual

525 transpiration and rainfall interception, particularly for fast growing evergreen species

526   such as pines and eucalypts (Farley et al., 2005). Gyenge et al. (2008) demonstrated

527   significantly greater water use by ponderosa pine plantations compared to natives

528   *Austrocedrus chilensis* forests in NW Patagonia. Hydraulic characteristics of *P.*

529   *ponderosa* (higher canopy-stomatal, whole hydraulic conductances and specific

530   hydraulic conductivity) allow high stomatal conductance for more hours a day than *A.*

531   *chilensis* trees, and therefore greater transpiration. In a study of more than 600

532   observations, Jackson et al. (2005) found reductions stream flows by almost 52% when

533   native vegetation was replaced by forest plantations. In some cases, establishment of

534   plantations caused streams to dry completely, especially in drier regions.

535   By contrast to afforestation, deforestation usually leads to increases in stream

536   flows and ground water recharge since evapotranspiration is considerably reduced

537   (Farley et al., 2005; Nosetto et al., 2011). Native forest clearing for cropping in

538   Australia and the Sahel has led to increased groundwater recharge, arising of water table

539   levels due to the lower evapotranspiration rates of croplands (Schofield, 1992; Leblanc

540   et al., 2008). Similarly, Nosetto et al. (2011) predict that replacement of large areas of

541   dry forests by soybean crops in central Argentina would reduce evapotranspiration in a

542   30% and would almost increase three fold deep drainage fluxes.

543   Nevertheless, the impact of the hydrological changes generated by land-use

544   changes varies depending on context where land use shifts occur (Van Dijk and Keenan,

545   2007; Nosetto et al., 2011). In drought prone regions the potential reductions of water

546   resources caused by forest plantations are smaller in absolute terms than in humid

547   regions, but the impact can be environmental, economical and socially more harmful

548   due to the already scarce water availability. Even more, hydrological modification could

549   trigger positive or negative impacts on water cycle depending on the context. For

550   example, tree plantation in flooding-prone places may be positive, since it can reduce

551   the risk of flooding and improve the soil drainage capacity. By contrast, afforestation in

552   semiarid environments would reduce water availability even more. The replacement of

553   forests by crops can improve stream flows and ground water recharge, but it could also

554   cause the rise of water table levels, flooding and salinization (Archibald et al., 2006;

555   Peck, 1978). In addition, for a given climatic condition, there are different options for

556   developing sustainable forest management strategies in order to control or minimize the

557   potential hydrological impacts of tree plantations: terrain conditions, planting

558   arrangement, species physiology, water use efficiency, variation in stand age, spacing,

559   site productivity, forestry operations, proportion of area planted etc.

560

561   *5 Main conclusions and remarks*

562

563   Water is a keystone element influencing performance of forest tree species

564   worldwide. The impact of water availability on the ecology and evolution of plants in

565   general, has been one of the most important subjects of study for functional plant

566   ecologists in the last decades. Main environmental factors influencing the species-

567   specific water use by forest tree species, and the different functional strategies, are

568   beginning to be elucidated. Nevertheless it must be recognized that there are important

569   gaps in current functional knowledge regarding water use for many forest tree species,

570   especially in tropical zones. Functional mechanisms governing water use at different

571   scales of biological integration have been assessed in detail during the last decades.

572 However, the complexity in the response to water availability, always interacting with

573 other factors of the environment such as light or nutrients, and the proper structural

574 complexity of forest ecosystems, explain the difficulties to implement water used by

575 forest tree species as criteria in management practice. In any case, management of

576 forests must guarantee the sustainability of forest stands in the future, taken into account

577 the well documented relationship between forest health, tree growth and water

578 availability. Management must make possible the difficult interplay between forests as

579 water spenders and carbon fixing sinks. Some natural and artificial forest could be in

580 serious risk of die-back and mortality of dominant trees as a consequence of a general

581 harshening of climate in terms of more acute dry periods. This reinforces the urgent

582 need to establish, despite the many aforementioned difficulties, the inclusion of water

583 use as one of the main targets in the management of forest in the future, and within the

584 context of a rapidly changing world. The issue is especially relevant for the new

585 plantations planned to provide different goodness from biomass for bioenergetics

586 purposes to soil protection from desertification.

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1065   Figure 1 Seasonal evolution in daily leaf stomatal conductance to water vapour (g_{wv}) for

1066   sun leaves at the top canopy in a mixed stand of beech (*F. sylvatica*) and sessile oak (*Q.*

1067   *petraea*) at the southern area distribution of both species in Europe. There was a

1068   progressive increase in drought intensity that peaked by the middle of September. Beech

1069   shows a progressive decrease in maximum daily g_{wv} that tends also to be earlier in the

1070   morning as drought intensifies. In the other hand, sessile oak showed a typical dome

1071   shaped daily evolution of g_{wv}, even for the most stressful dates when differences were

1072   maxima between both species. Data are for year 2000 at the beech-oak forest of

1073   Montejo de la Sierra (I. Aranda unpublished original data).

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1075   Figure 2 Daily water sap flow in two typical Mediterranean forest tree species (*Quercus*

1076   *ilex* and *Pinus nigra*) recorded with the HBT technique. Two contrasted periods were

1077   considered, late spring (top graph) and mid summer (down graph). Pines suffered a

1078   much more acute decrease in summer water use than oaks. The trends represent the

1079   mean $\pm$ SD for four trees per species (A. Forner original unpublished data).

1080

1081   Figure 3 Water is used by trees in Mediterranean mid-mountains conditions according

1082   to its hierarchical position in the stand. Sensitivity of species to the depletion of soil

1083   moisture as season advance is of prime importance as well. There were significant

1084   differences for *Fagus sylvatica* (Fs) and *Quercus petraea* (Qp) in the water use at

1085   midday, and whether dominant (Do) or co-dominant the status of tree in the stand. The

1086   differences were maintained only for Qp as the season progressed. Average values

1087   represent water use by trees at midday in three dates on July and August in the Beech-

1088   Oak forest of Montejo de la Sierra (n=4, ± S.E.). This forest represents one of the

1089   southernmost beech populations in west of Europe. (A. Forner original unpublished

1090   data).

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1092   Table 1 Decoupling factor from conifer to tropical forest tree species. The ranges for

1093   some species represent variation according to time in the growing season or degree of

1094   canopy closure.

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1096   Table 2 Impact on water use of outstanding trees after forest thinning. It was observed

1097   an increased water use in most cases in the following years after the treatment.

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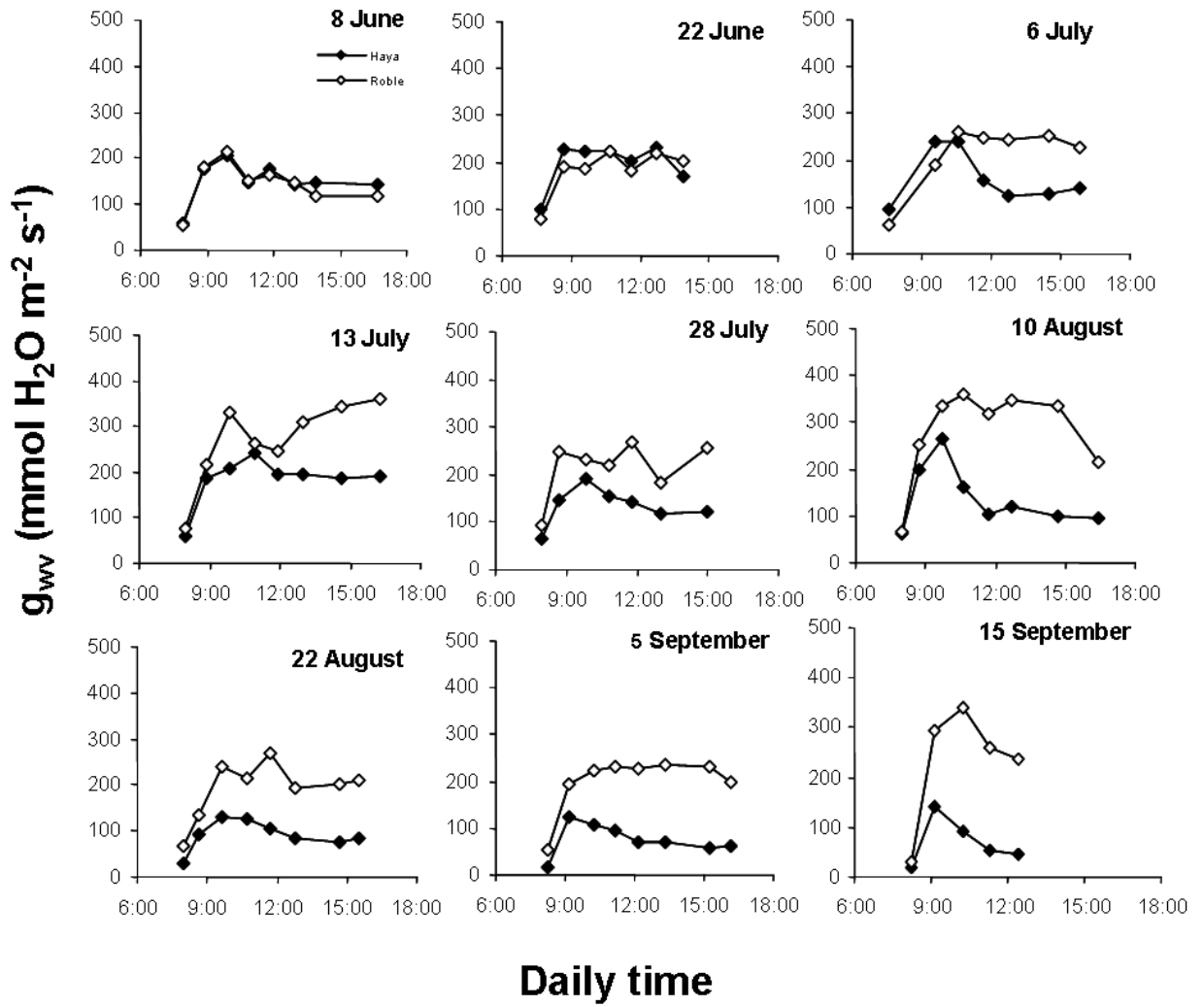1109

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1117   Figure 1

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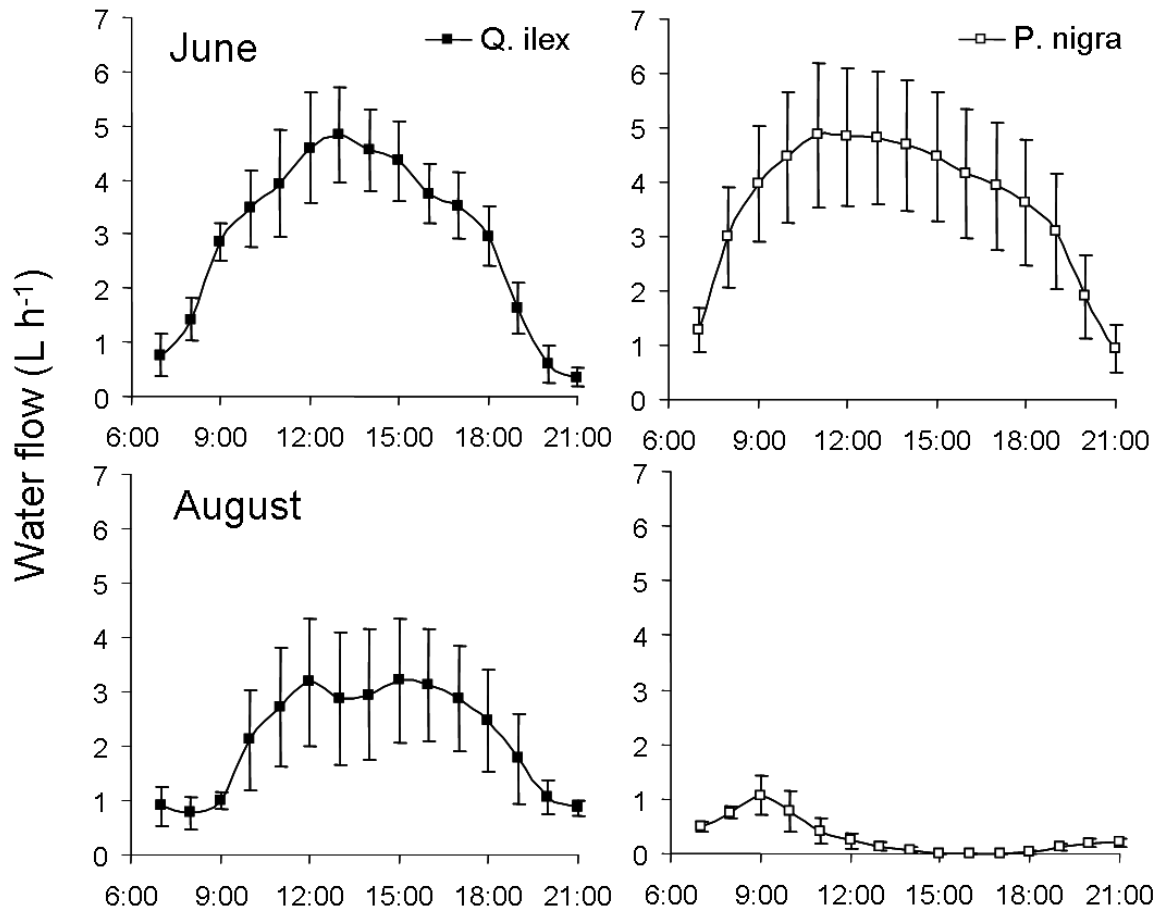
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1137 Figure 2

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1159   Figure 3

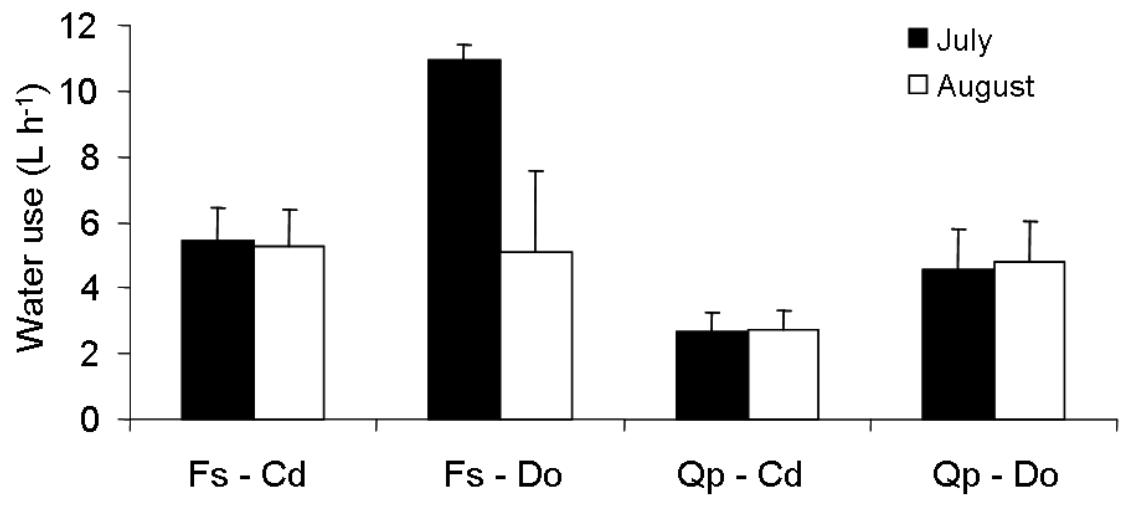1160

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