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1 **Increase in size and nitrogen concentration enhances seedling survival in**
2 **Mediterranean plantations. Insights from an ecophysiological conceptual model of**
3 **plant survival**

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29 **Abstract**

30 Reduction in plant size and tissue nutrient concentration is widely considered to increase
31 seedling drought resistance in dry and oligotrophic plantation sites. However, much evidence
32 indicates that increase in size and tissue nutrient concentration improves seedling survival in
33 Mediterranean forest plantations. This suggests that the ecophysiological processes and
34 functional attributes relevant for early seedling survival in Mediterranean climate must be
35 reconsidered. We propose a physiological conceptual model for seedling survival in
36 Mediterranean-climate plantations to provide a physiological explanation of the frequent
37 positive relationship between outplanting performance and seedling size and nutrient
38 concentration. The model considers the physiological processes outlined in the plantation
39 establishment model of Burdett (1990), but incorporates other physiological processes that
40 drive seedling survival, such as N remobilization, carbohydrate storage and plant hydraulics.
41 The model considers that seedling survival in Mediterranean climates is linked to high growth
42 capacity during the wet season. The model is for container plants and is based on three main
43 principles, 1) Mediterranean climates are not dry the entire year but usually have two
44 seasons of contrasting water availability; 2) summer drought is the main cause of seedling
45 mortality; in this context deep and large roots is a key trait for avoiding lethal water stress; 3)
46 attainment of large root systems in the dry season is promoted when seedlings have high
47 growth during the wet season. High growth is achieved when seedlings can divert large
48 amount of resources to support new root and shoot growth. Functional traits that confer high
49 photosynthesis, nutrient remobilization capacity, and non-structural carbohydrate storage
50 promote high growth. Increases in seedling size and nutrient concentration, strongly affect
51 these physiological processes. Traits that confer high drought resistance are of low value
52 during the wet season because hinder growth capacity. We provide specific evidence to
53 support the model and finally we discuss its implications and the factors that may alter the
54 frequent increase in performance with increase in seedling size and tissue nutrient
55 concentration.

56

57 **Keywords:** Carbohydrates, drought stress, fertilization, forest plantation, nitrogen, nutrients,
58 photosynthesis, plant quality, remobilization, root growth.

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60

61 **Introduction**

62

63 Water stress is a major cause of failure in forest restoration projects in Mediterranean
64 ecosystems (Alloza and Vallejo 1999; Mendoza et al. 2009). Summer drought is the main
65 cause of water stress and seedling mortality is concentrated during the first summer after
66 planting (Castro et al. 2004). Plants usually do not experience water stress during the
67 remainder of the year (Sala and Tenhunen 1994; Mediavilla and Escudero 2004), due to either
68 low air vapor pressure deficit or high rainfall. Consequently, forest plantations in the
69 Mediterranean basin are done in the wet season with the planting window spanning from
70 early November to early April in most sites. Most stocktype is container plant, which is
71 planted when seedlings are 8-12 months old in most species.

72 Mediterranean woody flora is mainly composed of evergreen species, which maintain
73 appreciable photosynthesis and root elongation during the wet season (Leshem, 1965; Sala
74 and Tenhunen 1994; López et al. 2001). Plant functional attributes exert a significant
75 influence on the carbon (C), water and mineral nutrient economy of plants and thus on their
76 fitness. Nursery cultivation regimes strongly influence seedling morphology and physiology
77 and, consequently, their potential outplanting performance (van den Driessche 1991a; Arnott
78 et al. 1993; Villar-Salvador et al. 2004). Shoot height and root collar diameter are the most
79 commonly functional attributes used for operational plant quality assessment due to their
80 measurement simplicity. European Union has regulated the shoot height and root-collar
81 diameter standards for acceptable seedlings for forest restoration in several Mediterranean
82 tree species (Alfá et al. 2005). For instance, one-year old *Quercus ilex* L. seedlings of
83 acceptable quality must have a shoot height ranging between 8 and 30 cm. Seedling size is
84 a relatively good predictor of outplanting performance in boreal and humid-temperate species

85 when seedlings are similar in physiological quality, with survival frequently increasing with
86 shoot size (Thompson 1985; Tuttle et al. 1988; Mexal and Landis 1990; Bayley and Kietzka
87 1997; South et al. 2005; Pinto et al. 2012). In the last 20 years, there has been a growing
88 body of evidence also in Mediterranean environments that, for a given species and for plants
89 of the same age, seedling survival increases with plant size (Guehl et al. 1989; Villar-
90 Salvador et al. 2004a; Tsakaldimi et al. 2005; del Campo et al. 2007; Luis et al. 2009; Oliet et
91 al. 2009; Cuesta et al. 2010b). For instance, *Q. ilex* seedlings that were 12.5 cm in height had
92 50% less survival than seedlings that were 16.4 cm in height (Villar-Salvador et al. 2004a). In
93 *Pinus canariensis* C.Sm. ex DC, 8-cm tall seedlings survived 40% less than 20-cm tall plants
94 (Luis et al. 2009). Similarly, differences in sapling survival across *Quercus suber* L.
95 provenances were also positively related to the height of planted seedlings (Ramírez-
96 Valiente et al. 2009). In this study, seedling size was closely related to acorn size, which was
97 bigger in populations from warm and drier locations. In their meta-analysis of 30 forest
98 plantation studies in Mediterranean-climate areas of Spain, Navarro et al. (2006) concluded
99 that plant size at planting significantly explained survival differences in 43% of the case
100 studies, whereas survival was not related to plant size in the remaining cases studies (Figure
101 1). Among the former, positive relationships between survival and seedling size were three
102 times more frequent than cases showing negative relationships. Rainfall differences among
103 sites did not affect the outlined pattern in this meta-analysis and both positive and negative
104 survival-plant size relationships have been reported in semiarid sites (Luis et al. 2009; Oliet
105 et al. 2009; Trubat et al. 2011). Navarro et al (2006) concluded that the target seedling for
106 Mediterranean forest plantations should be larger than the conventional seedling used in
107 most forestation programs. Many of the positive relationships between survival and plant size
108 are supported by nursery fertilization experiments, which suggests that plant nutritional
109 status (mainly of nitrogen) is also an important issue in explaining outplanting performance in
110 Mediterranean environments (Villar Salvador et al. 2004a; Luis et al. 2009; Oliet et al. 2009).

111 The outlined trends are in conflict with results indicating that reduction in seedling size
112 and tissue nutrient concentration increases drought resistance and performance in

113 oligotrophic soils located in dry environments (Tuttle et al. 1988; Tan and Hogan 1997; Leiva
114 and Fernández-Alés 1998; Trubat et al. 2011). Therefore, we believe that the physiological
115 processes and functional attributes underlying seedling survival in Mediterranean forest
116 plantations must be revisited based on a different view of the Mediterranean climate.

117 This study proposes a physiological conceptual model of seedling survival in
118 Mediterranean sites to explain why seedling survival frequently increases with seedling size
119 and tissue nutrient concentration. The conceptual model considers the physiological
120 processes outlined in Burdett's plantation establishment model (Burdett 1990) but
121 incorporates other relevant physiological processes driving seedling survival, such as
122 nitrogen (N) remobilization, carbohydrate storage and plant hydraulics, which were not
123 explicitly considered in Burdett's model. Additionally, our model also extends the timeframe
124 beyond the establishment phase and considers that dry season survival is strongly linked to
125 physiological activity in the wet season. Finally, we provide evidence for the model based
126 either on *ad hoc* designed experiments to test predictions derived from an earlier version of
127 the model (Villar-Salvador 2003) or published studies on transplanting performance of forest
128 species.

130 **The conceptual physiological model**

131 The model assumes the use of container stocktypes, that selected species and provenances
132 are appropriate for the planting site, seedlings are healthy and cold-hardy, and operational
133 activities before, during and after planting, such as soil preparation, irrigation, weed control or
134 herbivore exclusion, are properly implemented. It is based on three major principles:

- 136 1. Mediterranean climates have two seasons of contrasting water availability (Mitrakos
137 1980). Drought is usually concentrated in the summer when the combination of high
138 temperature and lack of rainfall occur for one to five months. Plants usually do not
139 experience drought stress during the wet season, except in very dry sites or during
140 extraordinary drought events and in sites that experience severe frost. In this scenario of

141 variable water availability in time, correct outplanting timing (*i.e.* during the wet season)
142 allows seedling establishment and growth to lessen dry season stresses.

143 2. Survival to summer drought is linked to the capacity of seedlings to avoid lethal water
144 stress, which is mainly achieved by having a large, deep root system during the dry
145 season.

146 3. Reallocation of large amounts of resources during the wet season is critical for great new
147 growth prior to the onset of the dry season. The model therefore, emphasizes the
148 physiological processes that underlie root and shoot growth.

149

150 *Model description*

151 New growth depends on seedling capacity to supply C and mineral nutrients (mainly N) as
152 long as the plant water potential does not limit cell elongation and gas-exchange (Willaume
153 and Pages 2006; Millard and Grelet 2010). Carbon can be supplied by both current
154 photosynthesis and carbohydrates stored during nursery cultivation. Most boreal and wet
155 temperate conifers rely mainly on current photosynthesis to support early root growth in
156 spring (van den Driessche 1987; van den Driessche 1991b; Hansen et al. 1996; Millard and
157 Grelet 2010). Some evidence also point out the importance of recently assimilated C for new
158 growth in conifers and in evergreen broadleaf Mediterranean species (Atzmon et al. 1994;
159 Cerasoli et al. 2004; Maillard et al. 2004). The importance of current photosynthesis and
160 stored non-structural carbohydrates (NSC) for early root growth in deciduous species
161 depends on whether roots resume their growth before or after shoot flush in spring. When
162 root growth initiates after shoot flushing, shoot growth is strongly dependent on NSC but root
163 growth is then supported by recently expanded leaves (Abod et al. 1991). When shoot and
164 root growth initiation occurs simultaneously in spring, as in *Q. rubra* L., early root growth
165 depends on stored NSC, but as new leaves mature current photosynthates assume a greater
166 role (Sloan and Jacobs 2008).

167 The greater the contribution of photosynthesis or stored NSC, the more C there is for
168 growth (Figure 2). Greater seedlings shoot size increases foliage biomass (del Campo et al.

169 2010; Trubat et al. 2011) and, consequently, photosynthesis per plant (Dyckmans and Flessa
170 2001). Higher foliage N concentration may also increase net photosynthesis rate (A) due to
171 higher stomatal conductance (g_s) and carboxylation capacity (Field and Mooney 1986;
172 Clearwater and Meinzer 2001).

173 Variations in seedling size determine NSC content if there is not any change in NSC
174 concentration. An increase in NSC content can enhance growth in species that chiefly rely on
175 NSC for early growth or disturbance recovery (Puttonen 1986; McPherson and Williams
176 1998). NSC availability also depends on the balance between photosynthesis and
177 maintenance respiration, which will be reduced if the proportion of “heterotrophic” organs in a
178 seedling increases. The shoot-to-root mass ratio (S/R) and the leaf mass ratio usually scale
179 up with increased seedling size if rooting volume does not vary (Villar-Salvador et al. 2005).
180 Therefore, it can be expected that maintenance costs will increase with reduction in seedling
181 size in container seedlings.

182 New organ growth depends on soil N and N remobilization from pre-existing organs
183 (Salifu and Timmer 2003; Millard and Grelet, 2010). Nitrogen remobilization is a source-
184 driven process, *i.e.*, the higher the N content of an organ the greater the amount of N
185 remobilized from it (Millard and Grelet 2010). Therefore, an increase in plant size and tissue
186 N concentration will increase N remobilization potential (Figure 2).

187 Plant hydraulic conductance is the water flow rate through the plant per change in
188 hydraulic pressure driving the flow (Sperry 2000). It is usually standardized with leaf area
189 (leaf specific conductance, LSC), the transversal sapwood area (specific conductance, k_s) or
190 by root surface area (k_r) when the root hydraulic conductance is studied. An increase in k
191 enhances water flow through the plant. This effect is attributed to the link between k and g_s ,
192 mediated by water potential. A higher k permits the plants to maintain higher water potential
193 at similar transpiration rate than a lower k (Bucci et al. 2006; Sperry 2000). Increase in
194 hydraulic conductance (k) can increase g_s and, consequently, A (Sperry 2000). k can
195 increase with plant size (Lovelock et al. 2004) and enhance water uptake capacity
196 (Grossnickle and Russell 1990; Sword Sayer et al. 2005) and, consequently, plant hydration.

197 Variations in photosynthesis, mediated by changes in foliage surface and g_s , also positively
198 affect transpiration and, therefore, negatively plant water potential.

199 Higher C and N availability can support higher root and shoot growth, leading to a
200 feed-back cycle where root growth supports photosynthesis and photosynthesis supports
201 root and shoot growth (Burdett 1990) (Figure 2). This process will ensure seedling
202 establishment right after planting (Burdett 1990; Grossnickle 2005) and extension of the root
203 system during the rest of the wet season. If seedlings exhibit vigorous root growth during the
204 wet season, root systems should be large and reach deep moist soil horizons at the onset of
205 the dry season. This increases water uptake capacity during the dry season (Padilla and
206 Pugnaire 2007) and, consequently, gas-exchange capacity. Root elongation during the wet
207 season should also favor soil nutrient uptake to support root and shoot growth along with
208 nutrient remobilization. Similarly, production of high photosynthetically active new shoots in
209 spring should foster photosynthesis in Mediterranean evergreen species, in which currently
210 formed leaves coexist with older less photosynthetically active leaves during spring (Milla et
211 al. 2005).

212 Plant water potential ultimately depends on the balance between plant water loss and
213 uptake. If the root system is too small in relation to the plant's transpiration capacity or too
214 shallow to reach deep moist soil layers, plant water uptake will not meet transpirational
215 demand and cause a reduction in water potential. This will reduce gas-exchange through
216 stomatal closure and growth. Increased water uptake during the dry season prevents the
217 plant from reaching lethal water potential, at which extensive embolism can cause
218 catastrophic hydraulic failure inducing leaf shedding and, lastly, seedling death (Vilagrosa et
219 al. 2003; Brodribb and Cochard 2009). Prolonged periods of very low photosynthesis can
220 lead to C starvation (Adams et al. 2009), which also might be also a potential cause of
221 seedling mortality (Canham et al. 1999; McDowell et al. 2008) (Figure 2). As high summer
222 temperature can exacerbate C starvation by increasing seedling respiration, maintenance of
223 a significant level of photosynthesis is critical for maintenance of plant metabolism during the
224 dry season.

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2 **226 Predictions from the model and evidence of the physiological mechanisms underlying**
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4 **227 the frequent outplanting performance improvement with seedling size and N**
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6 **228 concentration increase in Mediterranean plantations.**

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9 229 Several predictions can be established from the conceptual model and in this section we
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11 230 provide evidences that support main predictions and help to understand the frequent superior
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13 231 outplanting performance of larger and N-rich seedlings relative to smaller and poor-N plants
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15 232 in Mediterranean environments.

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20 234 *Prediction 1: Root system size and depth determines plant water status and survival in*
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22 235 *summer*

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26 237 Size of the root system drives drought survival of woody species in dry climate areas
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28 238 (Grossnickle 2005). Seedling survival differences among common woody species in the
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30 239 semiarid Iberian Peninsula were positively linked to the root depth achieved during summer
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32 240 (Padilla and Pugnaire 2007). Species that had high seedling survival produced roots that
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34 241 reached deeper moisture soil horizons than species that had low survival. Summer predawn
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36 242 water potential of *Quercus coccifera* L. seedlings that were planted within different
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38 243 treeshelters was positively related to the length of new roots (Bellot et al. 2002). Similarly, *Q.*
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40 244 *ilex* seedlings that differed in vigor and in planting date were also different in their mid-day
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42 245 water potential and survival by the end of the first summer, which were positively correlated
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44 246 with new root growth at the beginning of the summer among (Figure 3).

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51 248 *Prediction 2: An increase in seedling size and N content increases root growth*

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55 250 Many studies have shown that differences in seedling morphology and physiology status
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57 251 influence root growth capacity (RGC). Most RGC studies have been conducted under
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59 252 glasshouse or growth chamber conditions for short time periods but field studies are scarce.

253 RGC increases with plant size (South et al. 1989). High fertilized seedlings, which are
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2 254 bigger and richer in N than low fertilized plants, have greater RGC (van den Driessche 1992;
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4 255 Villar-Salvador et al. 2004a). Further, field studies rend similar results to those in controlled
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6 256 conditions. High N fertilized *Juniperus thurifera* L. seedlings grew deeper roots than low N
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8 257 fertilized plants when transplanted into 1 m long metacrylate tubes that were inserted into the
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11 258 soil. Deeper roots were attributed to higher root elongation rate in high fertilized plants
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13 259 (Figure 4). Using the same methodology, Cuesta et al. (2010a) found that larger *Pinus*
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15 260 *halepensis* Mill. seedlings had greater root systems than smaller seedlings, but no difference
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17 261 in root depth could be observed. Contrary to the results for *J. thurifera*, a greater root system
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19 262 in larger *P. halepensis* plants was attributed to a greater number of new roots rather than a
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21 263 higher elongation rate of each root.
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24 264 Large, nutrient rich *P. canariensis* plants produced greater root systems than small,
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26 265 nutrient-poor seedlings three years after outplanting (Luis et al. 2009). Similarly, large *P.*
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28 266 *halepensis* had greater new root mass at the beginning of the dry period than small
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30 267 seedlings, and this difference was more pronounced in the presence rather than in the
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32 268 absence of weeds (Cuesta et al. 2010b).
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38 270 *Prediction 3: N remobilization increases with increase in plant N content.*
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42 272 Greater plant size and tissue N concentration increases plant N content. The proportion of N
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44 273 remobilized to support new growth depends on species, source organ, and source/sink
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46 274 interactions (Silla and Escudero 2003; Millard and Grelet 2010). For instance, the proportion
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48 275 of new N in growing organs derived from remobilized N from old leaves and woody fractions
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50 276 varied from 17 to 88% in Mediterranean oak saplings (Silla and Escudero 2003). The amount
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52 277 of remobilized N depends on source strength, *i.e.* plant N content. Using ¹⁵N labeled fertilizer,
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54 278 Salifu and Timmer (2003) demonstrated that N-loaded *Picea mariana* (Mill.) BSP seedlings
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56 279 remobilized three times as much N as conventional fertilized seedlings did, which had lower
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58 280 N content than the former seedlings. Similar trends have also been reported for other wet
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281 temperate and boreal woody species (Millard and Neilsen 1989; Grelet et al. 2003; Millet et
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2 282 al. 2005).

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4 283 Using a N budget approach, Cuesta et al. (2010b) found that large *P. halepensis*
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6 284 seedlings remobilized four to six times more N than small seedlings to support spring growth.
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8 285 Both seedling types did not differ in their tissue N concentration but large seedlings
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10 286 contained five more times N than small seedlings. El Omari et al. (2003) reported that
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12 287 fertilized *Q. ilex* saplings remobilized higher amounts of N than N-deprived seedlings, which
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14 288 was attributed to greater N reserves in high-fertilized seedlings.
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20 290 *Prediction 4: Increase in seedling size and nutrient concentration at planting increases water*
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22 291 *potential and photosynthesis rate in the field during the dry season.*
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26 293 Large, nutrient-rich *P. canariensis* seedlings had higher water potential and photochemical
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28 294 efficiency than small, nutrient-poor seedlings three years after planting (Luis et al. 2009).
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30 295 Furthermore, large *P. halepensis* seedlings had greater field gas-exchange capacity than
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32 296 small plants, independent of their tissue N concentration (Cuesta et al. 2010b). These
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34 297 differences were apparent under moderate but not under high drought stress conditions.
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36 298 However, the authors did not observe differences in water potential between seedling types.
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38 299 Similarly, moderate and high N fertilized *Ceratonia siliqua* L. plants had greater *A* than low-
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41 300 fertilized plants after planting in a site with <200 mm of annual rainfall (Planelles González
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43 301 2004). High-fertilized *J. thurifera* seedlings had higher daily course of *A* in mid-summer than
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45 302 low-fertilized seedlings. Higher *A* was linked to significantly higher water potential in high-
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47 303 than in low-fertilized plants (Figure 5). Unfertilized seedlings of the deciduous Mediterranean
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49 304 oak *Q. faginea* Lam. had lower mid-day water potential in mid summer than fertilized
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51 305 seedlings at two inside Spain locations (Villar-Salvador, unpublished data; Figure 6).
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57 307 *Prediction 5: Increase in seedling size and new root enhances hydraulic capacity.*
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309 Large plants produced by high fertilization regimes have greater xylem transversal area,
310 wider xylem conduits and consequently higher k_s than small plants cultivated with low
311 fertilization (Krasowski and Owens 1999; Hacke et al. 2010). These changes in xylem
312 structure permit high fertilized plants to meet their greater transpiring capacity. However,
313 increases in xylem conduit diameter may increase vulnerability of xylem to embolism, as
314 reported in hybrid poplar (Hacke et al. 2010). Published studies on the effect of nursery
315 cultivation regimes on hydraulic properties of Mediterranean plants are scarce and show
316 varied trends. Trubat et al. (2006) found that N- and P-deficient *Pistacia lentiscus* L.
317 seedlings had lower k_r than well fertilized seedlings, which were larger and had higher
318 nutrient concentration than the former. On the contrary, high fertilization decreased k_r in *P.*
319 *lentiscus* and *P. canariensis* but did not have any influence in *Q. suber* seedlings (Hernández
320 et al. 2009; Luis et al. 2010).

321 Cuesta et al. (2010b) observed higher field gas-exchange in large compared to small *P.*
322 *halepensis* seedlings but no differences in their water potential, suggesting that higher gas-
323 exchange might be attributed to k differences between plant types.

324

325 **Discussion and concluding remarks**

326

327 We suggest that high resource mobilization capacity to support high growth during the wet
328 season is a key process for seedling survival during the dry season in seasonally dry climate
329 environments such in Mediterranean ecosystems. This ensures high growth capacity, which
330 allows rapid seedling establishment during the wet season and drought stress avoidance
331 during summer drought. Therefore, nursery cultivation should seedling promote functional
332 traits that confer seedlings high photosynthesis and nutrient remobilization capacity and low
333 maintenance costs. Fertilization regime, container volume, cultivation density, growing media
334 together with the length of the growing season have strong influences on these traits (van
335 den Driessche, 1991a; South et al. 2005; Oliet et al. 2009; Cuesta et al. 2010b, Verdaguer et
336 al. 2011). In this framework seedling size is an important attribute because it strongly

337 determines plant photosynthesis and nutrient storage capacity and, consequently, resource
338 mobilization and growth capacity. This explains why large seedlings frequently have higher
339 absolute growth than small seedlings (Puértolas et al. 2003; Villar-Salvador et al. 2004a).
340 Shoot and root elongation in small *P. halepensis* seedlings had an antagonistic pattern
341 through time, indicating that the growth of both organs depresses each other. In contrast,
342 large seedlings were able to simultaneously maintain high root and shoot growth without
343 interference, evidencing that large seedlings have the capacity to divert resources to sustain
344 two main resource sinks (Cuesta et al. 2010a).

345 Our model predicts that an increase in seedling size and N concentration can result in
346 higher transpiration, which increases plant vulnerability to drought on the short-term. This is
347 the main argument for using small seedlings in dry sites. However, seedlings with high
348 drought resistance traits (low transpiration) have low root growth capacity resulting in a long-
349 term survival cost. This idea is supported by results in Villar-Salvador et al (2004b), which
350 showed that osmotic adjustment and reduction in stomatal conductance in drought-
351 conditioned *Q. ilex* seedlings were associated with a reduction in RGC. Plantation of
352 seedlings in the wet season, long before summer drought onset, can minimize transpiration
353 costs associated to increasing seedling size. This is a critical issue for two reasons. First, air
354 vapor pressure deficit usually remains low during most of the wet season imposing low
355 transpiration demand on seedlings. This is very important for maintaining high water potential
356 immediately after transplanting until new root egress, especially in high transpiring seedlings.
357 Secondly, because root system size at the beginning of the dry season is directly related to
358 the length of the wet season lasting after plantation takes place. As root growth in
359 Mediterranean forests is inhibited during the dry season (Leshem 1965; López et al. 2001),
360 seedling survival is not expected to occur at the expense of root growth during the dry
361 season. In support to this reasoning, Corchero de la Torre et al. (2002) found that *P.*
362 *halepensis* seedlings planted in the fall had larger roots at the beginning of the dry season
363 than seedlings planted in early spring. This likely explains the higher mortality in late-planted
364 plantations of *Q. ilex* as compared to those planted during the early and mid wet season

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2 366 (Palacios et al. 2009). Studies on natural regeneration of Mediterranean woody species also
3
4 367 point to the importance of early seedling emergence in the wet season as a major driver for
5
6 368 resisting drought stress during the first summer (Castro 2006; De Luis et al. 2008). The
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8 369 length of the optimal root growth period determines the strength of the positive and negative
9
10 370 feedback physiological process of the model. Extreme climatic events, such as very low
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12 371 winter temperatures or very dry and warm spells during winter or lengthy delays in planting
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14 372 date will shorten the period of optimum growth and decrease the potential advantage of
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16 373 increase in seedling size and nutrient concentration. Results from an experiment performed
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18 374 under semi-arid condition in SE Spain on degraded soils and with a shallow soil preparation,
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20 375 where smaller, poor nutrient seedlings had higher survival better than larger, rich nutrient
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22 376 plants, supports this idea (Trubat et al. 2011).

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24 377 Shoot-to-root ratio scales up with above-ground seedling size when rooting volume
25
26 378 remains constant (Villar-Salvador et al. 2005). S/R reflects the amount of roots in the plug
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28 379 respect to shoot size. High S/R may cause drought stress immediately after transplanting
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30 380 (Burdett 1990). However, seedling establishment depends on the production of new high
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32 381 water-uptake capacity roots which grow out of the plug into the surrounding soil shortly after
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34 382 transplanting (Burdett 1990; Brissette and Chambers 1992; Sword Sayer et al. 2005). The
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36 383 proportion of new roots relative to shoot size (NR/S) is thus a more meaningful proxy of the
37
38 384 balance between transpiration demand and water uptake than S/R (Grossnickle 2012). Villar-
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40 385 Salvador et al. (2005) reported that large seedlings in several Mediterranean species had
41
42 386 similar or greater NR/S than small plants after RGC tests. This suggests that the “potential”
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44 387 vulnerability to water stress of larger seedlings due to higher S/R relative to smaller plants
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46 388 disappears soon after planting. This might explain the poor relationship between outplanting
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48 389 performance and S/R in container plants (Bernier et al., 1995).

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51 390 Enhanced root growth with greater seedling size and N concentration could be
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53 391 reduced in soils restricting root growth, thus reducing differences in outplanting performance.
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55 392 Compact or low air-filled porosity soils can constrain root growth even under optimal moisture
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393 extension, which can exacerbate drought vulnerability with increasing seedling size. This
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2 394 highlights the importance of soil preparation for the success of Mediterranean plantations
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4 395 (Palacios et al. 2009; Löff et al 2012).
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6 396 Most of the studies that inspired this model have been performed with Mediterranean
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8 397 conifers. Mediterranean flora has a high diversity of functional groups and it is likely that the
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10 398 relative importance of physiological processes outlined in the model may differ among
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12 399 functional groups. For instance, we expect that the potential negative effect of seedling size
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14 400 on its water status might be lower in water-saver plants (*e.g. Pinus* species) than in water-
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16 401 spending species (*e.g. oaks* and *Pistacia lentiscus*) (*sensu* Levitt, 1980). Similarly,
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18 402 performance differences associated with seedling size are expected to be greater in pioneer
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20 403 rather than in late-successional species. Therefore, future studies should consider the high
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22 404 functional diversity of Mediterranean ecosystems and directed to provide more solid
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24 405 evidence of the outlined physiological processes underpinning the proposed model.
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26 406 Specifically, we need information on how cultivation conditions affect seedling hydraulics and
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28 407 the role of plant hydraulics on seedling outplanting performance. We also need to understand
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30 408 better the role of current photosynthesis and stored NSC on root and shoot growth in most
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32 409 Mediterranean woody species. Although the model has been established from the
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34 410 experience gained in Mediterranean environments, we consider that it can be a suitable
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36 411 conceptual framework for other seasonal dry biomes, such as dry tropical forests. Moreover,
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38 412 it can be used to understand the effect of other planting and post-planting operational works
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40 413 on plant performance.
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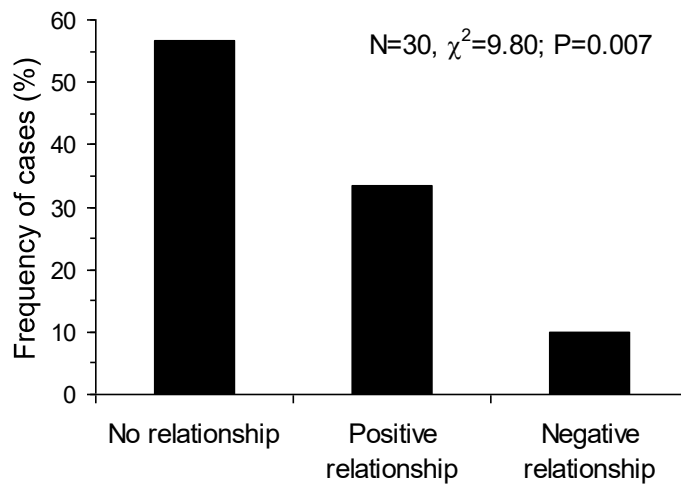
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34 673 Figure 1. Frequency of cases studies in which the relationship between seedling survival in
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36 674 Mediterranean-climate areas of Spain and seedling shoot size at planting was null, positive
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38 675 or negative. The figure has been redrawn from the meta-analysis in Navarro et al. (2006) that
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40 676 included 30 forest plantation studies, in which stocktype was container plant and in most
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42 677 cases 1+0 seedlings were used. The range in seedling size and other relevant information of
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44 678 each case study can be found in the original publication.
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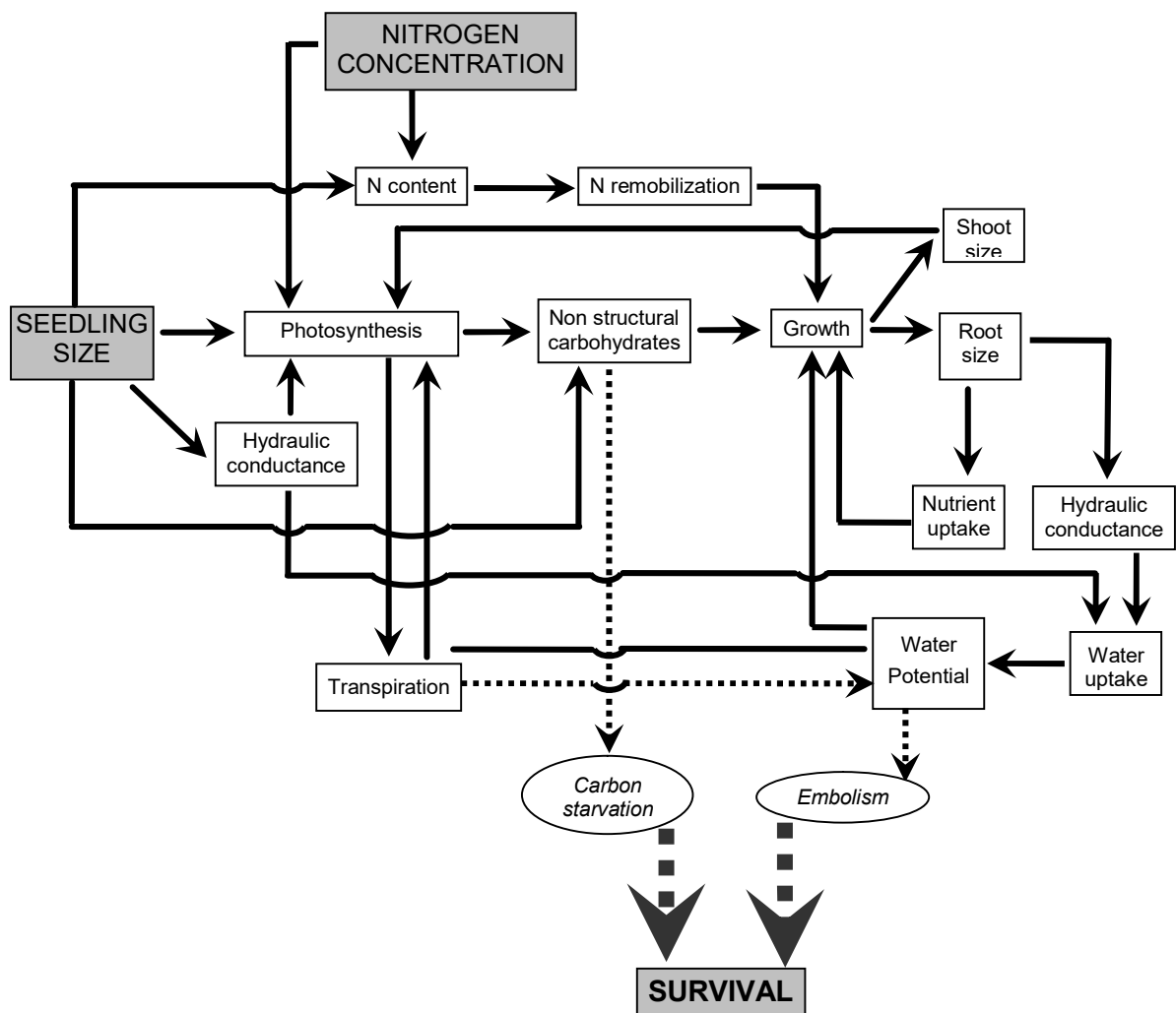
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Figure 2. Conceptual model of the physiological process that link seedling size and tissue N concentration with seedling survival in Mediterranean forest plantations. Continuous and dotted lines indicate positive and negative relationships, respectively.

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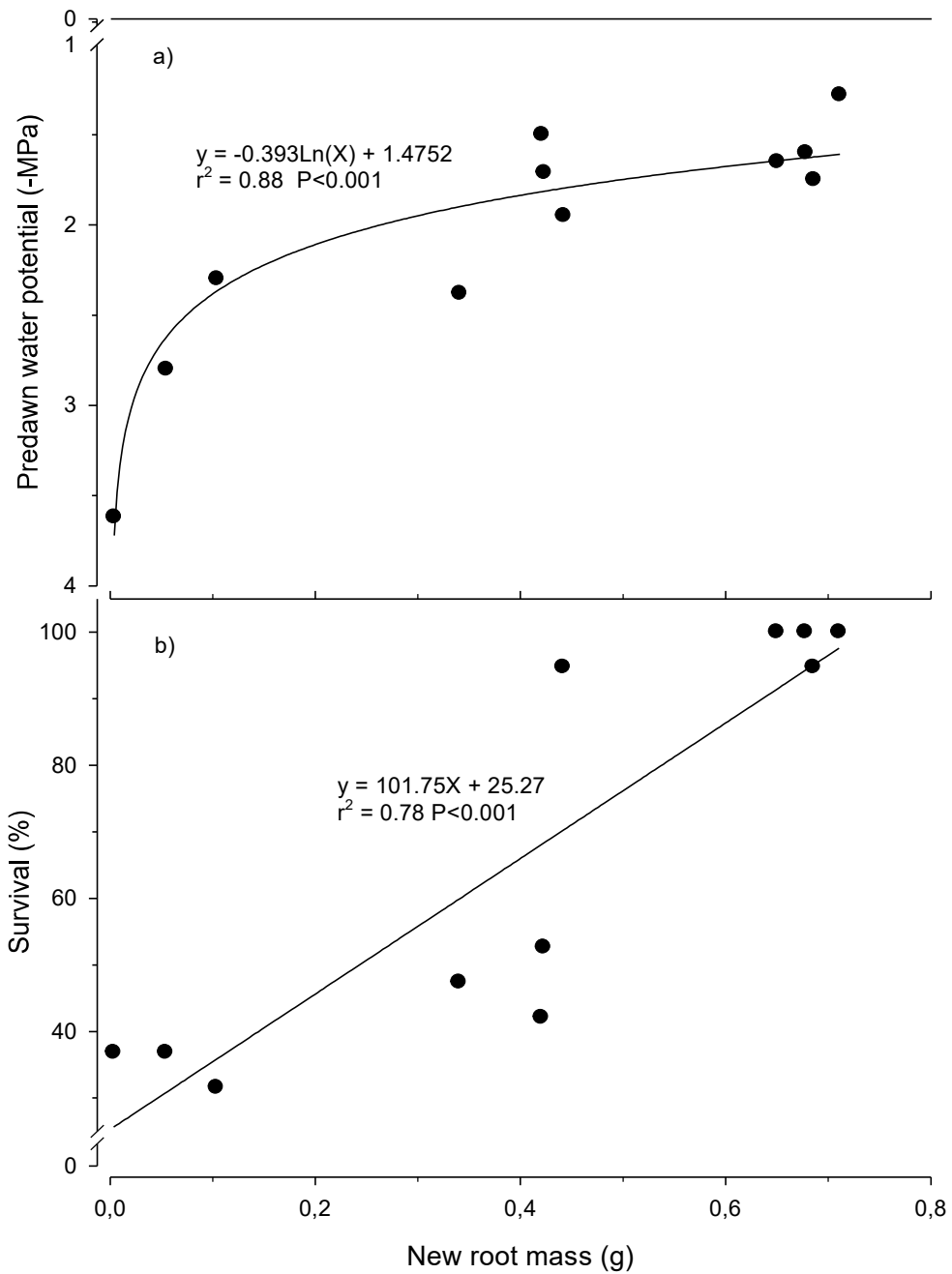
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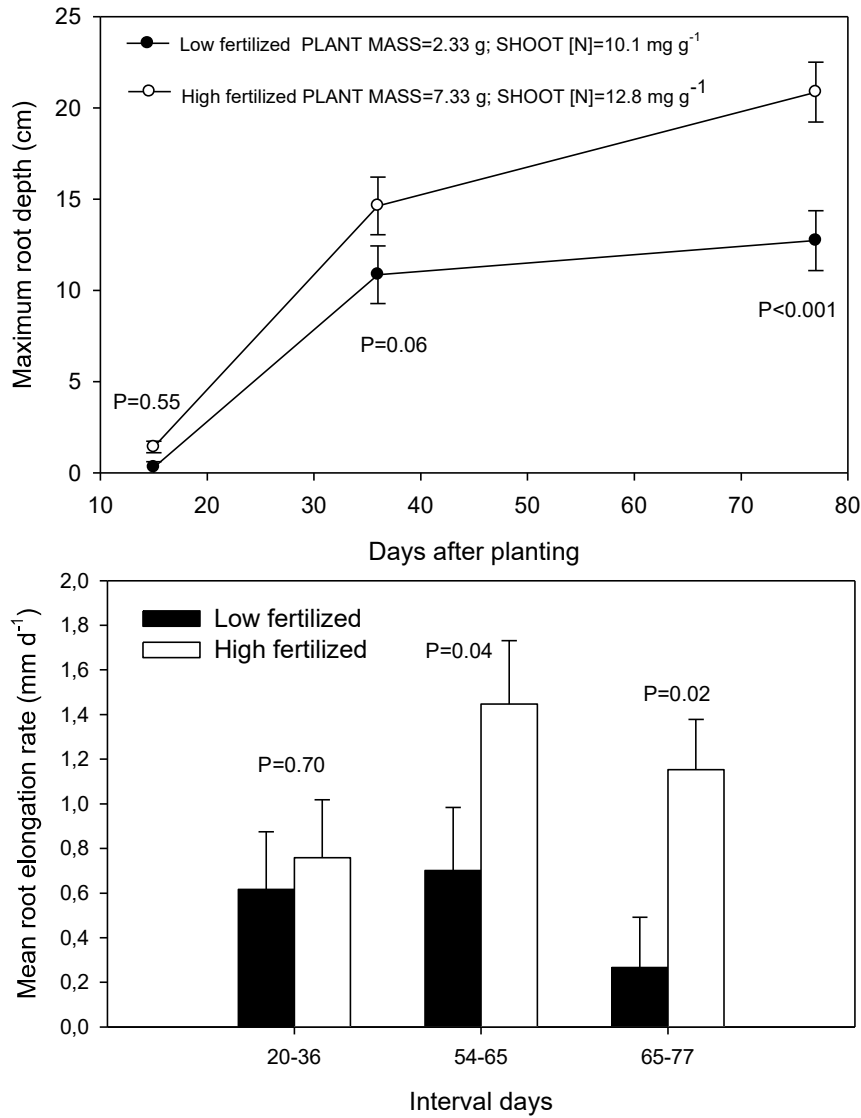


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703 Figure 3. Relation of a) predawn water potential in mid summer and b) survival at the end of

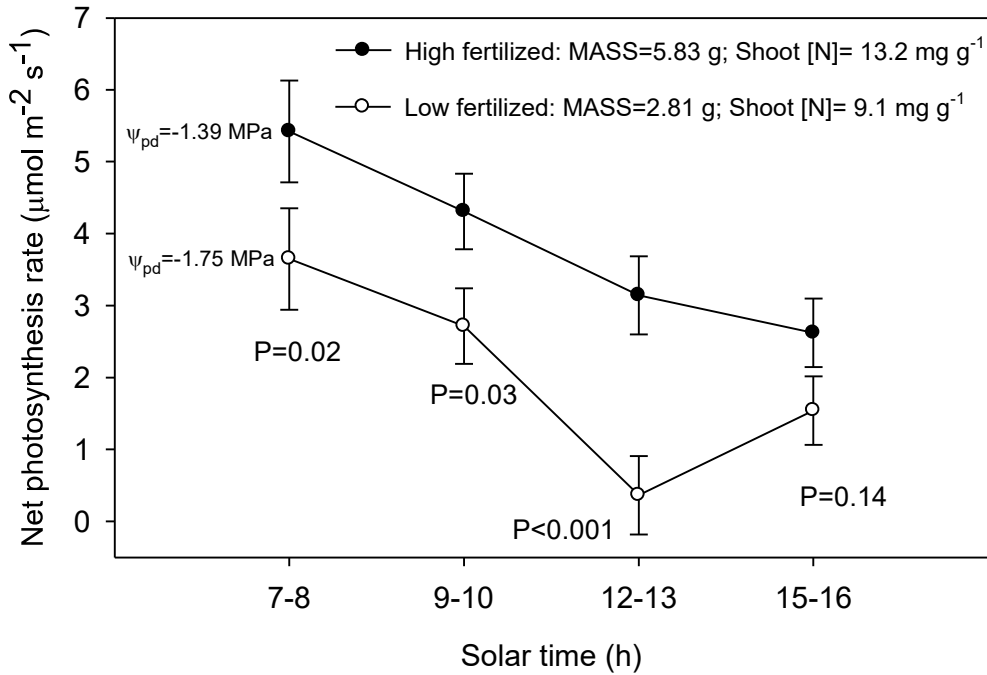
704 the summer with new root mass as determined at the beginning of the summer in *Quercus*

705 *il*ex seedlings. Each point in the graphs represents the mean of five plants for root mass and
 706 water potential, and 30 plants for survival (redrawn from data in Rodríguez-García 2003).



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 711 Figure 4. Time course of root depth (upper figure) and mean root elongation rate (lower
 712 figure) in three periods of high- and low-N fertilized *Juniperus thurifera* seedlings.
 713 Measurements were made by transplanting seedlings into 1 m long metacrylate tubes filled
 714 with sand that were inserted in the field. Data are means \pm 1 SE. N=6. In the upper figure the

715 mean plant mass and shoot N concentration of high- and low-fertilized seedlings is provided.
716 (modified from Martínez-Sanz 2006).



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720 Figure 5. Daily course of net photosynthesis rate in high and low fertilized two-year old
721 *Juniperus thurifera* seedlings in late July during the first summer after transplanting in the
722 field. The plant mass and shoot nitrogen concentration at the end of the cultivation of each
723 seedling type is shown together with the field predawn water potential (ψ_{pd}), which was
724 determined on the same day that gas-exchange measurements were obtained. Differences
725 in ψ_{pd} were statistically significant ($P=0.012$, $N=8$, Villar-Salvador, unpublished data).

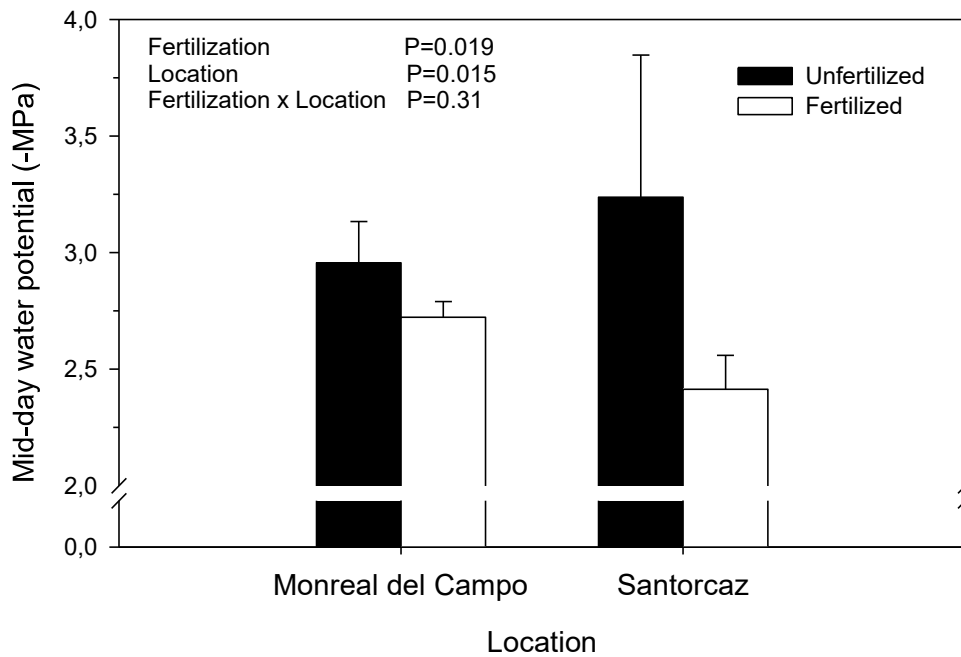
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739 Figure 6. Mid-day water potential of unfertilized and fertilized *Quercus faginea* seedlings
 740 transplanted at two locations inside Spain. Data are means \pm 1 SE. Measurements were
 741 taken in late July. Water potential of fertilized treatments is the average data of four nitrogen
 742 fertilization rate treatments, which did not significantly differ. N>5. Insert data show P-values
 743 derived from ANOVA. Mean height of unfertilized and fertilized plants was 9.6 and 16.1 cm,
 744 respectively (Villar-Salvador, unpublished data).

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