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1 **Genotypic variability in radial resistance to water flow in olive roots and its response to**

2 **temperature variations**

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Abstract

As radial root resistance (R_p) represents one of the key components of the soil-plant-atmosphere continuum (SPAC) resistance catena modulating water transport, understanding its control is essential for physiologists, modelers and breeders. Reports of R_p, however, are still scarce and scattered in the scientific literature. In this study we assessed genetic variability in R_p and its dependence on temperature in five widely-used olive cultivars. In a first experiment, cultivar differences in R_p at 25 ºC were evaluated from flow-pressure measurements in excised roots and subsequent analysis of root traits. In a second experiment, similar determinations were performed continually over 5 h periods in which temperature was gradually increased from 12 to 32 ºC, enabling the assessment of R_p response to changing temperature. Despite some variability, our results did not show statistical differences in R_p among cultivars in the first experiment. In the second, cultivar differences in R_p were not significant at 12 ºC, but they became so as temperature increased. Furthermore, the changes in R_p between 12 and 32 ºC were higher than those expected by the temperature-driven decrease in water viscosity, with the degree of that change differing among cultivars. Also, R_p at 25 ºC reached momentarily in the second experiment was consistently higher than in the first at that same, but fixed, temperature. Overall, our results suggest that there is limited variability in R_p among the studied cultivars when plants have been exposed to a given temperature for sufficient time. Temperature-induced variation in R_p might thus be partly explained by changes in membrane permeability that occur slowly, which explains why our values at 25 ºC differed between experiments. The observed cultivar differences in R_p with warming also indicate faster acclimation of R_p to temperature changes in some cultivars than others.

Introduction

Since the pioneering work by van den Honert (1948), the movement of water through the soil-plant-atmosphere-continuum (SPAC) is often treated as a catenary process that can be modelled following an Ohm's law analogy (Tyree and Ewers 1991). Accordingly, the water flux from soil to leaves is proportional to water potential gradient and inversely proportional to hydraulic resistance to flow between the extremes of the pathway. Studying the factors that determine the SPAC hydraulic resistance is therefore crucial for improving our understanding of plant water relations.

The hydraulic resistance to water transport from the soil to the leaves can be decomposed into four elements in series, namely, the soil (R_{soil}, from the soil to the root surface), radial (R_p, from the root surface to root vascular bundles), vascular (R_{xyl}, from the root xylem to the leaves) and mesophyll (R_{mes}, from the leaf veins to the evaporation sites) resistances. The first component of the catena, R_{soil}, is known to be strongly modulated by the soil matrix composition, by soil water content and by the amount of roots; and is very low as compared to the other components when the soil is wet (Campbell 1985). R_{xyl} is the main component of the resistance catena on a distance basis, but the high specialization of xylem conduits limits its magnitude as resistor (Sperry 2003, Venturas et al. 2017). R_{xyl} is mainly constrained by a number of anatomical and physiological factors, although harsh environmental conditions (e.g. severe water stress) can also result in the cavitation of xylem conduits. The extravascular plant resistances (R_p and R_{mes}) constitute the least-known components of the resistance catena despite probably being the most important bottlenecks in the whole-plant hydraulic continuum (Tyree and Zimmerman 2002). In this regard, R_{mes} has been suggested to account for up to 30 % of the whole-plant hydraulic resistance in well-watered plants (Sack et al. 2003, Sack and Holbrook 2006, Scoffoni and Sack 2017) while experimental evidence has revealed values of R_p 2–20 times higher than those of R_{xyl} (Nobel and Sanderson 1984).

59 R_p represents the degree of impermeability of the different tissues arranged in series that form

60 the root cylinder (Steudle and Peterson 1998), and is determined by anatomical root traits.

61 However, R_p can vary over time due to modifications in membrane fluidity, aquaporin

62 activation and suberization, which can be triggered under certain environmental conditions

63 (Running and Reid 1980, Passioura 1988, Lee et al. 2005a). In this regard, it is well documented

64 that both soil water deficits (Rodriguez-Dominguez and Brodribb 2019) and low temperatures

65 can lead to large increases in R_p (e.g. Ameglio et al. 1994, Wan et al. 2001, Lee et al. 2005a).

66 In fact, some studies have highlighted that the inclusion of algorithms describing the

67 temperature effects on R_p can improve substantially the predictive power of SPAC models

68 (Mellander et al. 2006, García-Tejera et al. 2016). Besides, diurnal variations in R_p associated

69 to plant circadian rhythms have been described for some species (Henzler et al. 1999, Caldeira

70 et al. 2014).

71 So far, not much attention has been given to the characterization of intra-specific variability in

72 R_p. This topic is highly appealing as, in theory, two ideotypes differing in R_p might have

73 different patterns of water use along a season. A high R_p could imply an impaired water uptake

74 and slow plant growth, but it may still be a desirable trait in dry environments if the so-reduced

75 water uptake results in higher soil water availability during critical periods at the end of the

76 crop cycle. On the other hand, genotypic differences in R_p have been associated with differences

77 in chilling sensitivity (Aroca et al. 2001) and frost resistance (Pérez-López et al. 2010).

78 This paper deals with the evaluation of cultivar variability in R_p for olive trees. This evergreen

79 species is one of the most important crops in the Mediterranean basin, where they cover around

80 10.5 Mha (FAOSTAT 2017). Earlier studies on olive trees demonstrated that low temperatures

81 produce a disturbance of water relations, often evidenced by low water potentials occurring

82 even under low evaporative demand and adequate soil water content (Pavel and Fereres 1998,

83 Pérez-López et al. 2010, López-Bernal et al. 2015). This chilling-induced dehydration has been

4

84 reportedly linked to increases in R_p in olive and other sensitive species (Aroca et al. 2012,

85 Centeno et al. 2018). Indeed, García-Tejera et al. (2016) characterized the response of R_p to

86 temperature for the cultivar 'Picual', showing that the values measured at 10 ℃ were c.a. three

87 times higher than those measured at 25 ℃.

88 The specific goals of the present study are the identification of cultivar differences 1) in R_p at

89 a mild and low temperatures and 2) in the response of R_p to short-term temperature variations.

90 In order to do so, two experiments were performed with rooted cuttings of five widely used

91 olive cultivars. In the first, we assessed cultivar variability in R_p at 25 ℃, while the second

92 explored the differences at 12 ℃ and during a subsequent gradual increase of temperature up

93 to 32 ℃.

94

95 **Materials and Methods**

96 *Plant material*

97 The experiments were conducted between June and July 2018 with rooted cuttings of five olive

98 cultivars, namely 'Picual', 'Arbequina', 'Hojiblanca', 'Arbosana' and 'Frantoio'. Plant

99 material was obtained from a commercial nursery by early spring and subsequently grown

100 outdoor at the Institute for Sustainable Agriculture (IAS-CSIC, Córdoba, Spain) in small pots

101 filled with peat moss and irrigated meeting evapotranspiration every day.

102 *Experiment I*

103 Experiment I was aimed to assess cultivar differences in R_p at 25 ℃. All the measurements

104 were performed inside a growth chamber with controlled temperature and a fixed 14-h

105 photoperiod with fluorescent lights at 360 µmol m^{-2} s^{-1}. Both the plant material and instruments

106 were placed in the chamber 24 h prior to the start of measurements to ensure that everything

107   was at 25 ºC by the beginning of the experiment. Five plants per cultivar were used for the

108   measurements.

109   The protocol followed for determining R_p was similar to that used by García-Tejera et al.

110   (2016). First, plants were extracted from their pots and immersed in water in order to remove

111   most part of the substrate, avoiding any injuries to the root systems. Then, the upper part of the

112   stem was cut 4 cm above the collar and the whole detached root system was placed in a pot

113   filled with water inside the vessel of a pressure chamber (Soil Moisture Equipment Corp., Santa

114   Barbara, CA, USA). The chamber was used to apply a constant 0.4 MPa pressure to root

115   systems for at least 45 min, in order to ensure a steady flux of xylem exudate (García-Tejera et

116   al. 2016). During this period, the xylem exudate was collected at 15 min intervals using cotton-

117   filled sample tubes. The average flux was determined by weighting the cotton-filled sample

118   tubes before and after each measurement period using a 0.0001 g precision balance (model

119   AV104, Mettler Toledo, Greifensee, Switzerland). Once flux determinations were completed,

120   root systems were washed with water to remove all the remaining substrate particles and then

121   scanned with a commercial scanner (HP Scanjet G3110). The WinRhizo software (Regent

122   Instruments Inc., Quebec City, QC, Canada) was used for estimating the values of several root

123   traits including average root diameter, root diameter frequency distribution and total root

124   surface (*A*). In all cases we assumed a maximum root diameter of 1.4 mm for absorbing roots

125   (Polverigiani et al. 2011, García-Tejera et al. 2016). Finally, an apparent value for the root

126   resistance (R_{root}, MPa m^2 s kg^{-1}) was estimated as:

127    $$R_{root} = \Delta P \, A/F \tag{1}$$

128   Where ΔP is the pressure applied to the root system (0.4 MPa), *A* is root surface expressed in

129   m^2 and *F*, the flux of xylem exudate during the interval (kg s^{-1}). Because the hydraulic

130   resistance in the root xylematic pathway is generally considered negligible when compared to

131 the radial component (Nobel and Sanderson 1984, García-Tejera et al. 2016), and since our

132 rooted cuttings had small root systems, we assumed that $R_p = R_{root}$.

Experiment II

134 The goal of Experiment II was to explore the responses of R_p to short-term changes in

135 temperature for the studied olive cultivars. In order to do so, we performed continuous

136 pressure-flux measurements similar to those of Experiment I over periods of five hours, during

137 which the temperature of the root systems increased from c.a. 12 to 32–35 ºC. Three plants per

138 cultivar were used.

139 In the evening preceding the measurements (at 17.00 GMT), the plants were transferred to a

140 growth chamber with controlled temperature at 12 ºC. Starting at around 7.00 GMT, flux

141 measurements were initially performed every 15 min inside the growth chamber with an

142 operation pressure of 0.4 MPa until the flux was steady. At such low temperature, we observed

143 that the time for the flux to stabilize was longer than that at 25 ºC, taking between 60 and 120

144 min (Table S1). In all cases, only the data collected at 120 min were used in further analysis.

145 Then, the equipment was moved to an outdoor site exposed to direct sunlight. The 15-min flux

146 determinations continued there until around 12.00 GMT, with the rising solar radiation and air

147 temperature driving a gradual increase in the temperature of the root system, which was also

148 monitored every second with a thermocouple (Type E) placed inside the water-filled vessel

149 within the pressure chamber and controlled with a data logger (CR1000, Campbell Scientific

150 Inc., Logan, UT, USA). Following the pressure-flux measurements, root structural properties

151 were analyzed as in the previous experiment and values of R_p were calculated. Figure 1 shows

152 the typical patterns of temperature and estimated R_p found during the pressure-flow

153 measurements in Experiment II.

154 Statistical differences in R_p between cultivars were tested at various specific temperatures: 12,

155 16, 20, 24, 25, 28 and 32 ºC. To do so, third degree polynomial functions were fitted to the

156 plots of R_p versus temperature for each replicate. Those fits were subsequently used for

157 estimating the values corresponding to the aforementioned temperatures.

158 In a further analysis, we assessed cultivar differences in the pattern and extent of the relative

159 decrease in R_p with temperature from the initial value measured at 12 ºC. Such relative

160 resistance value was calculated for each replicate by dividing the estimated R_p by the value

161 inferred from the polynomial fit at 12 ºC. Besides, the relative decrease in R_p that can be

162 theoretically ascribed to temperature-mediated variations in water viscosity (η) was also

163 calculated from the relative decrease in η in relation to its value at 12 ºC. To this end, the

164 relationship between η and temperature reported by Roderick and Berry (2001) was used:

165 $$\eta = 1.95 \times 10^8 / T^7 \tag{2}$$

166 where T is the liquid temperature in K and η is expressed in MPa s^{-1}.

167 *Statistics*

168 Statistical analyses were performed with Statistix (Statistix 10 for Windows, Analytical

169 Software, Tallahassee, FL, USA). Analyses of variance, with prior data transformation when

170 required, were used for comparing cultivars. Means were separated using the Tukey HSD test

171 when P<0.05. When the assumptions of ANOVA could not be satisfied, the Kruskal-Wallis

172 test was used, being the distribution of the scores compared with the Dunn's test.

173

174 **Results**

175 *Experiment I*

176   The flow-pressure measurements conducted at 25 ºC in Experiment I revealed average R_p

177   values ranging from $0.66 \cdot 10^4$ (in 'Picual') to $1.13 \cdot 10^4$ MPa m^2 s kg^{-1} (in 'Arbequina') (Figure

178   2a). Albeit considerable, these differences were not statistically significant due to large

179   variability between replicates (average coefficient of variation of 32 %). On the other hand,

180   root surface in 'Arbequina' was significantly lower than in 'Picual', 'Hojiblanca' and

181   'Frantoio' (Figure 2c).

182   The average cumulative distribution function of root diameters for each cultivar is shown in

183   Figure 3. In all cases, more than 50 % of the roots had diameters below 0.3 mm, while those

184   with diameters above 0.7 mm represented less than 10 %. The frequency distribution of root

185   diameters (Fig. S1) was unimodal, with roots between 0.2 to 0.3 mm in diameter being the

186   most frequent class. Apart from this, Figure 3 also reveals slight cultivar variability in the

187   frequency distributions leading to differences in the average root diameter. The latter ranged

188   from 0.27 to 0.36 mm for 'Hojiblanca' and 'Arbequina', respectively. Differences between

189   these two cultivars were significant (Figure 2e).

190   *Experiment II*

191   For all cultivars, pressure-flux measurements showed a progressive decrease in R_p as

192   temperature increased, changing from an average value of $3.5 \cdot 10^4$ MPa m^2 s kg^{-1} at 12 ºC to

193    $1.4 \cdot 10^4$ MPa m^2 s kg^{-1} at 32 ºC (Table 1). As in Experiment I, 'Arbequina' always exhibited

194   the highest R_p and 'Picual' showed the lowest values, except for the comparisons at 32 ºC,

195   when the lowest values were estimated for 'Hojiblanca'. Differences between cultivars were

196   not significant at 12 ºC, but they became so at higher temperatures: R_p values in 'Arbequina'

197   was significantly higher than those of 'Picual', 'Hojiblanca', 'Arbosana' and 'Frantoio' when

198   comparisons were conducted, respectively, at temperatures equal or higher than 16, 20, 20 and

199   32 ºC. Differences between 'Picual', 'Hojiblanca', 'Arbosana' and 'Frantoio' were never

9

200   significant. As an additional interesting finding, R_p values at 25 ℃ in Experiment II were higher

201   than those determined in Experiment I, irrespective of the cultivar (Figure 2b).

202   During the course of the outdoor measurements, R_p decreased as temperature increased, and

203   cultivar differences were found in the extent of the relative R_p reduction (Figure 4). In this

204   regard, the increase in temperature from 12 to 32 ℃ yielded a 65–70 % reduction in R_p for

205   'Hojiblanca' and 'Arbosana' and a 55–60 % reduction for 'Arbequina' and 'Frantoio'.

206   Nonetheless, it is also noteworthy that there was considerable variability in the extent of the

207   relative decay of R_p with temperature between replicates in some cases (e.g. 'Hojiblanca').

208   Finally, Figure 4 also illustrates that viscosity effects are only able to explain a 38 % decrease

209   in R_p for the temperature interval considered.

210   Root systems in Experiment 2 presented higher A than those of Experiment 1, with the

211   comparison between cultivars leading to similar results (Figure 2d). The root diameter

212   frequency distributions in both experiments were virtually the same, regardless of the cultivar.

213   A non-significant trend to higher d was observed in Experiment 2 (Figure 2e-f).

214

215   **Discussion**

216   So far, reports on R_p are scarcely found within the scientific literature, let alone papers

217   exploring the genotypic variability in this trait. In fact, to the best of our knowledge, only four

218   past studies have analyzed differences in R_p between cultivars or rootstocks of a given species.

219   Aroca et al. (2001) compared the response of root hydraulic conductivity (i.e. the inverse of

220   R_p) after exposing plants of two maize genotypes to chilling temperatures. Statistical

221   differences between genotypes were significant at 5 ℃, but not at a control temperature of 25

222   ℃. In a similar study, Lee et al. (2005a) found significant differences in the hydraulic

223   conductivity of cucumber (*Cucumis sativus*) and figleaf gourd (*Cucurbita ficifolia*) roots, both

224   at low and control (25 ºC) temperatures. By contrast, Bloom et al. (2004) found similar values

225   in the hydraulic conductance of excised roots when comparing cultivated tomato

226   (*Lycopersicum esculentum*) and a wild congener (*L. hirsutum*) irrespective of temperature.

227   Finally, García-Tejera et al. (2016) compared R_p for two common almond rootstocks (GF677

228   and GN15) at 25 ºC, finding significant differences between them. In the present study, we

229   explored the genotypic variability in R_p between five widely used olive cultivars. We did not

230   find statistical differences between them when determinations were performed at two

231   contrasting steady temperatures (i.e. 25 ºC in Experiment I and 12 ºC in the first measurement

232   in Experiment II) despite some variability was observed in root traits (Fig. 2, Fig. 3). Partly,

233   the lack of significant differences was due to the large variability between replicates. This was

234   not an exclusive issue of our study, as similar levels of variability between replicates have also

235   been observed in previous reports (e.g. Cochard et al. 2000, Lee et al. 2005a). An explanation

236   for this phenomenon is still missing and clearly deserves further research.

237   Despite the variability in the studied species, plant material characteristics and methods, the

238   current body of literature consistently indicates that R_p is particularly sensitive to temperature

239   conditions, so that the lower the temperature in the root environment, the higher the R_p (Ramos

240   and Kaufmann 1979, Cochard et al. 2000, Aroca et al. 2012, García-Tejera et al. 2016). The

241   same trend was reproduced in Experiment II, irrespective of the cultivar (Table 1, Fig. 4).

242   Changes in sap viscosity drive the inverse relationship between R_p and temperature, but

243   frequently R_p variations cannot be entirely ascribed to that cause alone (Kuiper 1964, García-

244   Tejera et al. 2016). In fact, in our study decreases in R_p in the 12–32 ºC interval were

245   considerably higher than the theoretical decrease in water viscosity (on average 17–32 %

246   higher, depending on the cultivar, Fig. 4). Modifications in cell membrane structure and

247   inhibition of aquaporin activity at low temperatures have been proposed as possible

248   explanations for the variations of R_p beyond the contribution of water viscosity (Wan et al.

249   2001, Aroca et al. 2005, Lee et al. 2005b, Murai-Hatano et al. 2008, Aroca et al. 2012).

250   Traditionally, temperature effects on R_p have been studied by determining R_p in different plants

251   (i.e. excised root systems) exposed to various temperatures (e.g. Aroca et al. 2001, Lee et al.

252   2005a, García-Tejera et al. 2016). This approach can generate some bias due to non-

253   homogeneity in root structural properties, as temperature comparisons are performed for

254   different plants. Alternatively, in some works, temperature comparisons have been made for

255   the same individuals by performing consecutive pressure-flow measurements changing

256   temperature in steps and waiting for the exudation rate to stabilize (Cochard et al. 2001, Wan

257   et al. 2001), with the only uncertainty arising from the fact that it implies working with a

258   detached root system for long periods. In Experiment II, we used a new approach aimed at

259   estimating short-term changes in R_p in response to a gradual continuous warming from 12 ºC.

260   This allowed us to perform the pressure-flow measurements for the same root system under a

261   wide range of temperatures and within a relatively short period of time (5 h). Moreover, the

262   employed experimental setup is more suitable to mimic the rapid temperature variations to

263   which roots in the upper soil layers are exposed on a diurnal time scale (Villalobos et al. 2016).

264   Results from those measurements revealed two interesting findings. First, the estimates of R_p

265   at 25 ºC were consistently higher than those obtained under steady conditions in Experiment I

266   (Figure 2a-b), which implies that it takes time for the non-viscous mechanisms inhibiting R_p at

267   low temperatures to deactivate completely after warming. This was not entirely unexpected, as

268   some reports indicate that it can take hours (Aroca et al. 2001, Lee et al. 2005a) or even days

269   (Wan et al. 1999) for R_p to reach an equilibrium value following a drastic temperature change.

270   In rice plants, this phenomenon has been linked to a coordinated up-regulation of root

271   aquaporin gene expression during the exposure to low temperatures (Ahamed et al. 2012).

272   Second, statistical cultivar differences were found in the short-term R_p responses to temperature

(Table 1), evidencing some genotypic variability in the inertia of the mechanisms controlling membrane permeability at low temperatures. In other words, our results suggest that the time required for olive roots to recover R_p back to initial values after a chilling period differs between cultivars. Besides, it must be noted that, coming from warm field conditions, plants in Experiment II were exposed to 12 ºC for around 14 h before the start of pressure-flow measurements. While this time might not have been sufficient for the plants to fully acclimate in terms of R_p, cultivar differences at such temperature were not significant. This should indicate that the differential response to temperature observed between cultivars is only apparent at a very short-term scale (minutes or few hours).

A common effect of low (non-freezing) temperatures on plants is leaf dehydration (Aroca et al. 2012). In olive trees and other sensitive species, low temperatures result in a decrease of leaf water potential, even when soil water content is not limiting (López-Bernal et al. 2015, Centeno et al. 2018). This chilling-induced dehydration is originated by an imbalance between root water uptake and leaf transpiration, which is reportedly associated with the low-temperature driven increase in R_p (Running and Reid 1980, Aroca et al. 2001, Centeno et al. 2018). Pérez-López et al. (2010) assessed the effects of soil chilling in the water relations of six olive cultivars, among which 'Picual', 'Arbequina' and 'Frantoio' were included. According to their results, the authors labelled the former two as 'tolerant' and the latter as 'sensitive' to chilling-induced dehydration. Of these three cultivars, 'Arbequina' and 'Picual' always exhibited the highest and lowest R_p values in our experiments, respectively, although the differences between them were not significant when measurements were performed at steady temperatures. This is at odds with the fact that both were classified in the same category ('tolerant'), while the 'sensitive' cultivar 'Frantoio' showed intermediate R_p values. Therefore, our findings suggest that there is no clear connection between the reported differences in the sensitivity to soil chilling and a hypothetical variability in the R_p responses to temperature

298   between olive cultivars. However, we might speculate about a possible link between R_p

299   responses to temperature, chilling-induced dehydration and the winter dormant state of this

300   species.

301   In olive trees, vegetative growth ceases in autumn and undergoes a winter rest period lasting

302   until favourable conditions return in early spring. López-Bernal et al. (2020) performed a series

303   of experiments indicating that low temperatures control growth cessation and dormancy

304   induction in olive shoot apical meristems. According to the present study, the low temperatures

305   (< 15 ºC) leading to dormancy induction in autumn should also trigger an increase in R_p and

306   chilling-induced dehydration (Pérez-López et al. 2010). Given that growth processes are

307   inhibited at high water potentials (Hsiao 1973), autumn growth cessation might be associated

308   with a progressive increase in R_p and worsening of water status. On the other hand, it is

309   noteworthy that even if mean daily temperatures are low in winter, appropriate conditions for

310   growth can still occur around midday in many areas of the Mediterranean Basin. The absence

311   of olive vegetative growth during these periods might be related to the occurrence of high R_p

312   and low water potentials, as soil temperature should remain similar to the mean daily air

313   temperature (García-Tejera et al. 2016).

314

315   **Conclusions**

316   In conclusion, our findings show limited variability in R_p between the studied olive cultivars.

317   Nevertheless, the wide number of cultivars of different origins and the outcrossing nature of

318   this species (Díez et al. 2015) makes the existence of substantial genetic variability in this trait

319   still possible. As a consequence, further research with other cultivars would be needed to

320   elucidate whether it is possible to find genetic variability in R_p. With regard to the temperature

321   responses, it seems that, beyond the associated viscosity variations, the current study suggests

14

322 that additional mechanisms, such as changes in membrane permeability, may affect R_p, as

323 pointed out by other studies. These changes are not immediate, taking some time to reach a

324 'steady state', which explains why our values of R_p at 25 °C varied between experiments. The

325 fact that R_p values became significantly different between cultivars with warming suggest that

326 the pace of temperature-induced changes in membrane permeability is cultivar-dependent. In

327 other words, some olive cultivars seem to have the capacity to acclimate R_p faster to rapid

328 temperature changes than others.

329

341

342 **Conflict of interest**

343 None declared.

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Figure captions

450 **Figure 1**: Time course of xylem flux and temperature (15-min averages) of the root system

451 over the measurement period of one of the 'Arbosana' replicates. The arrow marks the time at

452 which the equipment was transferred from the growth chamber to an outdoor sunlit location.

453

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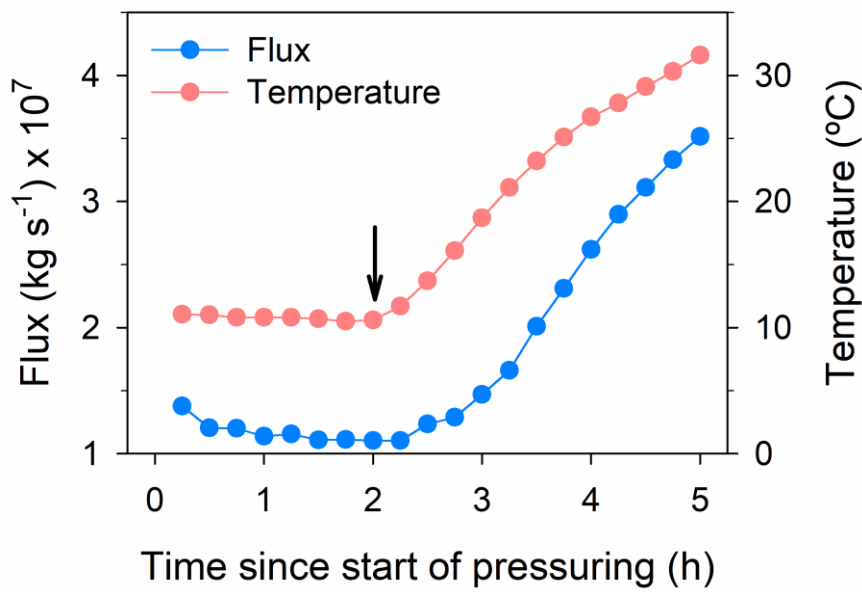
Figure 2: Measured values of (a, b) specific radial root resistance (R_p) at 25 ºC, (c, d) total root

456 surface (A) and (e, f) average root diameter for the different olive cultivars, both for Experiment

457 I (n=5, left panels) and Experiment II (n=3, right panels). Each point corresponds to one of the

458 replicates. Different letters denote significant differences (P<0.05) between cultivars.
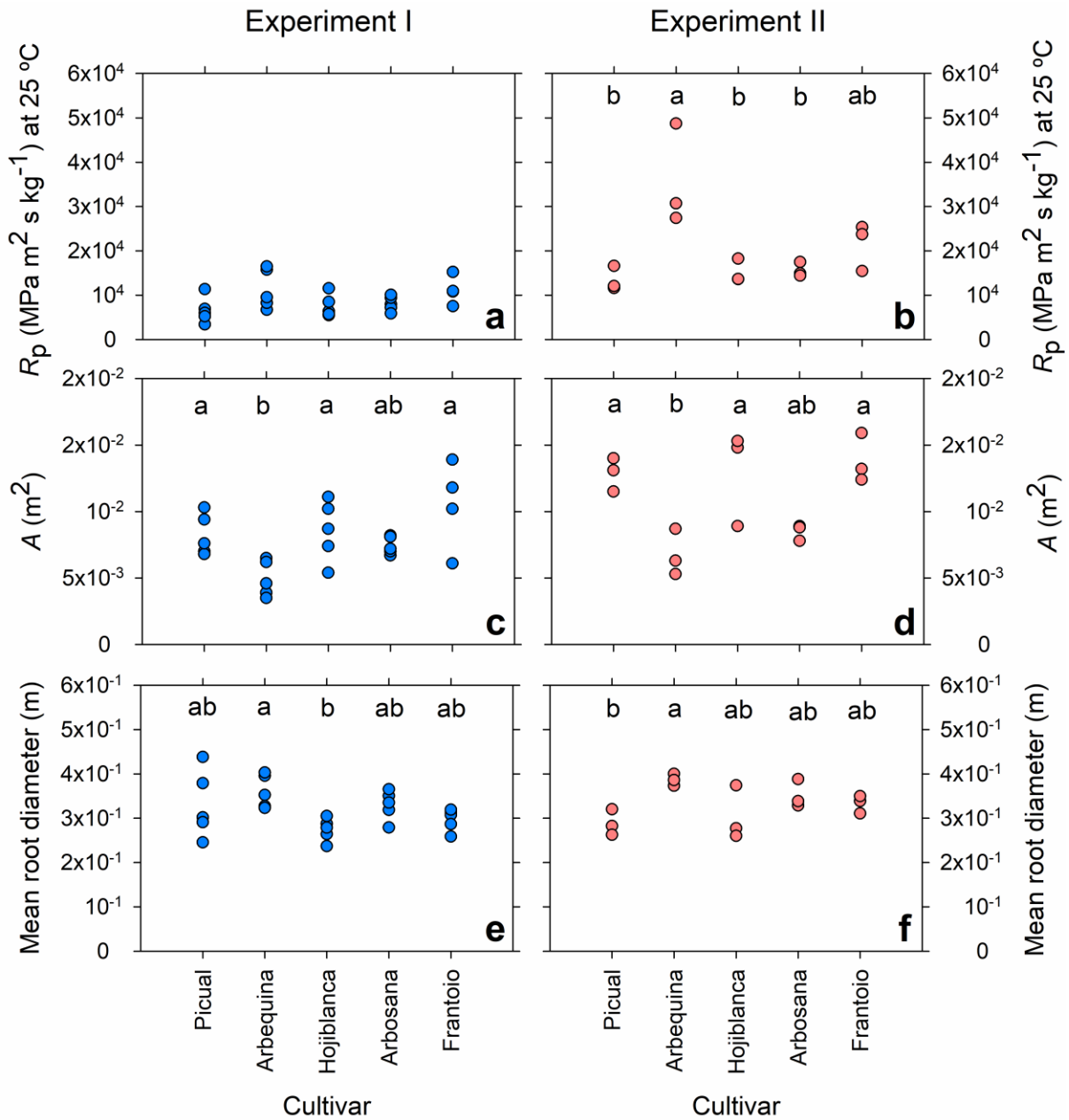

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461   **Figure 3**: Cumulative distribution function of root diameters below 1.4 mm for the studied

462   olive cultivars in Experiment I.
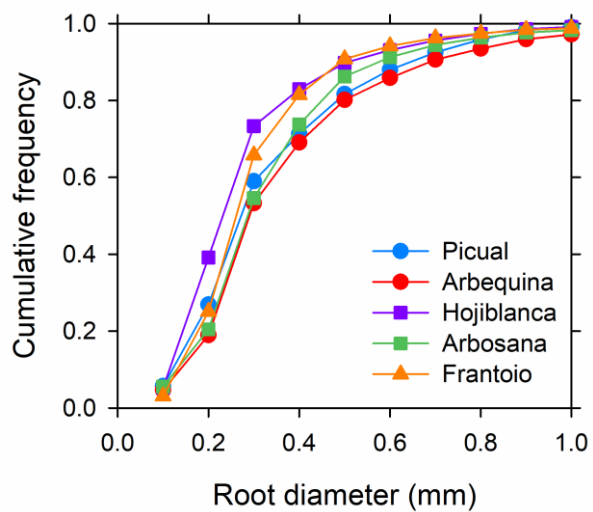
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465 **Figure 4**: Relative changes in specific radial root resistance (R_p) versus root temperature with

466 respect to the value estimated at 12 ºC in Experiment II. Each panel corresponds to one of the

467 studied cultivars: (a) 'Picual', (b) 'Arbequina', (c) 'Hojiblanca', (d) 'Arbosana' and (e)

468 'Frantoio'. Symbols correspond to the three replicates per cultivar. The solid line represents

469 the relative variations in R_p that can be ascribed theoretically to temperature-mediated changes

470 in water viscosity.

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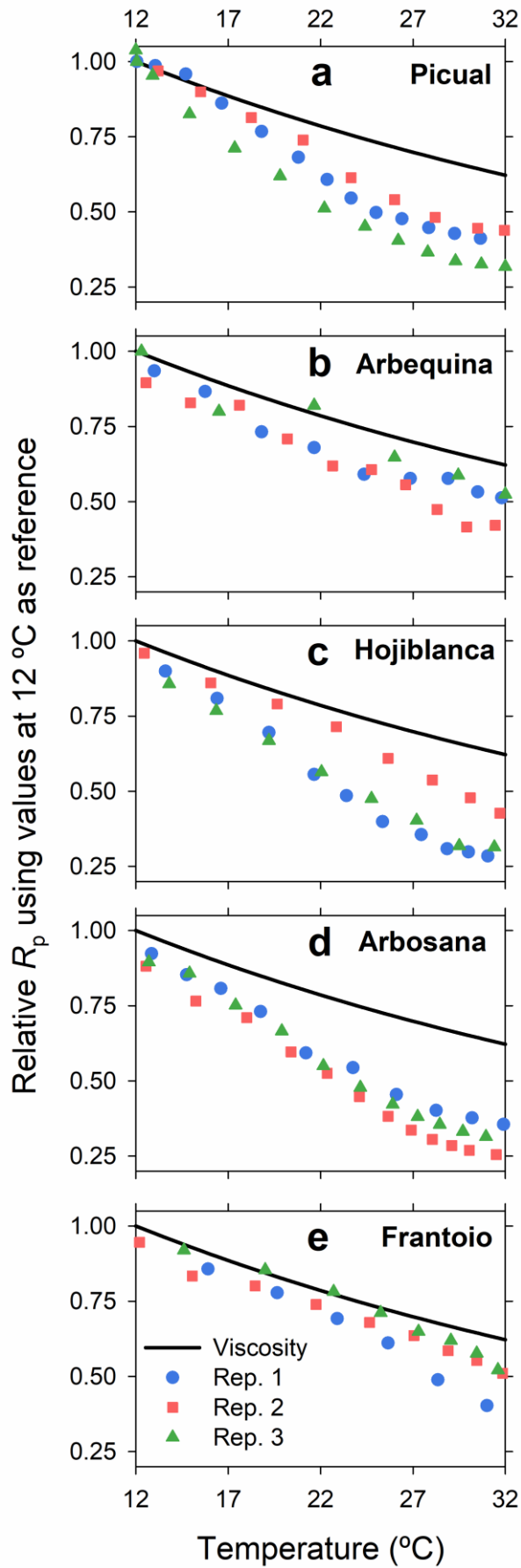
472 **Tables**

473 **Table 1**: Specific radial root resistance (R_p, MPa m^2 s kg^{-1} x 10^4) at different temperatures for

474 each of the olive cultivars in Experiment II. Values for each combination of temperature and

475 cultivars correspond to the average of three individuals. Different letters denote significant

476 differences (P<0.05) between cultivars.

477

Cultivar	Temperature (ºC)					
	12	16	20	24	28	32
Picual	2.77	2.31 b	1.84 b	1.44 b	1.15 b	1.04 b
Arbequina	5.52	4.83 a	4.22 a	3.67 a	3.13 a	2.60 a
Hojiblanca	2.88	2.50 ab	2.06 b	1.62 b	1.25 b	1.00 b
Arbosana	3.24	2.74 ab	2.20 b	1.69 b	1.26 b	0.98 b
Frantoio	3.13	2.83 ab	2.51 ab	2.19 ab	1.86 ab	1.50 b

478