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Abstract

The wild tomatoes and relatives constitute a group of closely related species inhabiting diverse habitats across South America. In order to test for the coordination of leaf traits related to venation, hydraulics, , morphology, and gas exchange in this clade, the wild tomatoes and some domesticated accessions were grown outdoors in a common garden under Mediterranean summer conditions. Results showed a coordination of leaf vein density with photosynthesis, stomatal conductance, leaf size and leaf mass per area, which was not found among the vast range of species, habitats and growth forms existing in literature data. Contrarily, the correlation of hydraulic conductance with photosynthesis and gas exchange found in literature data did not occur in the tomatoes, showing a decoupling of leaf hydraulics and venation traits in this group of close relative species. This fact indicated that limitations to gas exchange in the tomatoes are more related to CO_2 diffusion than hydraulics. Moreover, species from arid habitats followed a drought-escape strategy, favouring pulse-growth in suitable periods, resulting in leaf traits not predicted from global trends. In this framework, domesticated tomatoes had extreme values for most of the measured traits, reflecting modifications during domestication.

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Dear Editor,

Please find enclosed the manuscript entitled 'Leaf hydraulics and venation traits are decoupled in the tomatoes and relatives (*Solanum* sect. *Lycopersicon* sect. *Juglandifolia* and sect. *Lycopersicoides*)', by Conesa and co-workers, to be considered for publication in Environmental and Experimental Botany.

The study has been performed in the wild tomatoes and relatives, a clade of closely related species originated in very diverse environments across South America. Results show that the leaf hydraulics and venation traits are decoupled within this clade, which is contrary to the expectations based on the leaf hydraulics theory. Furthermore, venation, but not hydraulics, is coordinated with leaf morphology and gas exchange traits, denoting that the main limitation in the tomatoes is not hydraulics. This responds an open question left in a paper recently published in Environmental and Experimental Botany, dealing with growth capacity and biomass allocation in the same species (Conesa et al., 2017. Environ. Exp. Bot. 141, 181-190). Despite the narrow phylogenetic range covered by the tomatoes and relatives, results in this manuscript describe that the variation range in this group covers a wide part of the worldwide spectrum for some traits, but not others. Overall, this study is also a good example to show that global trait correlations expected from the leaf economics spectrum and the hydraulics theory do not necessarily exist among closely related species.

The inclusion of domesticated tomato accessions in the study allows pinpointing some of the leaf traits that have been modified during the domestication process, and to describe major differences in leaf hydraulics and venation in the domesticated tomato as compared to its wild counterparts.

We hope the manuscript merits publication in Environmental and Experimental Botany.

Sincerely,

Miquel À. Conesa and co-authors

Highlights:

-Leaf venation in wild tomatoes coordinates to gas exchange and photosynthesis

-Trends in the leaf economics spectrum are followed among closely related species

-Leaf venation in wild tomatoes is coupled to leaf morphology traits

-Contrary to theory, leaf hydraulics do not constrain gas exchange in wild tomatoes

1   **Leaf venation explains variation in leaf morphology and gas exchange in the**

2   **tomatoes and relatives (*Solanum* sect. *Lycopersicon* sect. *Juglandifolia* and sect.**

3   ***Lycopersicoides*)**

4

5   Miquel À. Conesa[a]*, José J. Peguero-Pina[a,b], Christopher D. Muir[c], Arántzazu Molins[a,d]

6   Emilio J. Roldán[a], Eustaquio Gil-Pelegrín[b] and Jeroni Galmés[a]

7   * ma.conesa@uib.es

8   [a] Research Group on Biology of Plants under Mediterranean Conditions. Departament

9   de Biologia, Universitat de les Illes Balears-INAGEA. Carretera de Valldemossa km

10   7.5, E-07122, Palma. Illes Balears. Spain.

11   [b] Unidad de Recursos Forestales, Centro de Investigación y Tecnología Agroalimentaria

12   de Aragón, Gobierno de Aragón, Avda. Montañana 930, 50059 Zaragoza, Spain

13   [c] Department of Botany, University of Hawai□i at Mānoa, 3190 Maile Way, Honolulu,

14   Hawaii 96822, USA.

15   [d] Dpto. Botánica, ICBIBE, Fac. CC. Biológicas, Universitat de València, C/ Dr. Moliner

16   50. 46100-Burjassot, Valencia, Spain.

17

18   **Abstract**

19   The wild tomatoes and relatives constitute a group of closely related species

20   inhabiting diverse habitats across South America. In order to test for the coordination of

21   leaf traits related to venation, hydraulics, morphology, and gas exchange in this clade,

22   the wild tomatoes and some domesticated accessions were grown outdoors in a common

23   garden under Mediterranean summer conditions. Results showed a coordination of leaf

24   vein density with photosynthesis, stomatal conductance, leaf size and leaf mass per area,

25   which was not found among the vast range of species, habitats and growth forms

existing in literature data. Contrarily, the correlation of hydraulic conductance with photosynthesis and gas exchange found in literature data did not occur in the tomatoes, showing a decoupling of leaf hydraulics and venation traits in this group of close relative species. This fact indicated that limitations to gas exchange in the tomatoes are more related to CO_2 diffusion than hydraulics. Moreover, species from arid habitats followed a drought-escape strategy, favouring pulse-growth in suitable periods, resulting in leaf traits not predicted from global trends. In this framework, domesticated tomatoes had extreme values for most of the measured traits, reflecting modifications during domestication.

Keywords: close relative species, gas exchange, leaf economics spectrum, leaf hydraulics, leaf trait decoupling, leaf venation, tomato.

Abbreviations: LES, leaf economics spectrum; M_{SP}, De Martonne aridity index for species; AR, arid habitat species; SA, semi-arid habitat species; HU-s, humid habitat species with shrub-like habit; HU-l, humid habitat species with liana-like habit; DO, domesticated accessions group; K_{leaf}, leaf hydraulic conductance; ε_{max}, maximum bulk modulus of elasticity; Ψ_{TLP}, leaf water potential at turgor loss point; π_0, osmotic potential at full turgor; RWC_{TLP}, relative water content at the turgor loss point; LA_1, leaf area per leaf; LMA, leaf mass area; A_N, net photosynthesis; g_s, stomatal conductance to water; V_{dL}, MV_{dL}, mV_{dL}, vein density on a length basis for total, major and minor veins, respectively; L average vein length; W average vein width.

1. Introduction

51   The hydraulics theory of leaf gas exchange states that because leaves need to be

52 continually supplied with water in order to keep stomata open, leaf hydraulics traits

53 evolve in concert with leaf photosynthetic function (Scoffoni et al., 2016). Since this

54 central role in photosynthetic function, leaf hydraulics traits play an important role in

55 plant evolution and adaptation to different ecological niches (e.g., Boyce et al., 2009;

56 Brodribb and Feild, 2010; Sack and Scoffoni, 2013; Rockwell and Holbrook, 2017).

57 Water transport through leaves accounts for more than 80% of the whole-plant

58 hydraulic resistance (Sack et al., 2012) and depends critically on leaf venation

59 properties (Sack and Holbrook, 2006; Brodribb et al., 2007; Flexas et al., 2013; Sack

60 and Scoffoni, 2013; Rockwell and Holbrook, 2017). Hence, there is a tight correlation

61 across plant groups and biomes between leaf venation and leaf hydraulics. In turn, leaf

62 hydraulics traits such as the leaf hydraulic conductance (K_{leaf}) and the bulk modulus of

63 elasticity (ε_{max}) among others, strongly affect stomatal control and closure (Brodribb

64 and Holbrook, 2003). Leaf venation properties that allow water supply more efficiently

65 facilitate stomata to stay open, increasing CO_2 supply for photosynthesis. Furhermore,

66 relationships between venation, hydraulics, and gas exchange are further modified by

67 leaf morphology and climate (e.g., Sack and Holbrook, 2006; Brodribb et al., 2007;

68 Flexas et al., 2013; Reich, 2014; Sack et al., 2015; Blonder et al., 2017).

69   Leaf hydraulics may also contribute directly or indirectly to leaf 'economics', the

70 balance between resources invested in building leaves and resources acquired during a

71 leaf lifespan. The Leaf Economics Spectrum (LES) delineates resource-conservative

72 and resource-acquisitive leaves based on their nutrient, structural, and photosynthetic

73 traits, indicating the existence of global tradeoffs (e.g., Wright et al., 2004; Blonder et

74 al., 2011; Sack et al., 2013; Reich, 2014; Díaz et al., 2016). In general, resource-

75 acquisitive leaves are cheap to build, have high mass-based photosynthetic rates, but

76   have shorter lifespan; while robust, resource-conservative leaves are expensive, have

77   low mass-based photosynthetic rates, but have longer lifespan. However, the anatomical

78   and physiological underpinnings of this tradeoff are not clear. Blonder et al. (2011,

79   2014) proposed that venation traits may directly underly the LES, but further

80   examination shows that coordination between venation and LES traits is probably

81   indirect (Sack et al. 2013).

82   If venation is the primary causal driver of leaf hydraulics and gas exchange, as

83   proposed by the leaf hydraulics theory, then similar patterns of trait covariation should

84   evolve repeadtedly (Scoffoni et al., 2016). This can be tested by measuring trait

85   covariation in multiple clades of closely related species. For example, Scoffoni et al.

86   (2016) showed that vein density, leaf hydraulic conductance and maximum

87   photosynthetic rates evolved in a coordinated fashion among *Viburnum* species,

88   consistent with a causal relationship. However, to test the generality or limits of the leaf

89   hydraulics theory, comparisons are needed from multiple clades spanning different

90   functional groups and geographies. For example, many LES tradeoffs have shown to be

91   dependent on the particular biome, species group or species (e.g., Li et al., 2015;

92   Niinemets, 2015; Grubb et al., 2015; Gleason et al., 2016; Males et al., 2017; Messier et

93   al., 2017 and references therein; Derroire et al., 2018).

94   Variation in trait correlations among different groups indicates multiple, complex

95   relatioships between leaf traits and physiological function (Sack et al. 2013; Blonder et

96   al., 2014; Blonder et al., 2016). If similar patterns of correlations among vein density,

97   hydraulic conductance and photosynthesis evolve independently in distantly related

98   clades, this would indicate that leaf hydraulics are the predominant limitations on

99   photosynthesis. Conversely, if correlations vary, then clearly other factors also drive

100   physiological variance. Phylogenetic or habitat-related constraints may limit variation in

101 specific parameters, pushing particular plant groups to increase variation in others (e.g.,

102 Jones et al., 2013, and references therein), which may be a major factor limiting the

103 existence of the global tradeoffs.

104   In this study, we examine the leaf hydraulics theory and its relationship to the

105 LES in wild tomatoes and relatives (*Solanum* sect. *Lycopersicon*, sect. *Lycopersicoides*

106 and sect. *Juglandifolia*), a group of 15-17 closely related species with monophyletic

107 origin (e.g., Peralta et al., 2008), radiated between 6 Mya (Särkinen et al., 2013) and >7

108 Mya (Nesbitt and Tanksley, 2002). Because of the extreme diversity in habitat

109 conditions across the species (ca. 3500 km in latitude, and ca. 3500 m in altitude;

110 reviewed in Peralta et al., 2008), this clade is well-suited to investigate how morpho-

111 physiological traits co-vary within a narrow group of species, potentially allowing

112 adaptation to diverse habitats. Past studies in the tomatoes and relatives showed weak

113 coordination of leaf morphology with gas exchange traits (Muir et al., 2017) and also

114 with growth-related traits (Conesa et al., 2017), suggesting that coordination between

115 leaf structure and function in this group, if it exists, may depend on other traits related

116 to leaf hydraulics. We also compared wild species to cultivated tomato varities in order

117 to understand which traits and trait relationships have been selected upon during

118 domestication.

119

120 **2. Material and methods**

121 *2.1. Plant material, germination and growth conditions*

122   In this experiment, 16 tomato accessions were grown at the University of the

123 Balearic Islands (Table 1). Wild accessions, obtained from the Tomato Genetics

124 Resource Center (http://tgrc.ucdavis.edu), included the two *Solanum* sect.

125 *Lycopersicoides* species (*S. lycopersicoides* LA2951, *S. sitiens*, LA4115), the two sect.

126   *Juglandifolia* species (*S. juglandifolium* LA3322, *S. ochranthum* LA2161), and 9 sect.

127   *Lycopersicon* taxa (*S. pennellii* LA1272, *S. arcanum* LA2153, *S. peruvianum* LA2964,

128   *S. neorickii* LA1322, *S. chmielewskii* LA1327, *S. pimpinellifolium* LA0114, *S.*

129   *cheesmaniae* LA1035, *S. galapagense* LA0930, and *S. lycopersicum* var. *cerasiforme*

130   LA1320). The domesticated accessions included a commercial tomato, 'Roma VF'

131   (Semillas Batlle S.A, Barcelona, Spain) and two 'Ramellet' tomato accessions from the

132   University of the Balearic Islands (UIB) seedbank (UIB1-48, with normal tomato-leaf,

133   and UIB1-30, with the potato-leaf morphology). 'Ramellet' tomato is a diverse Balearic

134   landrace selected under poor irrigation and adapted to drought conditions (Galmés et al.,

135   2011, 2013).

136   Seed pre-treatment, germination, plantlet growth and transplantation was

137   performed as in Conesa et al. (2017). Five plants per accession were grown in 19 L pots

138   containing a 4:1 mixture (v/v) of bog peat-based horticultural substrate (Prohumin-

139   Potting Soil Klasmann-Deilmann, Projar S.A., Valencia, Spain) and perlite

140   (granulometry A13, Projar S.A., Valencia, Spain). Plants were grown outdoors at the

141   UIB experimental field from May to July. The environmental conditions were the

142   typical under spring-summer Mediterranean climate, with average daily temperature

143   (ºC) during the day of 23.9±0.4, 25.4±0.8 and 27.6±0.4, average maximum daily

144   temperature of 25.39±0.4, 26.0±1.2, 29.1±0.4, and average minimum daily temperature

145   of 12.9±0.4, 15.7±0.5, 19.1±0.4, respectively for May, June and July. All plants were

146   irrigated daily to field capacity, and fertilized weekly with 50% Hoagland's solution.

147

148   *2.2 Classification of the wild accessions in climatic groups*

149   For each species, mean annual precipitation (P, mm) and temperature (T, ºC) for

150   all georeferenced accessions available in the TGRC were obtained from Worldclim

151   (Hijmans et al., 2005) and used to calculate the De Martonne aridity index (De

152   Martonne, 1926) at species level (M_{SP}; Table 1) as: P / (T+10).

153   The wild species were classified into three different climatic groups: arid (AR;

154   M_{SP} <12), semi-arid (SA; M_{SP} 12-24) and humid (HU; M_{SP} >24), based on

155   discontinuities among the tomato species studied (see Conesa et al., 2017 for more

156   details). As an exception, GAL, with a M_{SP} of 29, was considered here as SA. This is

157   because this species and CHE are Galápagos Islands endemics, thus inhabiting a narrow

158   geographic range. However, GAL is restricted to low elevations in saline seashore,

159   while CHE, with M_{SP} of 19 (i.e., SA), extends also to elevations up to 1300 m (Spooner

160   et al., 2005; Peralta et al., 2008). Therefore, it appears that GAL inhabits very similar or

161   even more arid habitats than CHE and thus, its M_{SP} should be lower. Given that, when

162   considering species into the different climatic groups, we included both endemics into

163   the SA group, despite the differences in the M_{SP} value.

164   The two sect. *Juglandifolia* species (JUG, OCH) present liana-like plant habit,

165   while the remaining tomatoes present a shrub-like plant habit. To consider these

166   differences, the HU group was separated into the shrub-like humid species (HU-s) and

167   the liana-like humid species (HU-l). The three domesticated tomato accessions were

168   considered as a separate group (DO).

169

170   *2.3 Leaf venation*

171   The terminal leaflet of 3-5 well developed healthy leaves was sampled and

172   preserved in a formalin-acetic acid solution according to Blonder (2018). From each

173   sample, 1 cm^2 pieces were taken from the space between the secondary veins, from a

174   minimum distance of 5 mm from the primary vein and the edge; considering midrib as

175   first order vein. Therefore, major veins correspond to secondary and/or tertiary order

176 veins. Clearing was performed in customized PVC mini-trays with 700 ml 1.25M

177 NaOH to maintain samples separated, with mechanical shaking at 20 rpm for three days,

178 plastic covered to prevent solution evaporation. Afterwards, samples were gently rinsed

179 in distilled water for 5 min and, soaked in a 2.5% NaClO solution for 5 min to remove

180 pigment depositions and rinsed again in distilled water. After that, samples passed

181 though EtOH series of 50% and 100%, and then stained in a 1% safranin solution (1 g

182 safranin/100 ml of 100% EtOH) for 5 min. Colorant clearing was performed in 100%

183 EtOH for at least 30 min. Finally, samples were rinsed in a 50% toluene/EtOH solution

184 and then in a 100% toluene solution, with the aim of spreading toluene based mounting

185 solution correctly. Picture series (720x576 pixels) were taken from the preparations at

186 50x magnification using an Olympus U-TVO 5XC digital camera mounted on an

187 Olympus BX60 microscope (Tokyo, Japan). The measured leaf portion corresponds

188 approximately to 3 mm^2.

189   Vein network identification was automated in LEAF GUI (Price et al., 2011) after

190 scaling and adjusting threshold with the same software. Prior to calculations, vein

191 recognition was manually screened and confirmed and all veins and areoles interrupted

192 by image margins were unselected. The venation parameters considered from LEAF

193 GUI were (see Price et al., 2011 for further detail): areole eccentricity (i.e, the ratio of

194 the minor and major axis in the ellipse that encodes the areole, where a value of 0 would

195 identify completely round areoles, and 1 may represent parallel veins not enclosing an

196 areole; *Eccentricity*), average vein length (*L*) and width (*W*), total vein density based on

197 vein length (V_{dL}, mm mm^{-2}), which was instead decomposed in the densities for major

198 veins (MV_{dL}; 1st to 3rd order in a leaflet, not considering the leaf rachis) and for minor

199 veins (mV_{dL}; 4th and further order veins).

200

2.4 Leaf gas exchange measurements

The net CO_2 assimilation rate (A_N) and stomatal conductance to H_2O (g_s) were

measured using an open-path infrared gas exchange analyzer (Li-6400, Li-Cor Inc.,

Lincoln, NE, USA) with a 2 cm^2 leaf chamber fluorometer. Point measurements were

taken after steady-state conditions (usually 15-30 min after clamping the leaf) at a leaf

temperature of 25ºC, 400 ppm of CO_2, saturating irradiance (1500 μmol quanta m^{-2} s^{-1})

with 10% of blue light, and 40-60% air relative humidity (vapor pressure deficit of 1.45

± 0.30 kPa).

2.5 Leaf morphology traits

The leaf area per leaf (LA_1) was measured with Image J (Ambrámoff *et al.* 2004)

on well-developed healthy leaves ($n = 5$), scanning all leaflets and discarding the rachis.

The leaflets were then dried in an air-forced oven at 70ºC to constant weight and

weighed to calculate the leaf mass area (*LMA*) as the dry weight of all leaflets divided

by LA_1.

2.6 Pressure-volume analysis and leaf hydraulic conductance (K_{leaf})

Pressure-volume relationships were determined in five leaves per species using a

pressure chamber and following the free-transpiration method (Corcuera et al., 2002;

Brodribb and Holbrook, 2003). The water-relation parameters analyzed were: leaf water

potential at the turgor loss point (Ψ_{TLP}), maximum bulk modulus of elasticity (ε_{max}),

osmotic potential at full turgor (π_0) and the relative water content at the turgor loss point

(RWC_{TLP}).

The leaf hydraulic conductance ($K_{leaf,}$) was measured following the methodology

described by Brodribb and Holbrook (2004). Five sun-exposed leaves from five plants

226 per accession were collected at 07:00-08:00 h (solar time), minimizing the possibility of

227 midday K_{leaf} depression (Brodribb and Holbrook 2003). The leaves were enclosed in

228 sealed plastic bags to prevent water loss, and stored in the dark for a period of at least 1

229 h until stomatal closure so that all leaflets from the same leaf could reach the same

230 water potential. The water potential measured on a leaflet under these conditions is

231 assumed to be the water potential of the leaves prior to rehydration (Ψ_0). Once this

232 value was obtained, the terminal leaflet was cut under water to prevent air entry and

233 allowed to absorb water for 20 to 40 seconds. The water potential after rehydration was

234 subsequently obtained (Ψ_f). The leaf hydraulic conductance was calculated as: $K_{leaf} = C_l$

235 ln $[\Psi_0/ \Psi_f]$ / t, where C_l (mol MPa^{-1} m^{-2}) is the leaf capacitance for each accession. C_l

236 was calculated as the initial slope of the *P-V* relationships, normalized by the leaf area

237 (Brodribb and Holbrook, 2004).

238   For hydraulics traits, as well as for gas exchange, morphology and venation traits

239 (see below), measurements were performed in completely developed and healthy leaves,

240 without symptoms of senescence, with South orientation and not shaded by other

241 leaves, minimizing trait variation related to leaf heterogeneity within the same plant.

242

243 *2.7 Statistical analyses*

244   One-way and nested analysis of variance (ANOVA) and correlation analyses

245 were conducted in SPSS (v. 15.0.1 for Windows; SPSS Inc., Chicago, IL, USA). The

246 ANOVAs were performed at 0.05 significance level, type III sum of squares with Tukey

247 *post-hoc* tests. One-way ANOVAs were performed to test for differences among

248 species, whereas nested ANOVAs were used to test for differences among climatic

249 groups, nesting "species" within "climatic group". Correlation analyses were performed

250 using bilateral significance and Pearson correlation coefficient.

251   Previous studies with the accessions here included showed that phylogenetic

252 relationships among species explained little of the trait variation, thus phylogenetic and

253 non-phylogenetic giving nearly identical results (Conesa et al., 2017; Muir et al., 2017).

254 To test directional hypotheses 1) between venation traits and K_{leaf} and 2) venation traits

255 and K_{leaf} with gas exchange and leaf morphology we used phylogenetic generalized least

256 squares (PGLS) using the R packages 'ape' (Paradis and Schliep, 2018) and 'nlme'

257 (Pinheiro et al., 2018). PGLS was not used when no clear causal effect can be tested.

258

259 **3. Results**

260 *3.1. Variation in leaf venation*

261   The total vein density on a vein length basis (V_{dL}) varied from 9.0 ± 1.0 mm mm^{-2}

262 in JUG to 20.7 ± 2.5 mm mm^{-2} in LYC (Table S1). The V_{dL} was mostly determined by

263 the density of the minor veins (mV_{dL}; correlation with V_{dL}, R^2=0.92; P<0.001), resulting

264 in very similar trends for both total and minor vein density. The mV_{dL} ranged from $6.5 \pm$

265 0.6 mm mm^{-2} in JUG to 17.7 ± 2.3 mm mm^{-2} in LYC. In contrast, the density for major

266 veins (MV_{dL}) did not differ among species (Table S1).

267   V_{dL} ranged from 15.3 ± 0.8 mm mm^{-2} in AR to 10.6 ± 0.5 mm mm^{-2} in DO (Fig.

268 1A; Table S1). The HU-l had significantly lower V_{dL} than AR and HU-s (Fig. 1A; Table

269 S1). Trends were similar for both MV_{dL} and mV_{dL}, with minimum values in both cases

270 in DO and HU-l, and the AR had higher mV_{dL} than HU-l (Table S1).

271   There was a negative relationship of V_{dL} with average vein length (L), (R^2=0.81;

272 P<0.001). Thus, L differences among climatic groups almost paralleled those indicated

273 for V_{dL}, although differences were more evident for L between AR, SA and HU-s (L

274 below 100 μm) and HU-l and DO (L above 120 μm), (Fig. 1B; Table S1). Among

275 species, L ranged from 66.1 ± 7.1 μm in LYC to 154.5 ± 25.6 μm in JUG (Table S1). In

276 turn, the average vein width (W) varied between 6.9 ± 0.3 μm in OCH and 14.9 ± 1.0

277 μm in CHE. Trends for W were not related to V_{dL} and L. Across climatic groups, the

278 maximum and minimum W corresponded to SA and DO, respectively (Fig. 1C; Table

279 S1).

280   There was no correlation between L and W, despite the coincidence of species

281 with both relatively long and thick veins (e.g., CHE, OCH, SIT) and short and thin

282 veins (e.g., PIM, LYC), (Table S1). On the other hand, all the DO accessions and the

283 close relative CER had consistently among the longest and thinnest veins (Table S1).

284   Across species, *Eccentricity* ranged between 0.76 ± 0.008 in PIM to 0.82 ± 0.005

285 in SIT, with a lack of significant differences across species (Table S1) and climatic

286 groups (Fig. 1D).

287   The correlation between K_{leaf} and V_{dL} was not significant across the published

288 data available (Fig. 3A). However, it was significant and negative ($R^2=0.28$; P<0.05)

289 considering only the wild and domesticated tomatoes (Fig. 3A). MV_{dL} did not correlate

290 with K_{leaf} (Fig. 3B), while results for mV_{dL} paralleled those described for V_{dL} (Fig. 3C).

291 The phylogenetic correlation between K_{leaf} and V_{dL} was slightly lower and significant

292 (PGLS $R^2=0.25$; P<0.05); the other PGLS correlations were similar and non-significant

293 (results not shown).

294

295 *3.2 Variation in leaf hydraulics traits*

296   The leaf hydraulic conductance on an area basis (K_{leaf}) varied widely among

297 species (see Table 1 for species' codes), ranging from 8.02 ± 0.78 mmol m^{-2} s^{-1} MPa^{-1} in

298 OCH to 44.1 ± 2.7 mmol m^{-2} s^{-1} MPa^{-1} in the domesticated RAP (Table S2). In spite of

299 the variability in K_{leaf} within each climatic group, some differences were observed

300 among groups, with HU and DO having the lowest and the highest values, respectively

301 (Fig. 2A).

302 There was little difference among climatic groups for water potential at turgor

303 loss point (Ψ_{TLP}) and osmotic potential at full rehydradion (π_0). The HU-l species JUG

304 had the most negative π_0 (-1.27 ± 0.06 MPa) and the domesticated RAN (-0.58 ± 0.03

305 MPa) the least negative π_0 (Table S2). For Ψ_{TLP}, the lowest value again corresponded to

306 JUG (-1.82 ± 0.06 MPa), while the highest was that of the AR species SIT (-0.88 ± 0.07

307 MPa). The HU-l had significantly the lowest values for Ψ_{TLP} (-1.51 ± 0.11 MPa) and π_0

308 (-1.11 ± 0.06 MPa), and the DO significantly the highest Ψ_{TLP} (-1.04 ± 0.05 MPa) (Fig.

309 2B,C). However, there was a high heterogeneity for Ψ_{TLP} within the AR (Table S2),

310 with PER having among the most negative values (-1.58 ± 0.047 MPa).

311 Compared to Ψ_{TLP} and π_0, the maximum bulk modulus of elasticity (ε_{max})

312 displayed higher variation. At the climatic group level, the maximum (7.72 ± 0.54 MPa)

313 and minimum (3.64 ± 0.38 MPa) values corresponded to the HU-l and DO, respectively;

314 although none of the groups was significantly different from the remaining (Fig. 2D). At

315 the species level, the minimum ε_{max} corresponded to RAP (2.30 ± 0.37 MPa) and the

316 maximum to PER (9.03 ± 1.28 MPa), (Table S2).

317 At species level, there was a significant correlation between Ψ_{TLP} and the

318 remaining parameters derived from the P-V curve, K_{leaf} (R^2=0.31; P<0.05), π_0 (R^2=0.53;

319 P>0.01), ε_{max} (R^2=0.58; P<0.001) and RWC_{TLP} (R^2=0.49; P<0.01).

320

321 *3.3. Variation in leaf morphological and gas exchange traits, and the relationship with*

322 *venation and leaf hydraulics traits*

323 There was a low number of significant correlations of hydraulics traits with

324 morphological and gas exchange traits or with climate across tomatoes, and none

13

325   involved K_{leaf} (Fig. 4A,C,E,G). The significant correlations were restricted to π_0, being

326   negatively correlated with M_{sp} (R^2=0.29; P<0.05) and positively correlated with A_N

327   (R^2=0.38; P<0.05), (data not shown). However, K_{leaf} correlated with g_s (Fig. 4G) and

328   especially A_N (Fig. 4E) in the literature data available (Table S4). After phylogenetic

329   correction, the correlation between K_{leaf} and A_N was marginally significant, but negative,

330   opposite to the predicted by the leaf hydraulics theory (PGLS R^2=0.25; P=0.05). The

331   other PGLS correlations with K_{leaf} were similarly non-significant (results not shown).

332   Contrary to hydraulics traits, most venation traits correlated with leaf

333   morphological and gas exchange parameters. V_{dL} correlated negatively with LMA (Fig.

334   4B) and especially MV_{dL} (R^2=0.45; P<0.01), but not M_{SP} (P>0.05; data not shown). LA_1

335   correlated negatively with V_{dL} (Fig. 4D) and MV_{dL}, but not mV_{dL} (P>0.05), probably as a

336   result of the positive correlation between LMA and LA_1. As expected from the

337   correlation between V_{dL} and L, L positively correlated with LMA and LA_1, while W was

338   uncorrelated. Moreover, $Eccentricity$ negatively correlated with both LMA and M_{SP} (R^2=

339   0.46 and R^2= 0.37, respectively; P<0.01; data not shown).

340   V_{dL} positively correlated with both A_N (Fig. 4F) and g_s (Fig. 4H). Such

341   correlations were virtually the same for V_{dL} and mV_{dL}, being non-significant for MV_{dL}

342   (P>0.05), which denotes the impact of the minor, but not major veins on gas exchange.

343   As occurred for the morphological traits, L paralleled V_{dL} results, while W showed no

344   significant correlation with gas exchange parameters. However, only the positive

345   correlation between V_{dL} and A_N was significant after phylogenetic correction (PGLS,

346   R^2= 0.32, P<0.05); whereas phylogenetic correlations between V_{dL} and LA_1, LMA, and

347   g_s were not significant (data not shown).

348

349   **4. Discussion**

4.1. Climatic groups in wild tomato species do not follow expectations from the leaf hydraulics theory because the lack of coordination between venation and hydraulics

The trend across tomato climatic groups for the total (V_{dL}) and minor vein density (mV_{dL}) was to decrease with humidity (Fig. 1A, Table S1). This depicts a positive relationship between hydraulic conductance (K_{leaf}) and V_{dL} across tomato groups (Figs. 1 and 2) that agrees with global observations by Sack and Holbrook (2006). These authors argued that higher mV_{dL} corresponded to a higher water supply capacity by increasing the xylem surface area for exchange of water with mesophyll, and reducing the outside-xylem water pathway. The correlation between K_{leaf} and V_{dL} was non-significant for wild species (P>0.05). Thus, there is a lack of coordination between leaf hydraulics and venation in the tomatoes, and also when considering the literature data available (Fig. 3A; Table S4). Accordingly, the K_{leaf} to vein density relationship is weak in eudicots, suggesting that further adaptations can be more important in particular species groups, such as extra-xylem and aquaporin traits, among others (McKown et al., 2010; Sack and Scoffoni 2013; Ohtuska et al., 2018). Nevertheless, the highest V_{dL} in the AR (Fig. 1A, Table S1) agrees with studies showing that V_{dL} correlates with aridity across diverse species (Sack and Scoffoni 2013). Thus, the maintenance of maximum V_{dL} in AR despite of the low K_{leaf} could respond to vein over-investment allowing maximization of net photosynthesis (A_N) and stomatal conductance (g_s), being as high as in SA and HU-s (Fig. 4).

The lowest K_{leaf} values were found in HU-s and HU-l (Fig. 2A). Within angiosperms, the hydraulics theory predicts higher K_{leaf} in species from moister habitats (Sack and Holbrook, 2006), the opposite to what we found in tomatoes. The unexpectedly high K_{leaf} in AR and SA (Fig. 2A) implies a water-profligate strategy in arid climate species, which can be an advantage in dry and nutrient-poor habitats

375 (Querejeta et al., 2018). In fact, AR species tended to exhibit a drought escape strategy

376 with pulse-growth behavior in suitable periods, having cheap leaves with lowest *LMA*

377 and fast turnover (Conesa et al., 2017). A similar conclusion arose in *Pelargonium*

378 species from Cape Floristic Region, where xerophytic species trends were broadly

379 opposite to the LES (Jones et al., 2013).

380   There were no differences in leaf water potential at turgor loss point (Ψ_{TLP}) and

381 osmotic potential at full turgor (π_0) among tomato climatic groups (Fig. 2B,C). The

382 hydraulics theory predicts that Ψ_{TLP} and π_0 correlate with water availability within and

383 across biomes (Bartlett et al., 2012). Ψ_{TLP} is considered a key indicator of drought

384 tolerance because leaves with lower Ψ_{TLP} are able to maintain function longer during

385 soil dehydration (Bartlett et al., 2014). Consequently, hydraulics traits did not explain

386 differences in aridity among tomato climatic groups. On the contrary, tomato species

387 from humid habitat and with liana-like plant habit (HU-l) had lower Ψ_{TLP} and π_0 than

388 any other group (Fig. 2). The low Ψ_{TLP} in HU-l can result from high solute

389 accumulation, because the main driver of Ψ_{TLP} seems to be π_0 (Bartlett et al., 2012),

390 which is also a main adaptive trait in lianas (Maréchaux et al., 2017).

391

392 *4.2. Variation in* A_{N} *and* g_{s} *is explained by vein density but is not correlated with leaf*

393 *hydraulics*

394   There was no correlation of K_{leaf} with A_{N} and g_{s} in the tomatoes (Fig. 4E,G),

395 reflecting the lack of coordination of hydraulics also with leaf gas exchange parameters.

396 On the contrary, the correlations were significant when considering diverse species (Fig.

397 4E,G), indicating the role of K_{leaf} in determining maximum g_{s} and A_{N} at broader

398 phylogenetic scales (Sack and Holbrook, 2006; Brodribb and Jordan, 2011; Blonder et

399 al., 2017). Despite this, the relationship between K_{leaf} and g_{s} has shown to depend on the

species and the climate, on different conditions of VPD, and on leaf and soil water

potential during peak activity (Sack et al., 2005). For example, Zhang et al. (2015)

found no correlation between both traits across cycads. They hypothesized that the main

reason affecting the coordination was related to the diversity of water availabilities

across the habitats in which the different species evolved, which may be also the case of

the wild tomatoes.

In contrast to hydraulic traits, V_{dL} correlated with gas exchange traits in the

tomatoes (Fig. 4F,H), reflecting the importance of venation rather than hydraulics in

explaining variation in leaf function in this clade. Several studies showed a lack of

coordination of A_N and g_s with vein density in particular biomes and species groups

(e.g., Gleason et al., 2016; Scoffoni et al., 2016), and such correlations were not

significant when considering the literature data available (Fig. 4).

4.3. Leaf hydraulics theory is not coordinated with the global leaf economics spectrum

because LMA *is not correlated to* K_{leaf}, *but to venation*

Across climatic groups, the highest *LMA* corresponded to HU-s and HU-l (Table

S3). This agrees with past studies in wild tomatoes showing a trend to increase *LMA*

with humidity (Easlon and Richards, 2009; Conesa et al., 2017; Muir et al., 2017),

which is opposite to predictions of the global leaf economics spectrum (LES), (Reich,

1998; Wright et al., 2005). Moreover, *LMA* did not correlate with K_{leaf} in the tomatoes

and across literature data (Fig. 4A), denoting the lack of coordination between two

prime traits in describing the LES (e.g., Wright et al., 2004; Poorter et al., 2009; Reich,

2014) and the hydraulics theory (e.g., Sack et al., 2006; Sack et al., 2013), respectively.

The low predictive power of *LMA* in tomatoes might relate to the narrow range that this

parameter covers along the LES spectrum; there is the 2-fold variation in the tomatoes (Fig. 4) and the up to 100-fold variation in the global LES (Wright et al., 2004).

Contrary to hydraulics traits, *LMA* correlated negatively with vein traits in the tomatoes (Fig. 4B). The inverse relationship between both traits has also been described across diverse species sets (Sack et al., 2013). However, V_{dL} did not correlate with *LMA* for the literature data available either (Fig. 4B), nor within other narrow species groups (e.g., Sack and Frole, 2006; Dunbar-Co et al., 2009; Nardini et al., 2012; Sack et al., 2013). Therefore, these results suggest a central role of the leaf vein system in explaining environmental adaptation in the tomatoes, while other traits thought to have a central adaptive role, like *LMA* and K_{leaf}, cannot explain the variation existing among the tomatoes regarding climatic distribution, leaf morphology and gas exchange function.

4.4. Domestication led to larger and denser leaves with more extreme hydraulic and venation traits

When compared to the wild species climatic groups, the domesticated accessions group (DO) had consistently higher K_{leaf}, Ψ_{TLP}, π_0 and RWC_{TLP} and among the highest A_N, and lower ε_{max}, V_{dL}, MV_{dL}, mV_{dL} and *W* (Figs. 1-4; Tables S1-S3). Furthermore, leaf morphology traits are the most obvious characterizing the DO, with ca. 3-fold larger LA_1 than those in the AR, SA and HU-s, and with the highest *LMA* among all groups (Table S3). Crop selection has been mainly determined by increased production (e.g., Darwin, 1868; Ladizinsky, 1998; Meyer et al., 2012), and leaf size increase seems to be related to the domestication process (Evans et al., 1993), as it seems also the high K_{leaf} values, since the latter have been described, on average, in the herbaceous crops (Sack and Holbrook, 2006). This is in agreement with the results

449   observed in the DO in this study, although A_N and g_s in the DO were not significantly

450   higher than the wild species groups (Table S3). This discrepancy might be related to the

451   fact that we grew species in common garden conditions, whereas past values were

452   measured under field conditions.

453   Adaptation to water shortage in drought adapted *Ramellet* tomato landraces

454   such as those included in the study (i.e, RAN, RAP) involves increasing mesophyll

455   airspaces, which improve CO_2 delivery to the chloroplast (Galmés et al., 2011, 2013).

456   This is a matter to consider in order to adapt tomato crop to future climate change

457   conditions. However, adaptations in wild tomatoes involve wider trait variation than

458   that available within the domesticated tomato. Despite several of the drought adaptive

459   traits in AR and SA, like increasing mV_{dL} and ε_{max}, have been described to be negatively

460   related to production, wild tomatoes are a meaningful source for morpho-physiological

461   adaptations in tomato crop.

462

463   *4.5. Lack of coordination between hydraulics theory and the LES in the tomatoes, a*

464   *matter of scale and particular adaptations to aridity*

465   At narrower phylogenetic ranges, global trait correlations predicted by the LES

466   and the hydraulics theory seem to be very dependent on the particular case studied (e.g.,

467   Sack and Frole, 2006; Jones et al., 2013; Zhang et al., 2015; Gleason et al., 2016;

468   Conesa et al., 2017; Ohtuska et al., 2018; Anderegg et al., 2018). Consequently, in

469   particular species groups, variation in traits with high adaptive importance may

470   dominate over the traits that are most important at a global scale. In the tomatoes, the

471   weak coordination of gas exchange with leaf morphology (Muir et al., 2017), growth

472   (Conesa et al., 2017) and hydraulics (Fig. 4E,G) indicates that different trait

473   combinations may be similarly adaptive. Results also indicate that hydraulic traits are

474 not the main limitation to gas exchange in the tomatoes, which could better relate to

475 CO_2 diffusion limitations (Muir et al., 2017) and affected by the venation system (Fig.

476 4F,H). Indeed, the pulse-growth behavior in arid habitat tomatoes (Conesa et al., 2017)

477 may shape varaition in leaf structure and function in this species group.

478

Author contributions

480 MAC, CDM, JJP-P and JG conceived and designed the experiment. All authors were

481 involved in the experiment establishment, data acquisition and analysis. JJP-P and AM

482 produced hydraulics data. CDM and EJR produced venation data. MAC drafted the

483 article, and CDM, JJP-P, EG-P and JG did important revisions. All authors critically

484 revised last versions of the manuscript and approved the submitted version. The authors

485 declare no conflict of interest.

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681   generality of leaf economic design principles in the cycads, an ancient lineage.
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683

684 **Table 1.** Species and accessions used in the study. Abbreviation codes are indicated.

685 The De Martonne aridity index (M_{SP}) was calculated as in De Martonne (1926), based

686 on temperature and precipitation values corresponding to annual means for the whole

687 species distribution. Climatic groups based on M_{SP} as follows: <12 arid (AR), 12-24

688 semi-arid (SA), >24 humid (HU); GAL is an exception (see Methods section). Different

689 plant habits in the HU were considered as separate groups: liana-like (HU-l) and shrub-

690 like (HU-s). The domesticated accessions are considered as a separate group (DO).

| Taxon	Code	M_{SP}	Climatic group
S. lycopersicoides Dunal	LYC	8.00	AR
S. sitiens I.M.Johnst.	SIT	2.33	
S. pennellii Correll	PEN	9.65	
S. peruvianum L.	PER	9.29	
S. arcanum Peralta	ARC	20.58	SA
S. pimpinellifolium L.	PIM	13.33	
S. cheesmaniae (L.Riley) Fosberg	CHE	18.73	
S. galapagense S.C.Darwin and Peralta	GAL	29.05	
S. chmielewskii (C.M.Rick, Kesicki, Fobes and M.Holle) D.M.Spooner, G.J.Anderson and R.K.Jansen	CHM	27.32	HU-s
S. neorickii D.M.Spooner, G.J.Anderson and R.K.Jansen	NEO	27.35	
S. lycopersicum L. var. *cerasiforme* (Alef.) Voss	CER	46.68	
S. juglandifolium Dunal	JUG	44.28	HU-l
S. ochranthum Dunal	OCH	47.47	
S. lycopersicum L. 'Ramellet'	RAN	-	DO
S. lycopersicum L. 'Ramellet'	RAP	-	
S. lycopersicum L. 'Roma VF'	ROM	-	

691

692
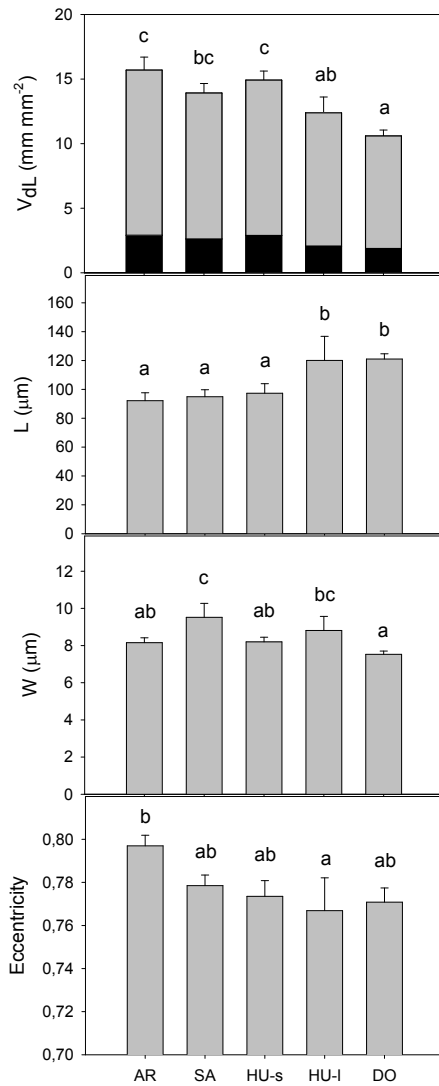
Fig. 1. Variation across climatic groups groups (arid, AR; semi-arid, SA; humid with

shrub habit, HU-s, and with liana-like habit, HU-l; domesticated, DO) for **A)** total vein

density (V_{dL}), separating major (black) and minor (grey) vein densities, **B)** average vein

length (*L*) and **C)** width (*W*), and **D)** vein areole eccentricity (*Eccentricity*), that ranges

from 0 to 1 (completely round areoles to parallel veins, respectively). Bars are averages

including all replicates per species, and error bars are the S.E. (in A correspond only to

total vein density). Letters on the error bars indicate nested ANOVA-Tukey (species

nested within climatic group) differences among groups at α=0.05.

Fig. 2. Variation across climatic groups (as in Fig. 1) for **A)** hydraulic conductance on area basis (K_{leaf}), **B)** leaf water potential at turgor loss point (Ψ_{TLP}), **C)** osmotic potential at full turgor (π_0), and **D)** modulus of elasticity at full turgor (ε_{max}). Bars are averages including all replicates per species, with S.E. Letters on the error bars indicate nested ANOVA-Tukey (species nested within climatic group) differences among groups at $\alpha = 0.05$
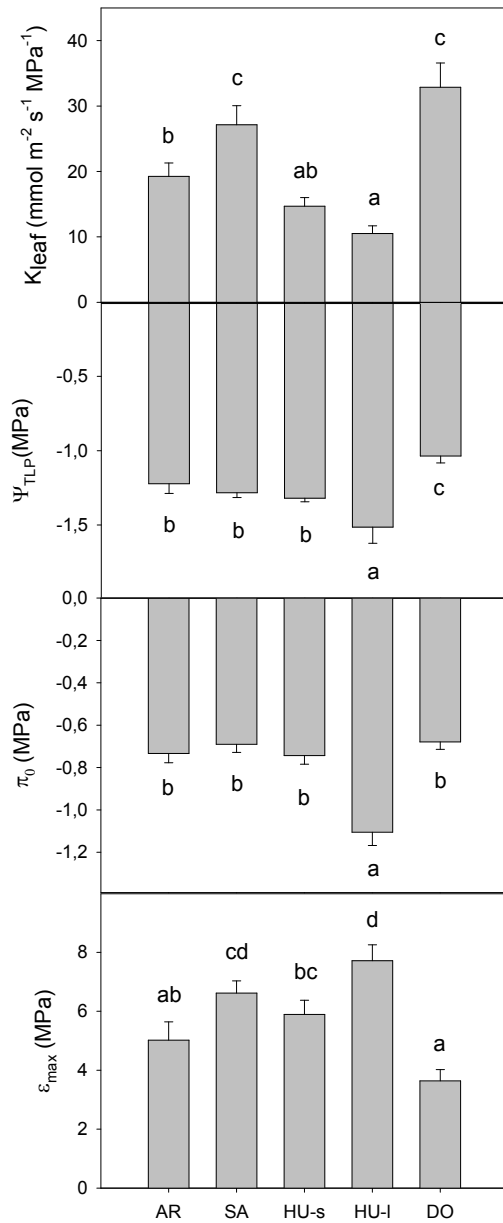
709
710
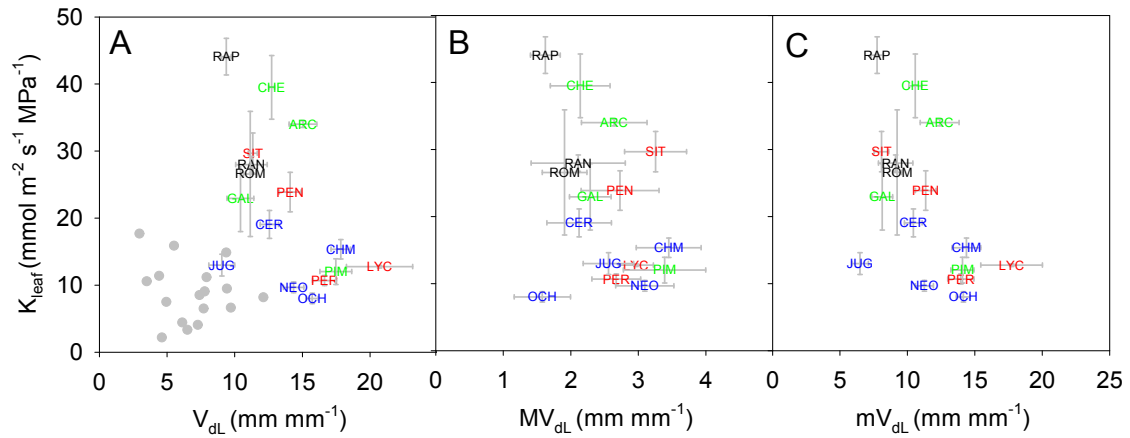
Fig. 3. Relationship between hydraulic conductance on area basis (K_{leaf}) and **A)** total vein density (V_{dL}), **B)** major vein density (MV_{dL}), and **C)** minor vein density (mV_{dL}). The S.E. is indicated for all parameters (n=3-5). Species codes as in Table 1. Species colors following climatic groups (see Fig. 1): AR in red, SA in green, HU in blue, and DO in black. Grey dots in A) represent the species in Flexas et al. (2013), (n=17). Regressions are non-significant (*P*>0.05) in all cases.
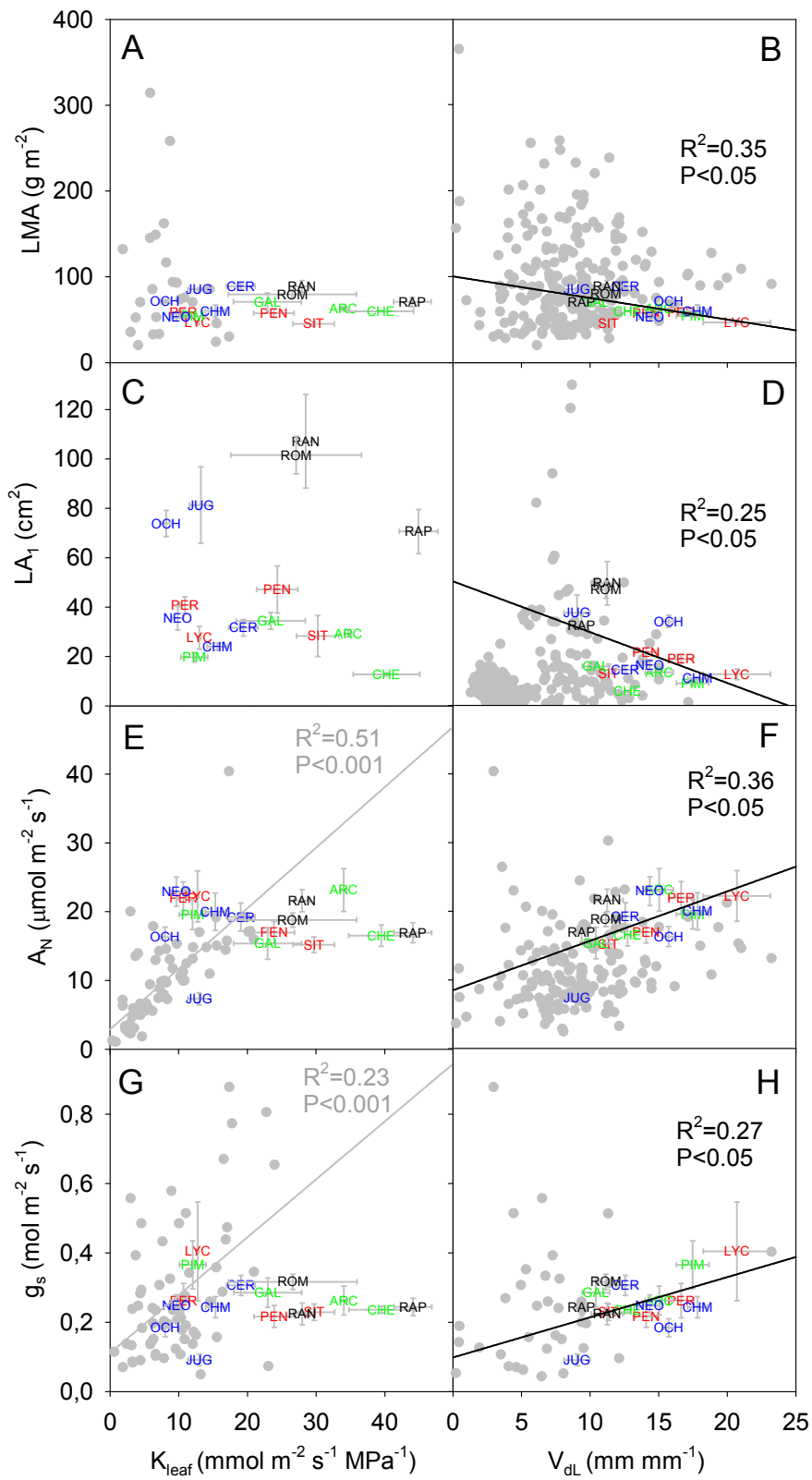
718   **Fig. 4.** Correlation of hydraulic conductance (K_{leaf}; A, C, E, G) and vein density (B, D,

719   F, H) with leaf mass per area (LMA; A, B), and leaf area per leaf (LA_1; C, D). net

720   photosynthesis (A_N; E, F), and stomatal conductance to water (g_s; G, H). Species codes

721   and colors as in Fig.3. The S.E. is indicated in the tomatoes for all parameters (n=3-5).

722   Grey dots represent data from higly diverse species from Brodribb et al. (2007), Flexas

723   et al. (2013), Sack and Scoffoni (2013), Sack et al. (2013), Price and Weitz (2014), and

724   Scoffoni and Sack (2017), compiled in Table S4. Vein density corresponds to total veins

725   (V_{dL}) for accessions in this study and for literature. Regression lines only indicated

726   when $P<0.05$, always separately for grey dots (grey line) and accessions in this study

727   (black line).

728 **Table S1**. Leaf venation traits for each accession. Vein density on a vein length basis,

729 for total (V_{dL}), major (MV_{dL}) and minor veins (mV_{dL}), average vein length (L) and width

730 (W), and vein areole eccentricity (*Eccentricity*), defining the shape of the areoles and

731 ranging from completely round areoles (value 0) to completely parallel veins (value 1).

732 For species, values are averages with S.E. (*n*=3-5) and letters denote ANOVA

733 differences. The averages per climatic group are shown in bold, with S.E. and

734 considering all the replicates per species. Capital letters correspond to nested ANOVA

735 differences among climatic groups (species nested within climatic group). Both

736 ANOVAs have been performed with Tukey *post-hoc* test.

Climatic group	Species code	V_{dL} mm mm^{-2}	MV_{dL} mm mm^{-2}	mV_{dL} mm mm^{-2}	L μm	W μm	*Eccentricity*
AR	SIT	11.33 ± 0.338 abcd	3.26 ± 0.46 a	8.08 ± 0.54 ab	121.97 ± 7.23 cde	9.7 ± 0.33 bc	0.815 ± 0.005 a
	LYC	20.7 ± 2.452 g	2.96 ± 0.26 a	17.74 ± 2.28 f	66.06 ± 7.06 a	7.2 ± 0.33 a	0.789 ± 0.008 a
	PEN	14.09 ± 0.81 bcdef	2.73 ± 0.58 a	11.36 ± 0.76 abcde	96.59 ± 4.82 abcd	7.82 ± 0.38 ab	0.781 ± 0.011 a
	PER	16.64 ± 0.887 efg	2.67 ± 0.36 a	13.97 ± 0.97 cdef	84.23 ± 5.62 abcd	7.9 ± 0.33 ab	0.802 ± 0.009 a
	AV.	**15.69 ± 1.01 C**	**2.91 ± 0.20 A**	**12.78 ± 1.01 C**	**92.21 ± 5.48 A**	**8.15 ± 0.27 AB**	**0.797 ± 0.005 B**
SA	ARC	15.04 ± 1.027 cdef	2.64 ± 0.49 a	12.4 ± 1.44 bcde	92.26 ± 4.2 abcd	8.34 ± 0.4 ab	0.79 ± 0.009 a
	PIM	17.47 ± 1.179 efg	3.39 ± 0.61 a	14.08 ± 0.86 def	73.27 ± 3.86 ab	6.98 ± 0.06 a	0.76 ± 0.008 a
	GAL	10.42 ± 0.993 abc	2.29 ± 0.31 a	8.13 ± 0.78 ab	115.42 ± 9.61 bcde	7.89 ± 0.09 ab	0.784 ± 0.013 a
	CHE	12.73 ± 0.211 abcde	2.14 ± 0.44 a	10.59 ± 0.48 abcde	98.81 ± 9.79 abcd	14.86 ± 0.98 d	0.781 ± 0.005 a
	AV.	**13.92 ± 0.74 BC**	**2.62 ± 0.24 A**	**11.30 ± 0.67 BC**	**94.94 ± 4.86 A**	**9.52 ± 0.76 C**	**0.779 ± 0.005 AB**
HU-s	NEO	14.35 ± 0.753 cdef	3.1 ± 0.43 a	11.26 ± 0.67 abcde	94.45 ± 5.62 abcd	8.22 ± 0.28 ab	0.776 ± 0.012 a
	CHM	17.83 ± 0.714 fg	3.45 ± 0.48 a	14.38 ± 1.07 ef	77.38 ± 3.78 abc	8.93 ± 0.48 abc	0.792 ± 0.008 a
	CER	12.56 ± 0.677 abcde	2.12 ± 0.48 a	10.44 ± 0.65 abcde	120.26 ± 13.48 cde	7.44 ± 0.28 a	0.753 ± 0.013 a
	AV.	**14.91 ± 0.70 C**	**2.89 ± 0.29 A**	**12.02 ± 0.63 BC**	**97.36 ± 6.62 A**	**8.20 ± 0.25 AB**	**0.774 ± 0.007 AB**
HU-l	OCH	15.73 ± 0.448 def	1.58 ± 0.42 a	14.15 ± 0.52 def	85.74 ± 2.53 abcd	6.85 ± 0.25 a	0.764 ± 0.002 a
	JUG	9.04 ± 0.954 a	2.56 ± 0.37 a	6.49 ± 0.62 a	154.5 ± 25.56 e	10.78 ± 0.75 c	0.77 ± 0.032 a
	AV.	**12.38 ± 1.22 AB**	**2.07 ± 0.31 A**	**10.32 ± 1.33 AB**	**120.12 ± 16.67 B**	**8.81 ± 0.75 BC**	**0.767 ± 0.015 A**
DO	RAN	11.24 ± 1.165 abcd	2.11 ± 0.7 a	9.13 ± 1.27 abc	113.43 ± 5.57 bcde	7.65 ± 0.49 ab	0.77 ± 0.011 a
	RAP	9.37 ± 0.369 ab	1.62 ± 0.22 a	7.75 ± 0.46 ab	126.1 ± 8.01 de	7.47 ± 0.23 a	0.772 ± 0.008 a
	ROM	11.15 ± 0.498 abcd	1.91 ± 0.33 a	9.24 ± 0.32 abcd	123.68 ± 4.68 cde	7.47 ± 0.18 a	0.77 ± 0.016 a
	AV.	**10.59 ± 0.47 A**	**1.88 ± 0.25 A**	**8.71 ± 0.47 A**	**121.07 ± 3.65 B**	**7.53 ± 0.18 A**	**0.771 ± 0.007 AB**

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738 **Table S2**. Leaf hydraulic traits for each accession. Leaf hydraulic conductance (K_{leaf}),

739 water potential at turgor loss point (Ψ_{TLP}), osmotic potential at full rehydration (π_0),

740 maximum bulk modulus of elasticity (ε_{max}) and relative water content at turgor loss

741 point (RWC_{TLP}). For species, values are averages with S.E. (*n*=3-5) and letters denote

742 ANOVA differences. The averages per climatic group are shown in bold, with S.E.

743 considering all the replicates per species. Capital letters correspond to nested ANOVA

744 differences among climatic groups (species nested within climatic group). Both

745 ANOVAs have been performed with Tukey *post-hoc* test.

Climatic group	Species code	K_{leaf}	Ψ_{TLP}	π_0	ε_{max}	RWC_{TLP}
		mmol m-2 s-1 MPa-1	MPa	MPa	MPa	%
AR	SIT	29.68 ± 3.01 defg	-0.88 ± 0.07 a	-0.66 ± 0.06 bc	3.7 ± 0.51 ab	0.88 ± 0.02 e
	LYC	12.75 ± 0.19 abc	-1.26 ± 0.08 bcde	-0.78 ± 0.06 bc	4.33 ± 0.49 abc	0.82 ± 0.02 cde
	PEN	23.89 ± 2.95 abcdef	-1.18 ± 0.08 abcd	-0.71 ± 0.11 bc	3.55 ± 0.51 ab	0.84 ± 0.01 de
	PER	10.68 ± 0.75 ab	-1.58 ± 0.04 ef	-0.77 ± 0.13 bc	9.03 ± 1.28 e	0.65 ± 0.05 a
	AV.	**19.25 ± 2.01 B**	**-1.22 ± 0.07 B**	**-0.73 ± 0.04 B**	**5.02 ± 0.62 AB**	**80.05 ± 1.10 AB**
SA	ARC	34.02 ± 0.49 efg	-1.22 ± 0.1 bcd	-0.69 ± 0.09 bc	6.14 ± 0.4 bcde	0.83 ± 0.01 de
	PIM	12.02 ± 1.92 abc	-1.38 ± 0.07 de	-0.75 ± 0.08 bc	6.06 ± 0.95 bcde	0.84 ± 0.01 de
	GAL	22.95 ± 4.95 abcdef	-1.27 ± 0.03 bcde	-0.71 ± 0.06 bc	5.81 ± 0.64 bcde	0.82 ± 0.01 cde
	CHE	39.5 ± 4.75 fg	-1.26 ± 0.02 bcde	-0.61 ± 0.08 bc	8.46 ± 0.8 e	0.69 ± 0.04 ab
	AV.	**27.12 ± 2.92 C**	**-1.28 ± 0.03 B**	**-0.69 ± 0.04 B**	**6.61 ± 0.41 CD**	**79.57 ± 1.04 A**
HU-s	NEO	9.67 ± 0.8 a	-1.25 ± 0.02 bcd	-0.66 ± 0.07 bc	4.35 ± 0.4 abc	0.83 ± 0.01 de
	CHM	15.35 ± 1.46 abcd	-1.38 ± 0.04 de	-0.88 ± 0.06 bc	6.38 ± 0.73 bcde	0.77 ± 0.02 bcd
	CER	19.05 ± 2.08 abcde	-1.33 ± 0.05 cde	-0.69 ± 0.05 bc	6.95 ± 0.91 bcde	0.71 ± 0.02 ab
	AV.	**14.69 ± 1.32 AB**	**-1.32 ± 0.02 B**	**-0.74 ± 0.04 B**	**5.89 ± 0.48 BC**	**77.29 ± 1.20 A**
HU-l	OCH	8.02 ± 0.78 a	-1.21 ± 0.06 bcd	-0.94 ± 0.02 ab	7.19 ± 0.94 cde	0.89 ± 0.01 e
	JUG	12.98 ± 1.63 abcd	-1.82 ± 0.06 f	-1.27 ± 0.06 a	8.24 ± 0.52 de	0.72 ± 0.03 abc
	AV.	**10.5 ± 1.19 A**	**-1.51 ± 0.11 A**	**-1.11 ± 0.06 A**	**7.72 ± 0.54 D**	**80.44 ± 1.47 AB**
DO	RAN	27.96 ± 1.21 cdefg	-0.96 ± 0.07 ab	-0.58 ± 0.03 c	3.67 ± 0.52 ab	0.86 ± 0.02 de
	RAP	44.08 ± 2.73 g	-1.02 ± 0.09 abc	-0.65 ± 0.06 bc	2.30 ± 0.37 a	0.85 ± 0.02 de
	ROM	26.59 ± 9.34 bcdef	-1.14 ± 0.07 abcd	-0.80 ± 0.04 bc	4.95 ± 0.48 abcd	0.83 ± 0.01 de
	AV.	**32.88 ± 3.70 C**	**-1.04 ± 0.05 C**	**-0.68 ± 0.03 B**	**3.64 ± 0.38 A**	**84.67 ± 1.20 B**

746

747 **Table S3**. Leaf-related morphological and gas exchange traits for all accessions. Leaf

748 mass per area (*LMA*), leaf area per leaf (*LA*$_1$), net photosynthesis (*A*$_N$) and stomatal

749 conductance (*g*$_s$). For species, values are averages with S.E. (*n*=3-5) and letters denote

750 ANOVA differences. The averages per climatic group are shown in bold, with S.E. and

751 considering all the replicates per species. Capital letters correspond to nested ANOVA

752 differences among climatic groups (species nested within climatic group). Both

753 ANOVAs have been performed with Tukey *post-hoc* test.

Climatic group	Species code	LMA	LA$_1$	A$_N$	g$_s$
		g m^{-2}	cm^2	µmol CO$_2$ m^{-2} s^{-1}	mol H$_2$O m^{-2} s^{-1}
AR	SIT	45.11 ± 2.74 a	28.26 ± 8.24 a	15.19 ± 1.13 ab	0.229 ± 0.024 abc
	LYC	46.66 ± 2.3 ab	27.61 ± 4.64 a	22.23 ± 3.69 b	0.405 ± 0.142 c
	PEN	57.61 ± 4.45 abcd	47.12 ± 9.5 abcd	16.98 ± 1.57 ab	0.217 ± 0.031 abc
	PER	58.83 ± 3.04 abcd	40.8 ± 3.38 abc	21.98 ± 2.34 b	0.262 ± 0.049 abc
	AV.	**52.45 ± 2.13 A**	**36.23 ± 3.59 A**	**18.91 ± 1.26 B**	**0.263 ± 0.030 B**
SA	ARC	62.78 ± 2.42 abcde	29.28 ± 1.39 a	23.13 ± 3.1 b	0.263 ± 0.042 abc
	PIM	53.92 ± 0.63 abc	19.67 ± 1.89 a	19.57 ± 2.15 b	0.366 ± 0.069 bc
	GAL	70.81 ± 10.4 bcdef	34.43 ± 3.39 ab	15.38 ± 2.29 ab	0.285 ± 0.042 abc
	CHE	59.76 ± 0.64 abcd	12.73 ± 0.83 a	16.51 ± 1.55 ab	0.236 ± 0.01 abc
	AV.	**61.82 ± 2.83 AB**	**24.03 ± 2.15 A**	**18.65 ± 1.28 B**	**0.288 ± 0.024 B**
HU-s	NEO	52.79 ± 4.21 abc	35.58 ± 4.84 abc	22.93 ± 2.1 b	0.248 ± 0.031 abc
	CHM	60.03 ± 7.08 abcd	23.99 ± 1.42 a	19.99 ± 2.7 b	0.243 ± 0.031 abc
	CER	88.8 ± 3.42 f	31.64 ± 3.34 ab	19.23 ± 2.03 b	0.306 ± 0.029 bc
	AV.	**66.09 ± 5.18 BC**	**30.80 ± 2.44 A**	**20.72 ± 1.29 B**	**0.266 ± 0.018 B**
HU-l	OCH	71.48 ± 1.62 cdef	73.87 ± 5.3 cde	16.31 ± 1.44 ab	0.184 ± 0.026 ab
	JUG	85.35 ± 1.75 ef	81.3 ± 15.48 de	7.33 ± 0.88 a	0.091 ± 0.017 a
	AV.	**76.68 ± 2.78 CD**	**76.66 ± 6.13 B**	**12.94 ± 1.88 A**	**0.149 ± 0.024 A**
DO	RAN	88.8 ± 6.73 f	107.14 ± 18.96 e	21.6 ± 1.62 b	0.224 ± 0.031 abc
	RAP	70.71 ± 5.34 bcdef	70.6 ± 8.92 bcde	16.94 ± 1.44 ab	0.244 ± 0.025 abc
	ROM	79.47 ± 3.94 def	101.53 ± 7.58 e	18.78 ± 1.02 b	0.316 ± 0.022 bc
	AV.	**79.66 ± 3.52 D**	**93.09 ± 8.11 B**	**19.11 ± 0.9 B**	**0.262 ± 0.017 B**

754

755 **Table S4.** Compilation of data in this study and in literature, represented in Figs. 3A

756 and 4A-H. Literature data from Brodribb et al. (2007), Plant Physiol. 144, 1890-1898;

757 Flexas et al. (2013), J. Exp. Bot. 64, 3965-3981; Sack and Scoffoni (2013), New Phytol.

758 198, 983-1000; Sack et al. (2013), J. Exp. Bot. 64, 4053-4080; Price & Weitz (2014),

759 BMC Plant Biol. 14, 234; Scoffoni and Sack (2017), J. Exp. Bot. 68, 4479-4496.

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