Effects of root phenotypic changes on the deep-rooting process of *Populus euphratica* seedlings under drought stresses

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Background. Deep roots are critical for the survival of *Populus euphratica* seedlings on floodplains in arid regions where they easily suffer drought stress. Drought typically suppresses root growth, but these seedlings can adjust phenotypically in terms of root-shoot allocation, root architecture, and morphology, thus promoting deep rooting. However, the *P. euphratica* seedling deep-rooting strategy achieved by these root phenotypic changes under drought remain unknown.

Methods. We quantified deep rooting capacity as the ratio of taproot length to plant biomass (RRD), which is controlled by root mass fraction (RMF), taproot mass fraction (TRMF), and specific taproot length (STRL). We recorded phenotypic changes in one-year-old *P. euphratica* seedlings under control/moderate/severe drought stress conditions and assessed the effects of RMF, TRMF, and STRL on RRD.

Results. Drought conditions significantly decreased root depth but substantially increased RRD via exerting positive effects on TRMF, RMF, and STRL. Under moderate drought conditions, TRMF contributed 55% to RRD variation, which was greater than 27% for RMF and 18% for STRL. Under severe drought conditions, the contribution of RMF increased to 37%, nearly equal to the 41% for TRMF. The contribution of STRL slightly increased to 22%.

Conclusion. These results suggest that adjustments in root architecture and root-shoot allocation were predominantly responsible for deep rooting in *P. euphratica* seedlings under drought conditions, while the role of morphological changes was marginal. Moreover, *P. euphratica* seedlings rely more on adjusting their root architecture to maintain root depth under moderate drought conditions but root-shoot allocation responds more strongly under severe drought conditions, to the point where it plays as important a role as root architecture on deep rooting.

1   **Effects of root phenotypic changes on the deep-rooting**

2   **process of *Populus euphratica* seedlings under drought**

3   **stresses**

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12

13 **Abstract:**

14 **Background.** Deep roots are critical for the survival of *Populus euphratica* seedlings on

15 floodplains in arid regions where they easily suffer drought stress. Drought typically suppresses

16 root growth, but these seedlings can adjust phenotypically in terms of root-shoot allocation, root

17 architecture, and morphology, thus promoting deep rooting. However, the *P. euphratica* seedling

18 deep-rooting strategy achieved by these root phenotypic changes under drought remain unknown.

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20 (RRD), which is controlled by root mass fraction (RMF), taproot mass fraction (TRMF), and

21 specific taproot length (STRL). We recorded phenotypic changes in one-year-old *P. euphratica*

22 seedlings under control/moderate/severe drought stress conditions and assessed the effects of

23 RMF, TRMF, and STRL on RRD.

24 **Results.** Drought conditions significantly decreased root depth but substantially increased RRD

25 via exerting positive effects on TRMF, RMF, and STRL. Under moderate drought conditions,

26 TRMF contributed 55% to RRD variation, which was greater than 27% for RMF and 18% for

27 STRL. Under severe drought conditions, the contribution of RMF increased to 37%, nearly equal

28 to the 41% for TRMF. The contribution of STRL slightly increased to 22%.

29 **Conclusion.** These results suggest that adjustments in root architecture and root-shoot allocation

30 were predominantly responsible for deep rooting in *P. euphratica* seedlings under drought

31 conditions, while the role of morphological changes was marginal. Moreover, *P. euphratica*

32 seedlings rely more on adjusting their root architecture to maintain root depth under moderate

33 drought conditions but root-shoot allocation responds more strongly under severe drought

34 conditions, to the point where it plays as important a role as root architecture on deep rooting.

Introduction

35

36 The root system is the main plant organ that acquires below-ground resources. To adapt to the

37 inherent scarcity and heterogeneity of below-ground resources in nature, plants can adjust root

38 phenotype on different integrated levels: they can change their relative investment of biomass in

39 shoots and roots on an individual-level, they can adjust root system architecture on an organ-level,

40 or alter root morphology on a module level (see Fig. 1). Most likely, plants adjust their roots on

41 all three levels. However, different environmental stresses may result in different degrees of root

42 phenotypic adjustments, resulting in different functional impact intensities for plants under

43 environmental stress. For instance, Freschet, Swart & Cornelissen (2015) found that root mass

44 fraction (RMF) responded more strongly than specific root length (SRL) to nutrient deficiency,

45 thus suggesting that an increased root-shoot allocation was emphasized by plants under nutrient

46 stress in order to favor an increase in fine root length versus root morphological changes.

47 Nevertheless, root architecture changes are a basic and generic way to improving fine-root function

48 efficacy (Lynch, 1995; McCormack et al., 2017). Increasing the density and length of the distal

49 roots can increase root absorptive area (Kong et al., 2014). Additionally, different root patterns

50 can influence plant uptake efficiency in heterogeneous resource environments (Lynch, 2005) and

51 can affect the ability of root systems to capture relatively immobile versus mobile soil resources

52 (Fitter, 1987). However, few studies have focused on the relative functional importance of the

53 different phenotypic changes in stressed plants, especially the relative role of root architectural

54 changes (Weemstra et al., 2016).

55 *Populus euphratica* Oliv. (Salicaceae) is a dioecious riparian tree species found

56 discontinuously within the continental-arid climate region in Central Asia (Browicz, 1977; Wang,

57 1996), which forms monospecific stands along continental rivers. This poplar is an obligate

58 phreatophyte which possesses a root system that continuously contacts the groundwater or the soil

59 water-saturated zone (Zhu et al., 2009), meaning that its growth and survival depends highly on

60 locating and acquiring groundwater (Gries et al., 2003). However, the plant's seedlings cannot

61 reach groundwater during the early stages, meaning that under harsh environments in arid regions,

62   *P. euphratica* only can propagate generatively in freshly deposited floodplain soils from May to

63   August (Cao et al., 2012). Even so, the optimal soil conditions in the floodplain for seedling

64   germination and growth only exist for a short time, as the surface soil post-flood rapidly becomes

65   increasingly dry and salty due to evaporation. The rapid onset of winter also shortens the growth

66   period for the seedlings. As a result, *P. euphratica* seedlings must establish a deep root system

67   during the early stage, as only seedlings with deep roots can secure water uptake during the dry

68   period and survive the following year (Zerbe & Thevs, 2011). According to Thevs et al. (2008),

69   Wiehle et al. (2009), and our previous field investigations, *P. euphratica* seedlings established in

70   floodplains possess deep root systems very asymmetrical in size to the shoots. Therefore, deep

71   rooting is considered a key process for early *P. euphratica* seedlings for survival and establishment

72   in an inconsistent riparian environment (Hukin et al., 2005; Wang et al., 2015).

73   In semi-arid regions, *P. euphratica* seedlings are, in general, naturally subjected to drought

74   stress, especially during the dry seasons which follow the annual spring floods (Stella et al., 2010;

75   Thevs et al., 2008). This weakens biomass accumulation and also limits root growth into the deep

76   soil. Accordingly, *P. euphratica* seedlings are able to make necessary phenotypic adjustments

77   under drought stress, including allocating more biomass to the root system (Wang et al., 2015),

78   changing the root architecture, and increasing the SRL (Lü et al., 2015). All of these are believed

79   to result in increased seedling root depth. However, as previously outlined, different levels of

80   phenotypic changes may have different functional contributions, and therefore we remain ignorant

81   regarding the exact effects of root phenotypic changes on *P. euphratica* seedling root depth under

82   drought conditions. Answering this question would aid in our understanding of the drought

83   adaptive strategy of *P. euphratica* and other similar deep-rooted plants in the arid regions.

84   In this study, we aimed to answer the following questions: (1) How do *P. euphratica* seedling

85   roots change phenotypically on individual-, organ- and modular- levels under drought stress? (2)

86   Which level of root phenotypic adjustment (root-shoot allocation, root architecture, or

87   morphology) plays a leading role in facilitating the deep rooting of the drought-stressed seedlings?

88   (3) Does the relative contribution of these different root phenotypic adjustments on deep rooting

89   vary with drought intensity? We therefore recorded root phenotypic changes in one-year-old *P.*

90   *euphratica* seedlings subjected to different drought conditions, focusing on root-shoot allocation,

91   root system architectural traits, and the morphological traits of the taproot, lateral roots, and distal

92   roots, and then assessed their relative functional contributions to deep rooting.

94 **Materials & Methods**

95 **Experimental design**

96 *Nursery phase*

97 This experiment was conducted at the State Forest Farm located in Ejin Banner, Inner Mongolia,

98 China. All seeds were collected randomly in a mature natural forest dominated by *P. euphratica*

99 (41°57 51.3″ N, 101°05 06.0″ E) along the Ejin River. Planted pots were 20 liters in volume, 40

100 cm in depth, and filled with 16 kg (dry weight) of substrate – a 4/6 (v/v) mixture of peat and sand.

101 A slow-release fertilizer (4 g L^{-1} Osmocote 16:9:12 NPK and trace elements, product code: 8840)

102 was pre-mixed within the substrate. From May to June 2016, countless *P. euphratica* seeds were

103 sown and germinated in 90 plastic pots placed in a greenhouse. After a month of growth with

104 normal management, three seedlings per pot, averaging 2.0 ± 0.5 cm in height with 4 to 6 leaves,

105 were selected and transferred to the open-air nursery. After two weeks of acclimation, only a single

106 healthy seedling per pot, averaging 7.0 ± 1.5 cm in height and 0.9 ± 0.2 mm in ground diameter,

107 was kept.

108 *Experimental treatments*

109 This experiment was conducted over a period of 60 days from July to September 2016, during

110 which the daily minimum and maximum temperatures averaged 19 °C and 34 °C, respectively.

111 The daily maximum temperature ranged between 39-44 °C. The experiment included three water

112 treatments: 70-80% of field capacity [(optimal water content (OW)], 50-60% of field capacity

113 [moderate drought stress (MD)], and 30-40% of field capacity [(severe drought stress (SD)]. Each

114 treatment was replicated 30 times. The seedlings were randomly assigned to these three treatments.

115 Because of the high evapotranspiration during summer day in Ejin, soil water was supplemented

116 every day according to weight in order to control water content. Prior to supplementation, the pots

117 were rearranged to avoid the effects of environmental heterogeneity. Plastic film was used to cover

118 the nursery to avoid rainfall, pests, and diseases. In the end, owing to the death of five seedlings

119 subjected to the severe drought treatment, a total of 85 seedlings were measured.

120 *Growth measurements and destructive sampling*

121   Intact root systems were cleaned of soil with a gentle water jet while a sieve was used to collect

122   any root fragments detached from the system during the process. The cleaned root systems were

123   then floated on water in a transparent tray and imaged using an Epson Expression Perfection V850

124   Pro Scanner with 800 dpi resolution. Adobe Photoshop CS6 software was used to reduce image

125   noise and black margins. Image analysis software (Win-RhIZO 2013a Pro Instruments Inc.,

126   Québec, Canada) was used to analyze images and estimate the length of total, lateral, and distal

127   roots, the average diameter of the total roots, the number of lateral roots, as well as the external

128   path length (p_e) and magnitude (μ) and altitude (a) (see Table 1). Lateral roots were defined as root

129   segments connected to the taproot with a root order greater than three so as to confirm that the root

130   in question serves conducting and foraging functions. The taproot was then severed from the root

131   system with scissors to measure length and dry mass. Meanwhile, three intact lateral root branch

132   segments were selected as random samples for scanning in order to estimate the average length

133   and diameter of the distal roots. Subsequently, a scalpel was used to dissect all distal fine roots in

134   order to measure dry mass, with the aim that the length of the selected branches exceeded 10 cm.

135   If it was impossible to meet that criteria, the whole root system was measured. The dry weights of

136   the taproot, sampled distal roots, and the other root parts were obtained by air drying plant matter

137   in an oven at 72 °C for 60 h. Total root biomass, specific root length, biomass-related variables,

138   and two topological indices were calculated using these dry weights (see Table 1).

139

140   **Introduction of calculated root variables**

141   **How to represent root architectural adjustments**

142   Like many other studies, we quantified root to shoot allocation as the fraction of biomass invested

143   in the roots (RMF; see Table 1 for definition), while we interpreted that taproot morphological

144   adjustments could be expressed as specific taproot length (STRL; see Table 1 for explanation).

145   It is difficult to fully measure root architecture, and previous studies commonly used topology

146   to describe the altered branching patterns indicative of changes in root architecture (Fitter, 1987;

147   Harper, Jones & Sackville, 1991; Lynch, 1995). Here, we not only use topological (Fitter, 1987;

148 Glimskär, 2000) and dichotomous branching indices (Šmilauerová & Šmilauer, 2002), which are

149 commonly applied to characterize topology (see Table 1), but also used taproot mass fraction

150 (TRMF; see Table 1) to characterize root architectural changes.

151   Adopting TRMF was a necessity since it is a mass proxy which can build a relationship with

152 other biomass-related variables such as RMF and make root architecture comparisons possible.

153 Also, it is reasonable to use the proportion of biomass in certain root segments to that in the total

154 roots to represent root architecture, especially the taproot mass fraction (i.e., TRMF). This is

155 because the root branching pattern simply refers to the growth relationship among different root

156 segments, and this relationship can also reflected using biomass proportion. In particular, an

157 extreme herringbone-like branching pattern has been found to be primarily confined to the main

158 axis (Fitter et al., 1991) – that is, possessing the largest proportion of taproot biomass. While not

159 the main aim of this study, the correlation between TRMF and topological and dichotomous

160 branching indices were also examined.

161 **How to represent deep rooting capacity**

162 To understand changes to plant root depth with environmental conditions, distinguishing between

163 absolute and relative plant dimensions is significant because while water deficit strongly

164 influences whole plant size in a negative manner, this commonly obscures the underlying deep-

165 rooting process (Schenk & Jackson, 2002). Therefore, following the method of Ryser & Lambers

166 (1995) who used root length ratio (root length per total plant biomass) to express the relative length

167 of the absorptive roots, i.e., root uptake capacity, we adopted the absolute root depth to total plant

168 biomass ratio to express relative root depth, i.e., deep-rooting capacity. *P. euphratica* has an

169 obvious taproot that determines root system depth, so here we used taproot length as the measure

170 of absolute root depth in order to measure relative root depth (RRD; see Table 1). RRD is a product

171 of RMF, TRMF, and STRL, with the three variables related as follows:

172 $$RRD = RMF \times TRMF \times STRL$$

173 **Data analyses**

174 Differences observed in biomass allocation as well as architectural and morphological variables

175   among the three drought treatments were tested using one-way ANOVA (Welch's F test). After

176   that, variations of statistical significance were further subjected to *post hoc* pairwise analysis by

177   applying *t*-tests with Bonferroni corrections or Games-Howell tests if the homogeneity of

178   variances was not assumed. A *P*<0.05 was considered significant. The dependence between TRMF

179   and TI or TRMF and DBI was determined by Pearson's correlation analysis. Statistical analysis

180   was performed with SPSS (SPSS Inc., version 19).

181   We calculated the relative contributions of variance in RMF, TRMF, and STRL to RRD,

182   referencing the variance partitioning method of Rees et al. (2010) and Freschet et al. (2015). Given

183   that $\text{RRD} = \text{RMF} \times \text{TRMF} \times \text{STRL}$, our calculation can be expressed as:

184    $\text{rrd} = \text{rmf} + \text{trmf} + \text{strl}$, where lowercase characters are used to indicate $\log_e$-transformed

185   variables (e.g., $\text{rrd} = \ln(\text{RRD})$). Consequently, the variance decomposition of rrd, for instance,

186   can be expressed as follows:

187
$$\begin{aligned}
\text{Var(rrd)} &= \text{Var(rmf)} + \text{Cov(rmf,trmf)} + \text{Cov(rmf, strl)} + \text{Var(trmf)} + \text{Cov(rmf, trmf)} + \text{Cov(trmf, strl)} + \text{Var(strl)} + \text{Cov(rmf, strl)} + \text{Cov(trmf, strl)}
\end{aligned}$$

188   Following this, as a sample, the contribution of variation in trmf to the variation in rrd can be

189   written as:

190
$$\text{Cont(trmf)} = \frac{[\text{Var(trmf)} + \text{Cov(rmf, trmf)} + \text{Cov(trmf, strl)}]}{\text{Var(rrd)}}$$

191   where Var is the variance and Cov is the covariance. This variance partitioning was only performed

192   when substantial variation (i.e., ≥15%) in rrd was observed across treatments, so as to avoid

193   meaningless results.

194

195   **Results**

196   **Drought-induced phenotypic changes in biomass, root morphology, and architecture**

197   *P. euphratica* seedling growth was inhibited by drought stress (Table 3). Drought conditions

198   brought upon a dramatic decrease in total root length and the length of the taproot, lateral roots,

199   and distal roots. However, when examining response to differing drought intensities, neither

200   taproot length nor taproot biomass displayed a consistent declining trend with increasing drought

201   intensity. Root system diameter did not change significantly under drought conditions, but distal

202   root diameter increased and lateral root diameter decreased significantly. Similarly, the SRL of the

203   whole root system was not changed by drought, but the SRL of the distal roots – the root

204   components more actively involved in water uptake – significantly decreased under drought

205   conditions.

206

207   *P. euphratica* seedlings showed a high root system branching pattern plasticity under different

208   drought stresses. DBI and TI measures the degree to which a root is perfectly herringbone (DBI

209   and TI equal to 1) or presents dichotomous branching (DBI equal to 0, TI close to 0.5). DBI and

210   TI values were significantly different in plants undergoing different drought treatments, with the

211   highest values in the SD group and the lowest in the OW. The minimum to maximum values

212   presented by the total samples was 0.650 to 0.844 for TI and 0.032 to 0.392 for DBI. Lateral root

213   branching density, a simple but direct trait reflecting root branching, showed a markedly decreased

214   trend from OW to SD groups.

215

216   **Different levels of root phenotypic changes are affected differently by drought**

217   Drought had a significant positive effect on RRD, but this increase was not proportionate, with

218   RRD variance in the severe drought group almost three times greater than in the moderate drought

219   group. Regarding the three indices representing different levels of root phenotypic changes, RMF

220   and TRMF increased markedly with increasing drought severity, while STRL did not significantly

221   increase under drought conditions. TRMF had significant increases in plants subjected to either

222   moderate or severe drought conditions, but RMF only increased significantly in plants subjected

223   to severe drought.

224

225   **Relative contribution of different root phenotypic changes to deep rooting**

226   These results indicated that drought stress had a positive effect on RRD via significant positive

227   effects on TRMF and RMF as well as a slightly positive effect on STRL. Generally, TRMF and

228   RMF contributed over 75% of the variation in RRD, with STRL contributing just 20%. Moreover,

229   whether examining the variation in RRD between MD and OW or between SD and OW groups, it

230   was always TRMF presenting the largest relative contribution (Fig. 3). Interestingly, the relative

231   contributions of RMF, TRMF, and STRL to RRD variation changed with drought intensity.

232   Variance partitioning results showed that TRMF contributed 55% of RRD variation between MD

233   and OW groups, which was larger than the 27% contributed by RMF and 18% by STRL, but under

234   severe drought stress, the relative contribution of RMF to RRD variation between SD and OW

235   increased to 37%, that of STRL slightly increased to 22%, and that of TRMF decreased to 41%.

236   In addition, the increase in RRD between SD and MD groups was more attributable to RMF

237   changes (41%) than TRMF (36%).

238

239   **Discussion**

240   **Root adaptive responses in terms of allocation, morphology, and architecture to drought**

241   **stress**

242   One of the most basic and general way for plants to adapt to a shortage of below-ground resources

243   is to maximize fine root area (e.g., decreased RD and increased SRL under drought stress) (Fitter,

244   1985; Cortina et al., 2008; Olmo, Lopez-Iglesias & Villar, 2014). However, in our results, the RD

245   and SRL of whole roots exhibited no significant change, with even the RD of distal roots increasing

246   and SRL decreasing under drought conditions (Table 3). Generally, a smaller RD under drought

247   stress is advantageous in that it conveys higher resistance to root embolism (Alameda & Villar,

248   2012) through smaller xylem vessel diameter (Fitter, 1987), while a larger SRL probably is meant

249   to commit limited carbohydrate supplies to extensional growth (Trubat, Cortin & Vilagrosa, 2006).

250   The unusual results observed in this study were likely due to the fact that a smaller SRL, being

251   positively correlated with root life span and respiration rate (McCormack et al., 2012), allowed *P.*

252   *euphratica* seedlings to save considerable energy in dry soil through a low root turnover rate.

253   Moreover, thicker fine roots would be able to penetrate into the more compacted soils imposed by

254   soil drying (Bengough et al., 2005). In addition, the thicker distal roots of *P. euphratica* seedlings

255 possess higher drought resistance, so as to preserve vitality in the topsoil of arid-region floodplains

256 with widely fluctuating soil water availability (Leon et al., 2011).

257 　　　Plants mostly elongate root internode lengths to adapt to drought environments (Nicotra &

258 Westoby, 2002) because increasing root internode length contributes to root volume extension

259 (Fitter & Stickland, 1992). However, in our results, average root length did not significantly

260 change and lateral root length clearly decreased under drought stress (Table 3). Ecologically,

261 floodplain soil possesses a high infiltration rate caused by a sandy layer several meters in depth

262 immediately below the 10-50 cm deep surface clay soil layer formed by floodwater sedimentation

263 (Thevs et al., 2008). As such, drought-stressed *P. euphratica* seedlings need to root downward

264 more than in other environments into deep soil in order to take up water. In such a circumstance,

265 shortening most of their lateral roots can avoid inefficient investments in horizontal soil zone

266 exploration (Padilla & Pugnaire, 2007; Bauerle et al., 2008).

267 　　　Root architecture plays a major role in determining root resource-uptake efficiency (Fitter,

268 1987; Lynch, 2005). This multidimensional root feature is generally described by measuring root

269 topology (Harper et al., 1991) or branching density/intensity (Kong et al., 2014). Our results show

270 that lateral root branching density, a simple but clear index of root architectural change, was

271 reduced under drought conditions (Table 4). From a functional point of view, the sparse lateral

272 root branching displayed by *P. euphratica* seedlings conserves the high metabolic cost of root

273 construction and maintenance, which can exceed 50% of daily photosynthesis (Lambers, Atkin &

274 Millenaar, 2002). It may also reduce the competition for water among the roots of an individual

275 plant (Fitter et al., 1991; Taub & Goldberg, 1996), which effectively increases the uptake

276 efficiency per unit of lateral root length (Postma, Dathe & Lynch, 2014).

277 　　　Topology is an important aspect of root architectural change that can be quantified by the

278 topological index (TI) and dichotomous branching index (DBI) metrics. Our results indicate that

279 *P. euphratica* seedlings tended to create a herringbone-like branching pattern under drought

280 conditions. This finding is in line with most modeling and empirical studies in droughted plants

281 (Fitter, 1991; Taub & Goldberg, 1996). Herringbone-like root systems possess greater exploration

282   efficiency, a significant factor in allowing *P. euphratica* seedlings to reach water-rich deep soils

283   quickly (Ho et al., 2005; Paula & Pausas, 2011). It is also worth noting that TI is not often used to

284   compare root systems with great distinct magnitudes (μ) (Šmilauerová & Šmilauer, 2002), with

285   DBI being more scale-independent than TI (scale here refers to root magnitude). However, in this

286   study, we were able to compare the TI values of individuals with differing root magnitudes

287   (Glimskär, 2000) because the theoretical ranges of TI measured by minimum magnitude and

288   measured by maximum magnitude were almost the same, at 0.37-1 and 0.31-1, respectively.

289   **The deep-rooting strategy of *P. euphratica* seedlings under drought conditions**

290   **Changes to root depth under drought**

291   The four-month-old *P. euphratica* seedlings grown in our experiment ultimately only had total

292   biomasses ranging from about 0.2 to 0.5 g (Table 2), but they developed taproots which were 26

293   to 35 cm long (Table 3). This indicates that despite a low biomass formation rate, *P. euphratica*

294   seedlings have a great capability to root deeply. The miniscule biomass accumulation by the first-

295   year seedlings may be caused by its extremely small and light seeds, weighing only 0.1-0.2 g per

296   thousand seeds. A similar ontogeny is also found in other studies of first-year riparian seedlings.

297   A drought experiment conducted by Wang (2015) showed that *P. euphratica* seedlings sown in

298   April had about 1 g dry mass and over 22 cm taproot length by the end of July. Likewise, a study

299   of riparian tree seedlings (family Salicaceae) by Stella et al. (2010) demonstrated that three-month-

300   old cottonwood seedlings (*P. fremontii*) had 0.3 g dry weight with roots over 20 cm in depth, and

301   that three-month-old *Salix exigua* and *S. gooddingii* seedling developed root depths exceeding 25

302   cm and 40 cm, respectively, despite dry weights of only 0.22 g and 0.4 g. Clearly, the tiny but

303   deep-rooting seedling phenotype seems common in riparian tree species growing in arid regions.

304   Changes to plant root depth under drought stress are controlled by two processes (Sultan,

305   2000). On the one hand, drought stress weakens photosynthesis, dwindles the accumulated

306   biomass and body size, and thereby shortens the root depth. On the other hand, the root depth is

307   influenced by different drought-induced root phenotypic responses. In this study, the root depth of

308   *P. euphratica* seedlings decreased significantly (Table 3) while the relative root depth (RRD)

309   increased significantly under drought conditions (Table 5), indicating that the limitation in growth

310   caused by drought had an overwhelming effect on root depth but *P. euphratica* seedlings

311   compensated by increasing relative root depth. Furthermore, RMF, TRMF, and STRL metrics all

312   showed increases with intensifying drought stress. Therefore, based on the relationship of these

313   three metrics with RRD, three different levels of root phenotypic changes all had positive effects

314   on root depth under drought stress.

315   Finally, TRMF was positively correlated with TI and DBI ($R^2 > 0.6$; Fig. 3), indicating that

316   TRMF can serve as a good proxy of TI and DBI. Therefore, the usage of TRMF to reflect root

317   architectural changes in this study was feasible.

318

319   Relative contribution of the three root phenotypic changes to deep rooting

320   Our results indicated that changes to root architecture and root-shoot allocation in *P. euphratica*

321   seedlings dominated for achieving deep rooting under drought conditions, while the role of

322   morphological changes was marginal (Fig. 3). This supports the perspective of Freschet et al.

323   (2015) that root-shoot allocation was more important than root morphological changes for plant

324   adaptations to changing environmental conditions.

325   The relative contributions of changes in root allocation, architecture, and morphology were

326   altered under different drought intensities (Fig. 3). Under MD, root architectural changes played a

327   decisive role (contribution over 50%) on increasing relative root depth. This is likely because the

328   negative influences brought by root architectural changes were more acceptable than those brought

329   by root-shoot allocation for *P. euphratica* seedlings under MD. Increased root-shoot allocation

330   would have decreased photosynthetic capacity and accumulation of photosynthates (Muller et al.,

331   2011), while root architecture changes under drought conditions would only weaken the horizontal

332   and surface soil exploration capacity (Thevs et al., 2008).

333   However, under SD, the root-shoot allocation response was stronger than before (Table 1),

334   and its relative contribution to deep rooting became as nearly important as that of root architectural

335   changes (Fig. 2). The variation of RRD from SD to MD is about three times that of the variation

336   from OW to MD. Changes in root architecture seems to be insufficient for *P. euphratica* seedlings

337   to root deeply under severe drought conditions. From a functional view, it was difficult to make

338   the seedlings acquire adequate water to maintain metabolic processes during increased drought

339   stress conditions. Consequently, the seedlings would rely more on allocating biomass to roots,

340   which was conductive to minimizing water loss through shoot transpiration and enhancing deep

341   rooting potential (Brunner et al., 2015). Moreover, the phenomenon that root-shoot allocation

342   responds significantly only to severe environmental stresses has been widely reported in many

343   plants (Poorter et al., 2012), including *P. euphratica* seedlings (Bogeat-Triboulot et al., 2007). A

344   general explanation is plants maintain their aboveground growth as long as possible under

345   moderate soil environmental stress (Padilla et al., 2009; Poorter et al., 2012), but if plants can

346   maintain shoot growth under moderate stress is still unclear. Our results indicate that plants are

347   able to adapt to moderate drought stress mainly via phenotypic adjustments within their root

348   systems. Furthermore, our study revealed a practical implication for breeding *P. euphratica*

349   seedlings. To promote the survival of container seedlings transplanted in the field, it is a good idea

350   to breed the seedlings under moderate drought stress before transplantation, in order to promote

351   deeper and steeper root systems while minimally affecting size.

352   In this study, STRL did not significantly increase under drought stress and always maintained

353   relatively slight contributions to deep rooting regardless of drought intensity (Table 3), although

354   taproot stretching seems to be an efficient way to increase root depth. The potential negative effects

355   of increased STRL on taproot function may account for this result. SRL is determined negatively

356   by the root diameter and root tissue mass density (Nicotra & Westoby, 2002), that is, increased

357   STRL means decreased taproot diameter or tissue density. This negatively affects taproot

358   conduction, anchorage, and penetration, which are all essential functions for droughted seedlings.

359   Our results could raise an assumption that plant root architecture strongly responds to drought

360   conditions before root-shoot allocation does, but as drought severity increases, the root-shoot

361   allocation response catches up. This is based on a perspective that plant root architectural changes

362   at the organ-level are always more economical than at the individual-level for drought adaptation.

363   To confirm this assumption, more functionally different species need to be studied in the future.

364

365   **Conclusion**

366   (1) *P. euphratica* seedlings showed a conservative resource-use strategy in response to drought

367   stress, presenting thicker and shorter distal roots with lower SRL, sparser lateral root

368   branching, and herringbone-like root architectures.

369   (2) The root depth of *P. euphratica* seedlings was strongly constrained by drought, but this effect

370   was alleviated by changes in root-shoot allocation, root architecture, and taproot morphology,

371   resulting in a significant increase in relative root depth.

372   (3) Root architectural changes and root-shoot allocation dominated in order to achieve deep

373   rooting, while the role of taproot morphological changes remained relatively marginal.

374   Interestingly, their relative contributions to deep rooting varied with drought intensity. Under

375   moderate drought conditions, root architectural changes exerted an overwhelming effect on

376   increased relative root depth, but under severe drought, root-shoot allocation and root

377   architecture played equally important roles.

378

379 **Acknowledgements**

386

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530

Figure 1

A sample of increasing root length through the three levels of root phenotypic changes separately.
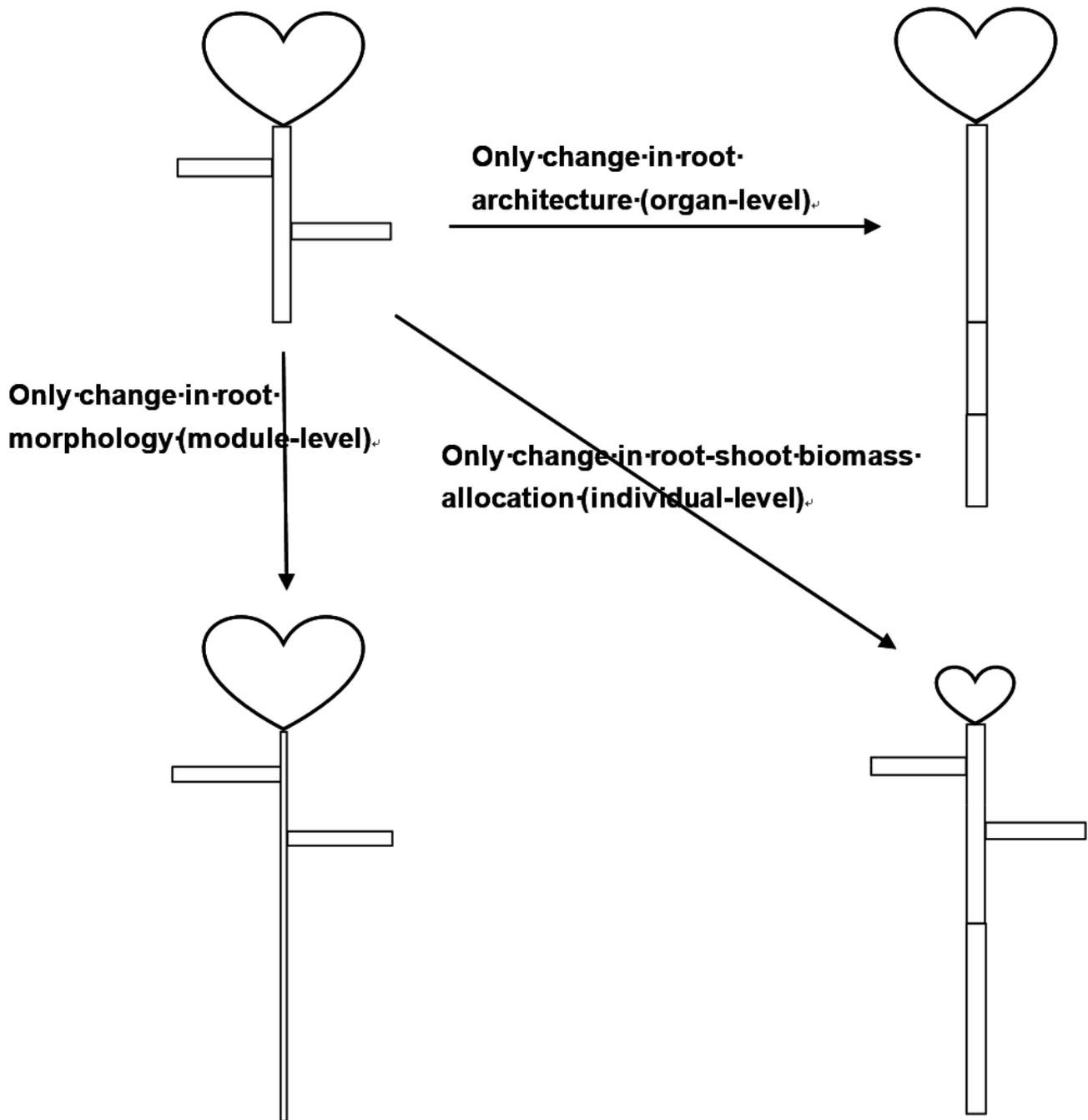
Figure 2

Relative contribution of root-shoot allocation (RMF, light grey bars), morphology (STRL, dark grey bars) and architecture (TRMF, black bars) variables to the total variation in relative root depth (RRD).

From left to right, the first bar represents whole contributions to the variation in RRD between OW and MD, the second bar represents that between OW and SD, and the thrid bar represrents that between MD and SD.
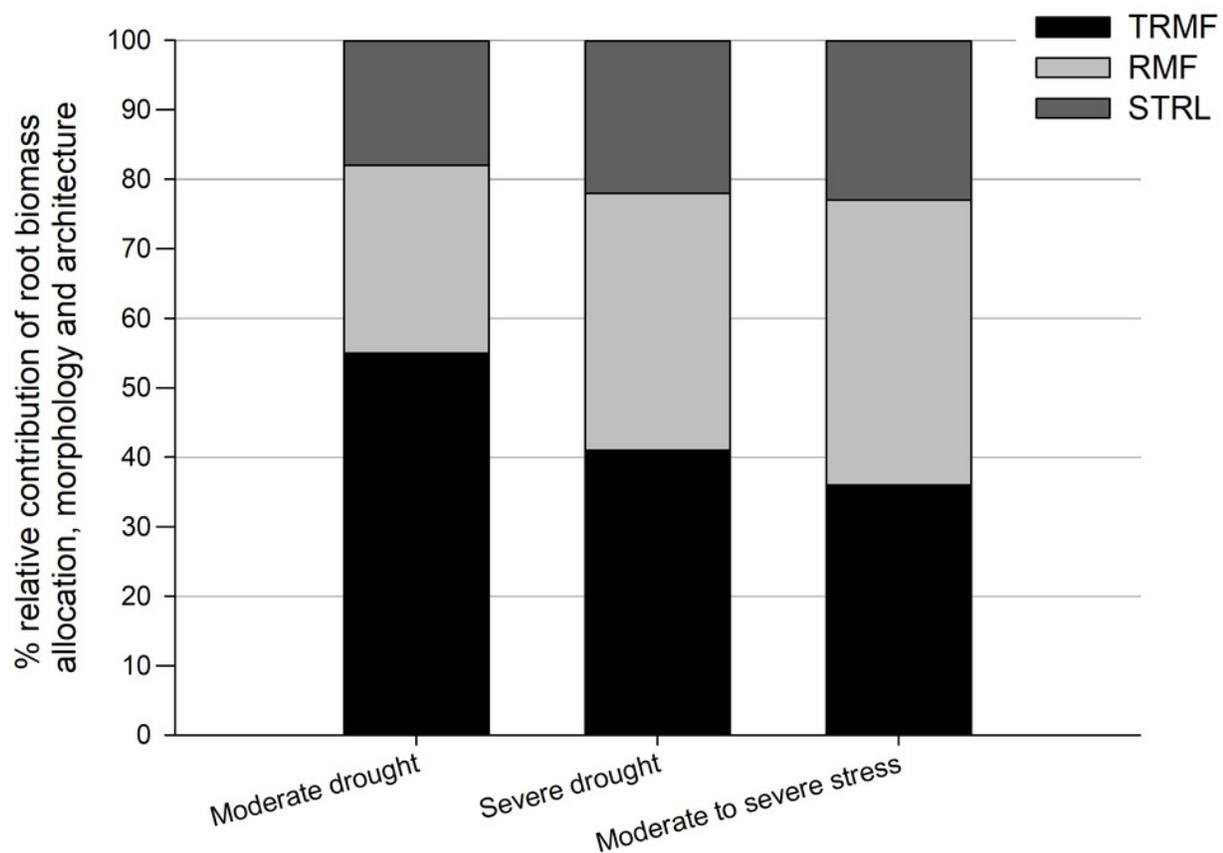
Figure 3

The correlation analysis of TRMF to TPI and of TRMF to DBI
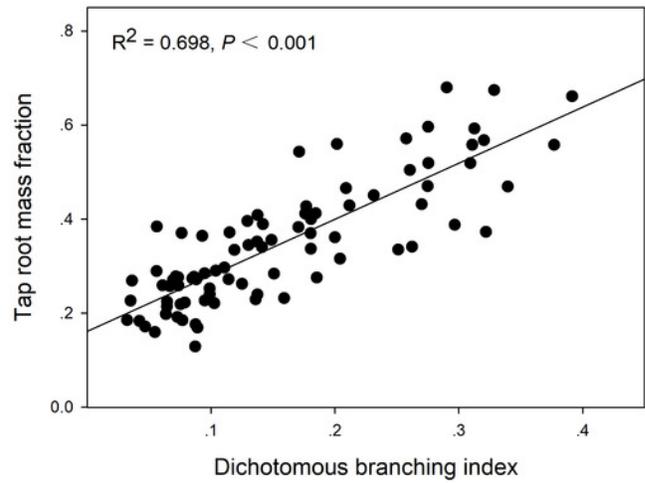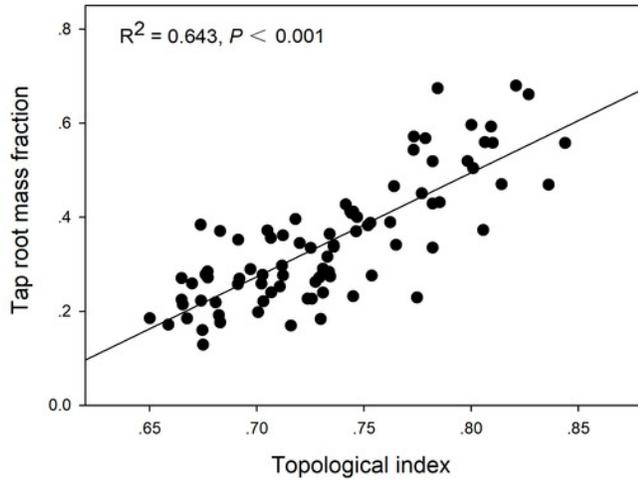
Table 1(on next page)

Calculated root variables and its abbreviations, units, description and functional role

1 **Table 1 Calculated root variables and its abbreviations, units, description and functional role**

Root variables (Abbrev.)	Units	Description	Functional role
Relative root depth *(RRD)*	cm g^{-1}	Taproot length per total plant dry mass	Rooting capacity for deep soil.
Root mass fraction*(RMF)*	g root [g plant]$^{-1}$	the proportion of total plant mass allocated to roots	Total plant resources allocated to root functions (e.g. absorption, transport, foraging, anchoring) (Markesteijn & Poorter, 2009)
Taproot mass fraction *(TRMF)*	g tap root [g root]$^{-1}$	the proportion of total root mass allocated to taproot	Total root resources allocated to the taproot functions.(e.g., anchoring, foraging, transport)
Specific tap root length *(STRL)*	cm g^{-1}	Taproot length per amount of taproot biomass invested	The efficiency of taproot resources used to deep rooting.
Lateral root branching density *(LRBD)*	number cm^{-1}	Lateral roots branching number per unit of primary root length	Potential capacity of exploration and exploitation to horizontal soil resources
Topology Index *(TI)*		TI = log$_{10}$(a)/log$_{10}$(μ); altitude a is number of links in the longest path from base to tips; magnitude μ is number of external links or the number of root tips (Glimskär, 2000)	Both topological indices vary between 0 and 1, with large values indicative of a more herringbone-like root system that are thought to be more efficient at intercepting mobile resources , such as water, by extensive soil exploration, contrasted with dichotomous-like systems that are better at

Dichotomous branching index *(DBI)*	$DBI=[p_e-\min(p_e)]/[\max(p_e)-\min(p_e)]$; p_e is the sum of the number of links in all paths from each external link to the base link; $\max(p_e)$ and $\min(p_e)$ respectively is the theoretical external path length for a system of given magnitude that has a completely herringbone and dichotomous topology, detail mathematical calculation see Šmilauerová & Šmilauer (2002)	acquiring immobile resources, such as phosphorus by intensive soil exploration (Fitter, 1987)

2

Table 2(on next page)

Biomass-related variables of *P. euphratica* seedlings under different drought treatments

Notes: Values are means± standard error (OW: n=25; MD: n=30; SD: n=30). Within a row, means followed by different letters are significantly different (P<0.05). OW, MD and SD refer to optimal water content, moderate drought stress and severe drought stress separately.

1 **Table 2 Biomass-related variables of *P. euphratica* seedlings under different drought**

2 **treatments**

Variables	OW (control)	MD	SD
Total biomass (g)	0.456±0.022 [a]	0.346±0.021 [b]	0.216±0.018 [c]
Above-ground biomass (g)	0.298±0.021 [a]	0.225±0.022 [b]	0.127±0.011 [c]
Below-ground biomass (g)	0.158±0.011 [a]	0.121±0.009 [b]	0.087±0.008 [c]
Taproot biomass (g)	0.043±0.003 [a]	0.032±0.002 [b]	0.030±0.002 [b]

3 Notes: Values are means± standard error (OW: n=25; MD: n=30; SD: n=30). Within a row, means

4 followed by different letters are significantly different (P<0.05). OW, MD and SD refer to optimal

5 water content, moderate drought stress and severe drought stress separately.

6

Table 3(on next page)

Root morphological variables of root system and classified roots under different drought treatments

Notes: Variables are means± standard error (OW: n=25; MD: n=30; SD: n=30). In each row, means followed by different letters are significantly different (P<0.05). OW, MD and SD referring optimal water content, moderate drought stress and severe drought stress separately.

1 **Table 3 Root morphological variables of root system and classified roots under different**

2 **drought treatments**

	Variables	OW(control)	MD	SD
Root system	Total root length (cm)	662±37 [a]	516±44 [b]	393±41 [c]
	Average root length (cm)	0.376±0.048	0.367±0.038	0.236±0.027
	Root diameter (mm)	0.348±0.007	0.357±0.006	0.359±0.009
	SRL (cm/g)	4766±290	4846±357	5141±343
Distal roots	Average distal root length (cm)	0.319±0.122 [a]	0.279±0.191 [b]	0.156±0.057 [c]
	Distal root diameter (mm)	0.278±0.006 [c]	0.302±0.007 [b]	0.337±0.007 [a]
	SDRL(cm/g)	10032±425 [a]	9487±661 [ab]	7843±361 [b]
Lateral roots	Average lateral root length (cm)	5.113±0.324 [a]	4.680±0.333 [ab]	3.765±0.298 [c]
	Lateral root diameter (mm)	0.881±0.035 [a]	0.757±0.034 [b]	0.653±0.029 [c]
Taproot	Taproot length (cm)	35.3±1.1 [a]	27.3±0.8 [b]	26.2±0.7 [b]
	Taproot diameter (mm)	1.60±0.091	1.48±0.093	1.35±0.082

3 Notes: Variables are means± standard error (OW: n=25; MD: n=30; SD: n=30). In each row, means

4 followed by different letters are significantly different ($P<0.05$). OW, MD and SD referring

5 optimal water content, moderate drought stress and severe drought stress separately.

6

Table 4(on next page)

The root branching pattern of *P. euphratica* seedlings under three drought treatments

Notes: Variables are means± standard error (OW: n=25; MD: n=30; SD: n=30). In each row, means followed by different letters are significantly different (P<0.05). OW, MDS and SDS referring optimal water content, moderate drought stress and severe drought stress separately.

Table 4 The root branching pattern of *P. euphratica* seedlings under three drought treatments

Variables	OW（control）	MD	SD
TI	0.713±0.007 [b]	0.731±0.008 [ab]	0.757±0.010 [a]
DBI	0.101±0.010 [b]	0.153±0.016 [ab]	0.216±0.020 [a]
Lateral root branching density (n/cm)	1. 21±0.09 [a]	1.03±0.05 [b]	0.85±0.04 [c]

Notes: Variables are means± standard error (OW: n=25; MD: n=30; SD: n=30). In each row, means followed by different letters are significantly different (P<0.05). OW, MDS and SDS referring optimal water content, moderate drought stress and severe drought stress separately.

Table 5(on next page)

Representative variables of different root phenotypic changes and deep-rooting capacity of *P. euphratica* seedlings under three drought treatments

Notes: Values are means± standard error (OW: n=25; MD: n=30; SD: n=30). Within a row, means followed by different letters are significantly different (P<0.05). OW, MD and SD refer to optimal water content, moderate drought stress and severe drought stress separately.

1   **Table 5 Representative variables of different root phenotypic changes and deep-rooting**

2   **capacity of *P. euphratica* seedlings under three drought treatments**

Indices	OW (control)	MD	SD
RMF	0.338±0.009 [b]	0.353±0.013 [b]	0.418±0.013 [a]
TRMF	0.304±0.018 [b]	0.333±0.026[ab]	0.393±0.030 [a]
STRL (cm/g)	889±37	919±45	1020±67
RRD (cm/g)	90.8±7.26 [b]	108.0±11.0 [ab]	166.0±15.9 [a]

3   Notes: Values are means± standard error (OW: n=25; MD: n=30; SD: n=30). Within a row, means

4   followed by different letters are significantly different (P<0.05). OW, MD and SD refer to optimal

5   water content, moderate drought stress and severe drought stress separately.

6