1   **Rehydration rates and the prevalence of xylem-hydration of**

2   **flowers**

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7   Word count:

8   Abstract   146

9   Introduction   914

10   Methods   605

11   Results   458

12   Discussion   1175

13   References   683

14   Total   3987

15

16   **Abstract**

17   Angiosperm flowers are remarkably diverse anatomically and morphologically, yet they all

18   must satisfy the physiological constraints of supplying sufficient amounts of water and

19   carbon effectively promote pollination. Flowers often occur in the hottest, driest parts of

20   the plant canopy and can face harsh abiotic conditions. Prior evidence suggests that extant

21   species vary dramatically in how water is delivered to flowers, with some evidence that

22   water may be imported into flowers by the phloem. Here we measured midday water

23   potential gradients between flowers, leaves, and stems of ten phylogenetically diverse

24   species. We further tested the likelihood of xylem-hydration by measuring rates of

25   rehydration after experimentally induced desiccation. There was no significant difference

26   in rehydration rates between leaves and flowers. These results are consistent with xylem-

27   hydration of flowers and suggest that there has been little modification to the mechanisms

28   of water transport despite the diversity of floral form.

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Introduction

33 Among the angiosperms reproduction has involved the evolution of complex floral

34 structures to attract pollinators, increase outcrossing rates, and protect developing seeds.

35 This critical phase in the life history of a plant can be costly in terms of carbon and water,

36 but these costs can vary widely [1]. Given that most flowers do not assimilate substantial

37 amounts of carbon [2] but may still transpire large quantities of water [3–5], floral

38 transpiration can negatively impact whole plant water balance. Indeed, water lost to floral

39 transpiration can reduce leaf water potential beyond the threshold that induces stomatal

40 closure, thereby suppressing carbon gain and further compounding the costs of

41 reproduction [6–8].

42 Because of the negative effects of floral water loss and the high carbon invesment into

43 building and maintaining flowers, these costs of reproduction may have driven selection

44 for physiologically cheaper flowers. At a broad phylogenetic scale, floral hydraulic traits

45 vary substantially among lineages [9]. Compared to ANITA grade and magnoliid flowers,

46 monocot and eudicot flowers have lower whole-flower hydraulic conductance, minimum

47 epidermal conductance, and fewer stomata [5]. This trend is in contrast to leaves, which

48 have evolved traits facilitating higher rates of transpiration [10]. This disparity between

49 leaf and flower hydraulic architecture suggests that limiting water loss from floral

50 structures may have been critical in the evolution of their large, morphologically complex

51 flowers.

52 Furthermore, some evidence suggests that the pathways of water entry into flowers vary

53 substantially among species. Flowers of some ANITA grade and magnoliid species exhibit

54   water potentials consistent with water delivery by the xylem (i.e. flower water potentials

55   more negative than stems and leaves) [11,12], but flowers of some eudicots maintain

56   higher (i.e. less negative) water potentials than leaves. These trends have been used to

57   suggest that they may be hydraulically isolated from the stem xylem and hydrated instead

58   by the phloem [13,14]. The difference in water potential between flowers and vegetative

59   structures can be quite dramatic; petals of cotton plants experiencing drought can maintain

60   water potentials 3 MPa higher than subtending bracts connected to the stem less than one

61   centimeter from the petals [13]. How such large water potential gradients are maintained

62   is unclear, yet may be linked to variation in the pathways of water entry into flowers.

63   The possiblity of two fundamentally different mechanisms of delivering water to flowers-

64   hydration by the xylem versus the phloem–is appealing because of the potential

65   physiological differences between these two strategies and because of their implications

66   for floral evolution. Long extinct, early angiosperm flowers are thought to have evolved as

67   highly modified leaves, consistent with xylem-hydration of basal angiosperm flowers

68   [11,12]. A transition to phloem-hydration could be beneficial if it helps to buffer flower

69   water potential from variation in plant water potential. Phloem-hydration could result

70   from a combination of reduced transpiration rates and xylem dysfunction. Whether the

71   phloem could supply enough water to maintain turgid, showy flowers given the high

72   hydraulic resistance of the phloem is unclear. Many flowers have lower stomatal densities

73   than leaves [5,15,16], which might allow floral transpiration rates during anthesis to be low

74   enough that water supplied by the phloem and water stored in floral hydraulic capacitors

75   would be sufficient to meet the demands of transpiration. However, while flowers have

76   much higher hydraulic capacitance than leaves [14], they also have significantly higher

77 minimum epidermal conductances [17]. Xylem disconnection between the stem and the

78 flower–due either to discontinuity in the receptacle [18] or to occlusion of the xylem [19]–

79 could physiologically isolate petals from other floral organs and from the stem xylem,

80 allowing petal water potential to vary widely and independently of leaf and stem water

81 potentials.

82 Data supporting this hypothesis, however, are lacking. To date, water potentials have been

83 measured on flowers of only nine species. Chapotin et al. [14] report water potentials of

84 flowers and leaves of three tropical trees, but for one species flowers and leaves were

85 measured on different individual plants, and no measurements of stem water potentials

86 were made. Inferring directions of water flow from flower and leaf water potentials

87 without measurements of stems is problematic because flowers may have water potentials

88 intermediate between stems and leaves, consistent with xylem-hydration. Indeed, this has

89 been shown in *Illicium* and *Magnolia* flowers, which suggests that these flowers remain

90 hydraulically connected to the stem xylem [11,12]. Although flowers of *Magnolia*

91 *grandiflora* generally have lower water potentials than stems, inner whorl tepals maintain

92 higher water potentials than stems, which is the only example of floral structures

93 maintaining higher, less negative water potentials than stems [12]. While Trolinder et al.

94 [13] showed that petals can remain significantly more well hydrated than both bracts and

95 leaves, water potentials of stems were not reported, making interpretation of their results

96 difficult.

97 Thus, the lack of water potentials measured simultaneously on stems, leaves, and flowers

98 hinders our understanding of the potential variation in pathways for water entry into

99   flowers and of floral hydraulic architecture more generally. Here, we report midday water

100   potentials of flowers, leaves, and stems from ten species spanning most of the extant

101   phylogenetic diversity of the angiosperms. We also combine measurements under natural

102   conditions with measurements on slowly desiccating, excised shoots to estimate both the

103   natural variation of midday flower water potential and the magnitude of water potential

104   gradients between flowers and stems under extreme drought conditions. Additionally,

105   these excised shoots were allowed to rehydrate and their water potentials remeasured

106   after 3-4 hours to determine whether and at what rates flower water potentials can

107   recover from declines in water content.

Methods

109   Plants growing in the Marsh Botanical Garden (New Haven, CT, USA) and the Arnold

110   Arboretum of Harvard University (Roslindale, MA, USA) were sampled in the spring and

111   summer 2017. These included two *Rhododendron* hybrids, one a likely cross between

112   *Rhododendron catawbiense* and *Rhododendron ponticum* and the other a cultivar in

113   subgenus *Azaleastrum* that has a double corolla (referred to as *Rhododendron catawbiense*

114   *x ponticum* and *Rhododendron* subg. *Azaleastrum*, respectively), as well as *Magnolia x*

115   *loebneri*, which is a cross between *Magnolia kobus* and *Magnolia stellata*. Because of

116   differences in floral phenology, species were sampled opportunistically as flowers became

117   available for measurement.

118   In all experiments, samples were sealed into thermocouple psychrometer chambers within

119   five seconds of excision (Merrill Specialty Equipment, Logan, UT, USA). Within ten minutes

120   of sampling, chambers were triple-bagged in the laboratory, and submerged in a water

121   bath maintained at 25˚C for five to seven hours, at which time sequential water potential

122   measurements had stabilized. Water potentials of all structures were made using

123   thermocouple psychrometers interfaced to a CR6 datalogger via an AM16/32B multiplexer

124   (Campbell Scientific, Logan, UT, USA). Measurements of the microvolt output from the

125   psychrometers were converted to MPa using sensor-specific calibration curves generated

126   from measurements of eight NaCl solutions of known water potential [20].

127   Midday water potentials were measured between 1300 and 1500 hrs on each day from at

128   least three individuals of each species, with the exception of *Clematis montana* var. *rubens*,

129   for which only one individual was available. In the drydown and rehydration experiments,

130   flowering shoots were collected in the morning and immediately enclosed in sealed,

131   humidified plastic bags. After 2-3 hours of equlibration in the plastic bags, initial water

132   potentials were measured. Flowers and leaves were sampled by excising two 6-mm

133   diameter discs of each tissue from midway down the length of the leaf, petal, or tepal and

134   from midway between the midrib and margin, avoiding major veins if possible. The newest,

135   fully expanded leaves on the same shoot as the flower were chosen. Short (~1 cm length)

136   stem segments were excised from below the leaves. All samples were enclosed in

137   thermocouple psychrometer chambers immediately after sampling. In the rehydration

138   experiment, the cut surface of each shoot was placed in distilled water and the shoot

139   allowed to rehydrate for 3-4 hours, at which time water potentials of each structure were

140   resampled. In species with unfused corollas, adjacent tepals or petals of the same flower

141   were sampled, and for species with fused petals, separate but adjacent flowers were

142   sampled. Stem samples after rehydration were taken from just below the sampled leaves,

143   avoiding the approximately 1-cm segment that had been sitting directly in water. This

144   sampling scheme for leaves and flowers assumed that adjacent flowers (or leaves) had the

145   same water potential.

146   We calculated tissue-specific rehydration rates as:

$$rate = \frac{\Psi_f - \Psi_i}{t}$$

147   where Ψ_i and Ψ_f are the water potentials immediately prior to and following rehydration,

148   respectively, and t is the time (hours) the sample was allowed to rehydrate. The absolute

149   rate of water potential recovery depends on the water potential gradient between source

150   (approximately 0 MPa for pure water) and the tissue water potential, Ψ_i. The slope of the

151   relationship between the rehydration rate and Ψ_i is the intrinsic time constant of

152   rehydration (τ; hr^{-1}). This time constant was calculated for leaves and flowers of each

153   species and compared using a paired t-test.

154   Because we are not interested in statistical comparisons of water potentials of the same

155   structures between species but rather in the water potential differences between

156   structures within each species, we performed separate mixed-effect ANOVA modeling for

157   each species. For each model, time of day and structure were treated as fixed effects and

158   date and individual as random effects. All analyses were performed in R [21]

159   **Results**

160   Of the ten species for which there were measurements of midday water potentials, four of

161   them had flower water potentials more negative than stem water potentials, and four of

162   them had flower water potentials indistinguishable from stem water potential (Figure 1).

163   Only two species, *Clematis montana* var. *rubens* and *Weigela coraeensis* had flower water

164   potentials consistently higher (i.e. less negative) than stem water potentials, gradients

165   which have been used previously to argue for phloem-hydration of flowers.

166   Of the four species that had flower water potentials close to stem water potential, two of

167   these were precociously flowering species (*Magnolia* x *loebneri* and *Forsythia* sp.) that

168   flower early in the spring when vapor pressure deficits are low and before leaves have

169   flushed. These species may, therefore, not compete with leaves for water. One of these

170   species, *Calycanthus floridus*, has been shown previously to have whole-flower water

171   potentials more negative than stems (Roddy et al., in press), suggesting that while the

172   overall $\Psi_{stem\text{-}flower}$ gradient may drive water flow towards flowers, there may be intrafloral

173   variation in water potential gradients between individual tepal whorls.

174   To determine the ranges of water potentials and the rates of rehydration, we allowed

175   excised flowering shoots to dry on the bench and sampled water potentials periodically

176   over time (Figure 2a). The driest flowers measured of each species showed signs of

177   necrosis, having shriveled and begun turning brown. Yet, mean water potentials of flowers

178   from this experiment never exceeded -1.5 MPa (Figure 2a), and the species with the lowest

179   mean $\Psi_{i,flower}$ were tepals of *Calycanthus floridus*, bracts of *Cornus florida*, and petals of

180   *Syringa pubescense*. Mean $\Psi_{i,flower}$ of other species were all above -1.0 MPa. $\Psi_{i,leaf}$ was

181   generally lower than $\Psi_{i,flower}$ for most species.

182   However, mean $\Delta\Psi_i$ never exceeded 1 MPa, indicating that leaf and flower Ψ remained very

183   close to Ψ_{stem} even during benchtop dehydration (Figure 2b). In only five of ten species was

184   mean $\Delta\Psi_i$ higher than $\Delta\Psi_{midday}$ (*Calycanthus floridus, Magnolia macrophylla, Rhododendron*

185   *catawbiense* x *ponticum, Leucanthemum vulgare, Weigela coraeensis*). In two species,

186   *Clematis montana* and *Rhododendron* subg. *Azaleastrum*, leaves and flowers remained more

187   well hydrated than stems during dehydration.

188   More useful information on the effects of water potential declines on hydraulic functioning

189   comes from the rehydration phase of the drydown experiment (Figure 3). For all structures

190   of all species, Ψ_i was a strong predictor of rehydration rate; samples allowed to desiccate

191   longer with lower Ψ_i had faster rates of water potential recovery. There was little variation

192   among species and structures in the relationship between Ψ_i and rehydration rate. To

193   quantify this relationship, we calculated the slope, τ, which is the intrinsic time constant of

194   rehydration. τ did not differ significantly among leaves and flowers (t = 1.64, df = 9, P =

195   0.14; Figure 4).

Discussion

197   In contrast to previous reports, water potential gradients between flowers and stems

198   suggest that flowers of many species remain hydraulically connected to the stem xylem

199   during anthesis. Results from the rehydration experiment further corroborate this result.

200   Together these experiments help to clarify the dynamics of water potential gradients in

201   flowering shoots under natural conditions and during experimental desiccation and

202   rehydration cycles.

203   The direction of water potential gradients between stems and flowers has been

204   surprisingly unclear, with some reports suggesting that flowers may not be hydraulically

205   connected to the stem xylem during anthesis. Reports of flowers having higher water

206   potentials than leaves have been used to suggest that flowers may be hydrated by the

207   phloem [13,14], while other reports have shown that water potentials of flowers are more

208   negative than stems, suggesting that flowers remain hydrated by the stem xylem during

209   anthesis [11,12]. While a single transition from xylem- to phloem-hydration is not

210   necessarily expected, the apparently strong phylogenetic signal in the pathways of water

211   entry to flowers is reinforced by similarly strong phylogenetic signal in other floral

212   hydraulic traits [5]. Our data strongly suggest that most flowers–even those of eudicots,

213   which are purported to be phloem-hydrated–may remain hydraulically connected to the

214   stem xylem. Indeed, $\Delta\Psi_{stem\text{-}flower}$ is often in the same direction as $\Delta\Psi_{stem\text{-}leaf}$ though the

215   magnitude of $\Delta\Psi_{stem\text{-}flower}$ is lower (Figure 1). Therefore, previous data used to show

216   phloem-hydration of flowers are consistent with our results for xylem-hydrated flowers.

217   However, among some species, it is certainly possible that $\Delta\Psi_{stem\text{-}flower}$ may be negative,

218   which would allow water to flow from the flower to the stem. This occurred among two

219   magnoliids (*Calycanthus floridus*, *Magnolia macrophylla* var. *ashei*), the basal eudicot

220   (*Clematis montana*), and one of the eudicots (*Weigela coraeensis*). Even with these reverse

221   water potential gradients, how much water may flow from flowers to stems depends upon

222   the resistance in the hydraulic pathway. In this case, flowers may actually supply water to

223   the stem, as do some fruits [22]. Athough the relative contributions of the various

224   resistances in the hydraulic pathway into and through flowers have not yet been

225   quantified, measurements of whole-flower hydraulic conductance suggest that the

226   hydraulic resistances can be high, but not substantially higher than in leaves [5].

227   The midday water potential gradients reported here also suggest that flower hydraulic

228   architecture may differ between species that flower before or after leaf out. Two of the

229   species measured here were precociously flowering, producing flowers prior to leaf flush

230   (*Magnolia* x *loebneri* and *Forsythia* sp.). Flowers of both of these species had water

231   potentials equal to Ψ_{stem} (Figure 1). Without the need to compete for water with co-

232   occurring leaves, Ψ_{flower} in these species may not need to decline much below Ψ_{stem} in order

233   to drive water flow into the flower. Although precocious flowering has been hypothesized

234   as a way to eliminate competition for water between flowers and leaves, even leaves on the

235   same branch may not compete with each other for water [23], suggesting that there may be

236   little or no competition for water between leaves and flowers. The hydraulic architecture of

237   precocious flowers may differ in other ways from flowers that co-occur with leaves. For

238   example, precocious flowers appear earlier in spring, when atmospheric conditions are

239   cooler and more humid, which limits their transpiration rates [24]. Furthermore, in ring-

240   porous species current-year vessels in the stem bole are mature only once leaves are

241   mature [25], suggesting that the water used by precocious flowers may be provided by

242   localized stem water storage.

243   The water potential gradients reported also aid in interpreting the role of embolism

244   formation and spread in flowers. Zhang and Brodribb [26] recently reported that water

245   potentials at 50% loss of xylem function in flowers of four species ranged from -2 to -4

246   MPa, while leaves of the same species ranged from about -1.5 to -7 MPa. The extent to

247   which embolism may influence flower function, phenology, and floral longevity is unclear.

248   Recent evidence suggests that *Calycanthus floridus* flowers rarely encounter water

249   potentials low enough to induce embolism under natural conditions (Roddy et al., in press).

250   Here, we show the lowest midday Ψ_{flower} measured was -1.63 MPa in an outer tepal of

251   *Magnolia acuminata* var. *subcordata*. Thus, it is unlikely that the flowers measured in the

252   present study experienced embolism at midday. Even when shoots had been excised and

253   allowed to desiccate, Ψ_{flower} of almost all species remained higher than -2 MPa. Only petals

254   of *Rhododendron catawbiense* x *ponticum* displayed water potentials substantially below -2

255   MPa, and these petals did not rehydrate, suggesting that there may have been embolism-

256   induced hydraulic failure or other structural damage to outside-xylem pathways that

257   prevented rehydration. While water loss and the threat of desiccation impact floral display

258   [6–8], our results suggest that under natural conditions, flowers rarely encounter

259   embolism.

260   Flowers and leaves differed little in their rates of rehydration. While leaf water potentials

261   tended to decline more than flowers during the desiccation experiment, leaves and flowers

262   followed similar rehydration trajectories with no difference in their intrinsic rates of

263   rehydration (Figures 3, 4). With the exception of one *Rhododendron* species, flowers

264   rehydrated just as quickly as leaves for a given initial water potential, suggesting that their

265   lower vein densities and hydraulic conductances did not hinder their capacity to recover

266   from desiccation-induced water potential declines. In contrast to the other species,

267   rehydration rates of *Rhododendron catawbiense* x *ponticum* petals did not follow the same

268   trajectory as leaves or flowers of other species when the initial water potential was below

269   approximately -1 MPa (Figure 3d). Between 0 and -1 MPa, however, this species showed

270   rehydration patterns consistent with the other species studied, suggesting that they may

271   have suffered failure in the hydraulic pathway. Importantly, though, while the rate of water

272   potential recovery did not differ among flowers and leaves (Figure 4), because flower

273   water potentials did not decline as much as leaves, the absolute change in water potential

274   was less in flowers.

275   Under natural conditions, water potentials of flowers during anthesis deviate little from

276   stem water potentials, with $\Delta\Psi_{stem-flower}$ rarely exceeding 0.5 MPa, and only in some species

277   were reverse water potential gradients observed (Figure 1). While these Ψ gradients

278   cannot unequivocally determine whether flowers are hydrated by the xylem or by the

279   phloem, the prevalance of positive $\Delta\Psi_{stem-flower}$ among species is consistent with xylem-

280   hydration of flowers, even among the eudicots. Given that flowers lose turgor at higher

281   water potentials than leaves [12], minimizing $\Delta\Psi_{stem-flower}$ may be critical to preventing

282   turgor loss. Furthermore, these results suggest that flowers can rehydrate as rapidly as

283   leaves. Unlike leaves, however, which must remain turgid to continue assimilating carbon,

284   it is possible that wilted flowers may still attract pollinators as long as ovary water

285   potentials remain high. Although the pathways for water movement into flowers remain

286   unclear, our measurements of midday water potentials and of rehydration dynamics do not

287   rule out the possibility of xylem hydration. Indeed, xylem hydration of flowers is certainly

288   possible, and the apparent dichotomy between xylem-hydration of basal angiosperm

289   flowers and phloem-hydration of eudicot flowers may very well be spurious.

Acknowledgments

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361

362   Figure legends

363

364   Figure 1. Midday water potential gradients ($\Delta\Psi_{\text{stem-leaf}}$ or $\Delta\Psi_{\text{stem-flower}}$) for ten species

365   measured under natural conditions. Different floral structures are differentiated by

366   different symbols. The grey, horizontal line represents the condition when Ψ of the

367   structure is equivalent to Ψ_{stem} (i.e. $\Delta\Psi$ = 0 MPa). Positive values indicate that leaf or floral

368   structures have Ψ lower than stems and negative values indicate that leaf or floral

369   structures have Ψ higher than stems. Shading indicates presumed hydration pathway

370   based on water potential gradients (blue: xylem-hydrated; green: phloem-hydrated;

371   yellow: equivocal). Points and error bars represent mean ± s.e.

372

373   Figure 2. (a) Leaf and flower water potentials and (b) stem-leaf and stem-flower water

374   potential gradients after bench drying and prior to rehydration. The dashed, horizontal

375   line represents the condition when Ψ of the structure is equivalent to Ψ_{stem} (i.e. $\Delta\Psi$ = 0

376   MPa). Points and error bars represent mean ± s.e.

377

378   Figure 3. Rehydration rates of leaves, flowers, and stems as a function of initial water

379   potential for (a) *Clematis montana* var. *rubens*, (b) *Leucanthemum vulgare*, (c) *Magnolia*

380   *macrophylla* var. *ashei*, and (d) *Rhododendron catawbiense x ponticum.*, with data for all

381   species in lighter colors. Species-specific regression lines for leaves and flowers are shown.

382 In (d), the solid line for flowers represents only points with initial water potentials greater

383 than -1 MPa, while the dashed line represents all flowers of this species.

384

385 Figure 4. The time constant of rehydration (τ, the slope of rehydration rate versus water

386 potential as shown in Figure 3) did not differ between leaves and flowers.

387

Figure 1. Midday water potential gradients ($\Delta\Psi_{\text{stem-leaf}}$ or $\Delta\Psi_{\text{stem-flower}}$) for ten species measured under natural conditions. Different floral structures are differentiated by different symbols. The grey, horizontal line represents the condition when Ψ of the structure is equivalent to Ψ_{stem} (i.e. $\Delta\Psi$ = 0 MPa). Positive values indicate that leaf or floral structures have Ψ lower than stems and negative values indicate that leaf or floral structures have Ψ higher than stems. Shading indicates presumed hydration pathway based on water potential gradients (blue: xylem-hydrated; green: phloem-hydrated; yellow: equivocal). Points and error bars represent mean ± s.e.
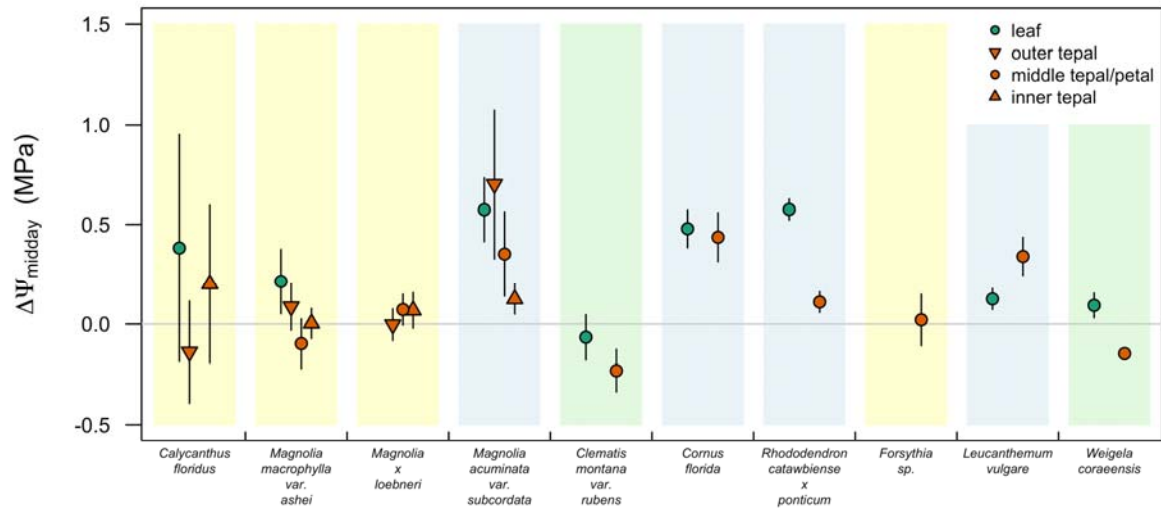
Figure 2. (a) Leaf and flower water potentials and (b) stem-leaf and stem-flower water potential gradients after bench drying and prior to rehydration. The dashed, horizontal line represents the condition when Ψ of the structure is equivalent to Ψ_{stem} (i.e. $\Delta\Psi$ = 0 MPa). Points and error bars represent mean ± s.e.
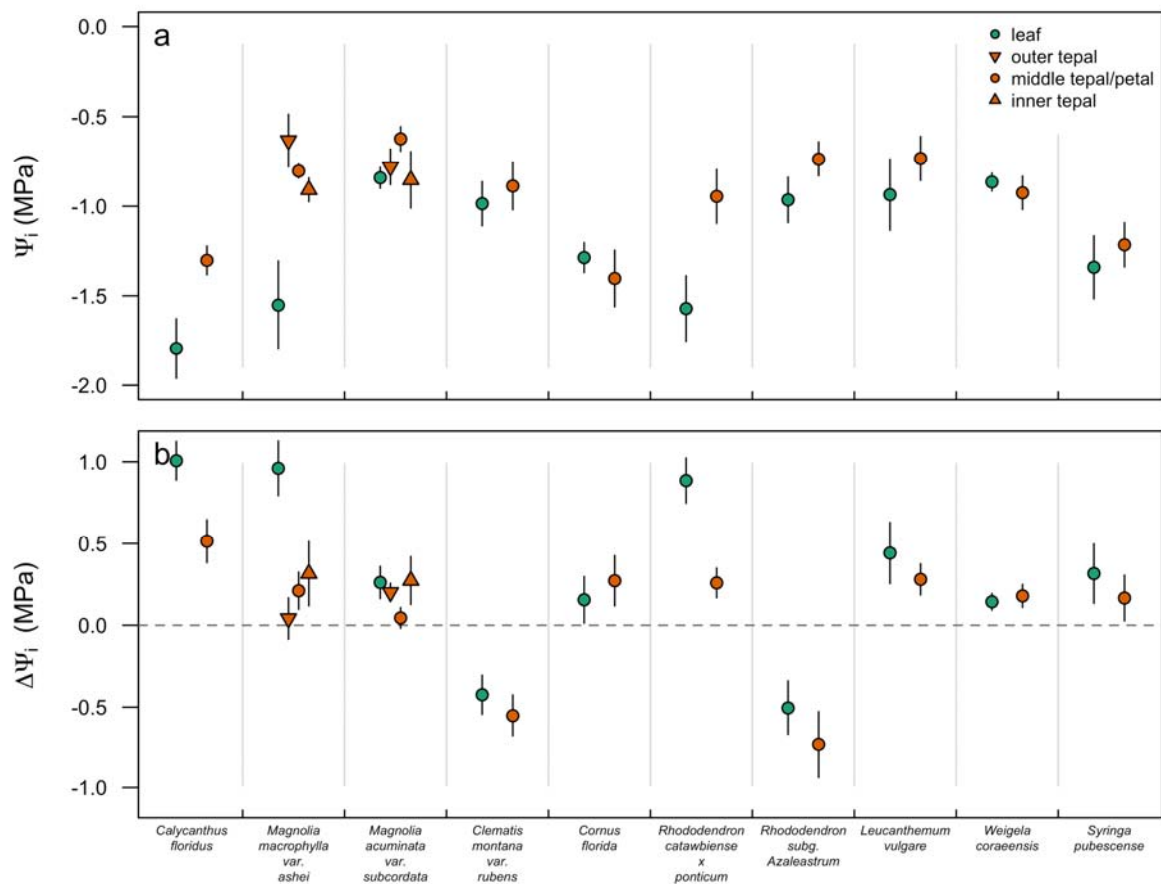
Figure 3. Rehydration rates of leaves, flowers, and stems as a function of initial water potential for (a) *Clematis montana* var. *rubens*, (b) *Leucanthemum vulgare*, (c) *Magnolia macrophylla* var. *ashei*, and (d) *Rhododendron catawbiense x ponticum.*, with data for all species in lighter colors. Species-specific regression lines for leaves and flowers are shown. In (d), the solid line for flowers represents only points with initial water potentials greater than -1 MPa, while the dashed line represents all flowers of this species.
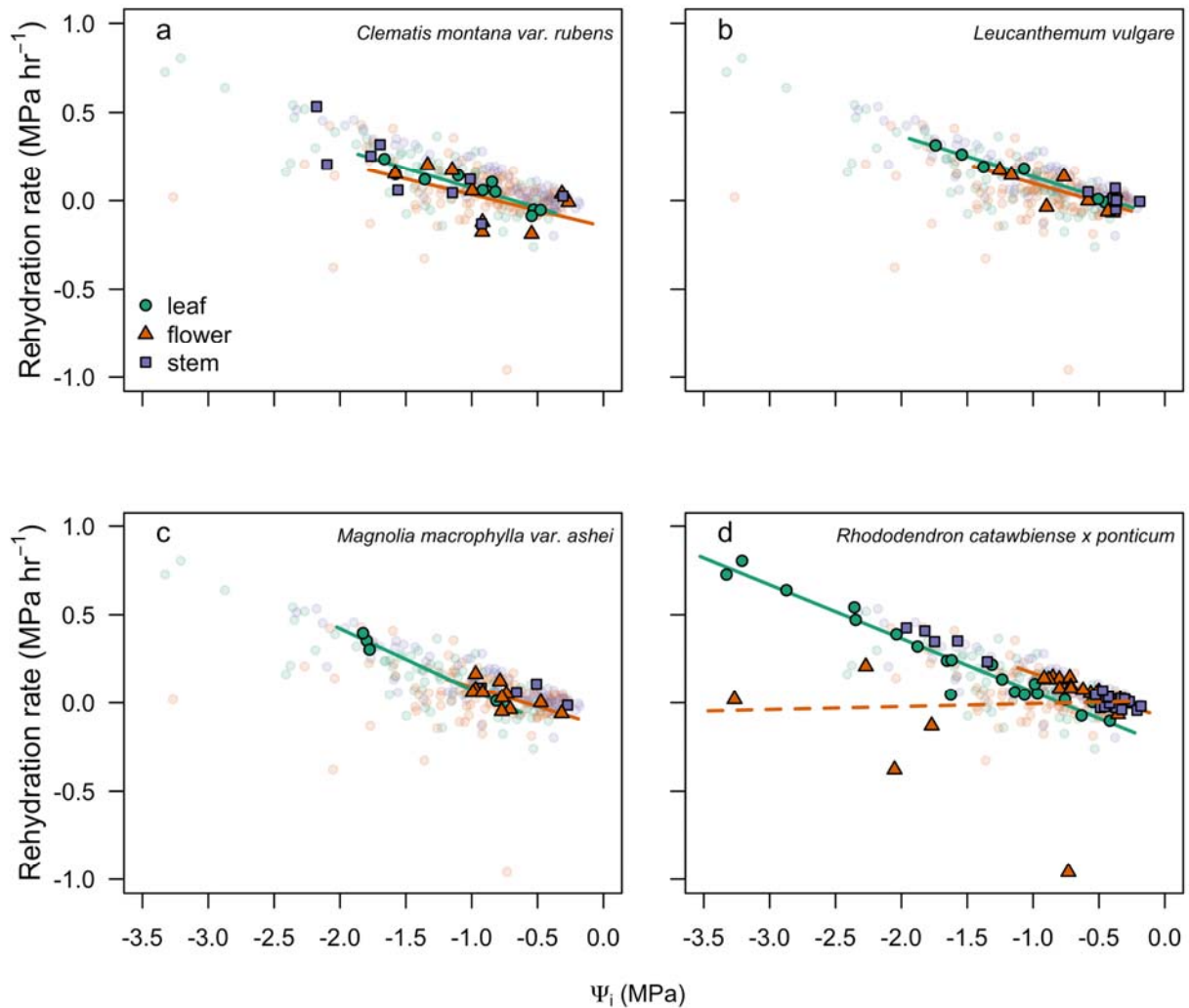
Figure 4. The time constant of rehydration (, the slope of rehydration rate versus water potential as shown in Figure 3) did not differ between leaves and flowers.