1	Growth response of cuttings to drought and intermittent flooding for three Salix
2	species and implications for riverbank soil bioengineering
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16 Abstract

Willows are used as cuttings or in fascines for riverbank soil bioengineering, to control 17 erosion with their high resprouting ability and rapid growth. However, water availability 18 is highly variable along riverbanks both in time and space and constitutes a major stress 19 limiting willow establishment. A species-specific understanding of willow cutting response 20 21 to water stress is critical to design successful riverbank soil bioengineering projects given exclusive use of local species is often recommended. In a three-month greenhouse 22 experiment, we investigated the effects of three soil moisture treatments (drought - soil 23 24 saturation - intermittent flooding) on survival, biomass production and root growth of cuttings of three willow species used for soil bioengineering along NE American streams 25 (Salix discolor – S. eriocephala – S. interior). Cutting survival was high for all species and 26 treatments (>89%). Biomass production and root volume only differed between species. S. 27 eriocephala produced the highest biomass and root volume, and S. discolor invested more 28 29 in below- than aboveground biomass. Root length responded to soil moisture, but differently between species. Under intermittent flooding, S. eriocephala produced shorter 30 roots, while S. interior produced longer roots. For riverbank soil bioengineering, S. 31 32 *eriocephala* should be favoured at medium elevation and S. *interior* at lower elevation.

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34 Keywords

35 Bioengineering; Biomass allocation; Root growth; Salicaceae; Water stress; WinRHIZO

36 Introduction

Willows (Salix spp.) encompass up to 500 species of shrubs and trees that dominate 37 riparian habitats across different biomes (Rechinger 1992; Malanson 1993; Karrenberg et 38 al. 2002; Kuzovkina et al. 2009). These pioneer plants are characterized by morphological 39 and dispersal strategies adapted to fluvial environments (Naiman et al. 2005). One female 40 41 willow can produce thousands to millions of seeds annually to be dispersed by wind and water, which confers these species a high colonization ability in the open, bare and moist 42 riverbank surfaces that flooding disturbance leaves behind (Karrenberg et al. 2002; 43 González et al. 2016; Bourgeois and González 2019). Once established, their dense and 44 relatively deep root system further reduces uprooting risk during flooding and fosters soil 45 stabilization (Karrenberg et al. 2002; Catford and Jansson 2014). Moreover, willows 46 possess a rapid growth rate and a high capacity for vegetative propagation, which promotes 47 their fast re-establishment after disturbance (Krasny et al. 1988; Kollmann et al. 1999; but 48 see Douhovnikoff et al. 2005). Owing to this extraordinary resprouting ability, willows are 49 frequently introduced as cuttings or fascines during soil bioengineering projects designed 50 to control erosion along riverbanks (Evette et al. 2009; Kuzovkina, et al 2009). 51

Along riverbanks, hydrological conditions fluctuate widely both in time following high flow-baseflow cycles, and in space, as less topographically elevated surfaces (e.g., lower banks) experience flooding more regularly than more elevated ones (e.g., upper banks). Tolerance to water stress (drought and flood-induced anoxia) is therefore a major constraint that can limit willow establishment and survival along bioengineered riverbanks (Francis et al. 2005; Pezeshki et al. 2007). In that regard, riparian willows have developed specific strategies to better cope with drought (e.g., by deepening their root system; Garssen et al.

2014) or anoxia (e.g., by developing lenticels and adventitious roots; Kozlowski 1997; Li 59 et al. 2006; Parent et al. 2008), but these vary markedly across species, but also within 60 species in relation to phenotypic plasticity. Many experiments have been conducted under 61 controlled conditions to test the survival and growth of *Salix* species along a gradient from 62 permanent anoxia to extreme drought (Krasny et al. 1988; Jackson and Attwood 1996; 63 64 Amlin and Rood 2001), as such responses can be less detectable under field conditions (but see Shields et al. 1998; Caplan et al. 2013). For example, Salix eleagnos tolerates both 65 water table declines and periodic inundation well (Francis et al. 2005). S. subfragilis has 66 67 higher tolerance to anoxia than S. gracilistyla (Nakai and Kisanuki 2011). Shoot and root elongation of S. exigua increased under inundated conditions but remained constant for S. 68 lutea (Amlin and Rood 2001). S. alba and S. matsudana x S. alba hybrids showed reduced 69 growth after six weeks under drought compared to continuous flooding (Doffo et al. 2017). 70 Wikberg and Ögren (2004) reported higher tolerance to drought for S. purpurea, 71 72 intermediate tolerance for S. viminalis, and lower tolerance for S. schwerenii x S. viminalis. Similarly, S. purpurea exhibits higher drought tolerance than S. suchowensis, as shown by 73 less growth reduction (Jia et al. 2020). Some species also perform better at field capacity, 74 75 such as S. nigra, which showed reduced growth under both drought and flooding (Pezeshki et al. 1998). Given these species-specific responses, carefully selecting local willow 76 77 species according to their tolerance to water stress could greatly improve the success of 78 riverbank soil bioengineering projects (Kuzovkina and Volk 2009). To meet this objective, a greater understanding of local willow species' response to water stress is required, 79 80 notably in regions where such information is scarce, such as North-Eastern America.

This study investigated the effect of three soil moisture treatments (drought, soil 81 saturation, and intermittent flooding) on survival as well as on the biomass production, root 82 length and root volume of cuttings from three willow species: Salix discolor Muhlenberg, 83 S. eriocephala Michaux, and S. interior Rowlee. These species, native to North America, 84 were selected as they are commonly used for riverbank soil bioengineering projects due to 85 86 their high biomass production, high resprouting ability and distinct lateral distribution along riverbanks (Marie-Victorin et al. 2002). We hypothesized that S. discolor, which 87 naturally occurs on upper banks should be more tolerant to drought, while S. interior, which 88 89 is mostly restricted to lower banks, should be more tolerant to intermittent flooding. As a generalist species distributed on both upper and lower banks, S. eriocephala was expected 90 to be highly tolerant to both drought and intermittent flooding. Based on results from our 91 three-month greenhouse experiment, we provide insights for willow species selection in a 92 context of riverbank soil bioengineering. 93

94

95 Materials and methods

96 *Cutting collection*

97 Cuttings of *Salix discolor*, *S. eriocephala* and *S. interior* were collected during the 98 dormancy phase (November 2017) from four natural populations per species established in 99 seven riparian areas surrounding Quebec City, Canada (supplementary Table S1). For each 100 species, a total of 12 individuals (from two to five individuals per population) measuring 1 101 to 2.5 m tall were selected, from which three cuttings were obtained, for a total of 108 102 cuttings. More precisely, newly produced willow branches, that were 20-cm long and 103 similar in diameter (around 0.6 cm), were harvested as cuttings. Only young willow 104 branches from the last growing season were therefore selected as their reduced lignin content promotes resprouting compared to older branches. All these cuttings were 105 harvested at the apex of parent shoot, given cutting location on the parent shoot (i.e., near 106 the base of the parent shoot, or near the apex) can influence their rooting ability (Zalesny 107 and Wiese, 2006). These cuttings were also visually inspected to ensure for their 108 109 homogeneity within species and among sites. Each of the three cuttings obtained from a single individual was dedicated to one of the three soil moisture treatments. After a large-110 spectrum fungicide was applied, cuttings were stored in vacuum sealed bags at -4°C until 111 112 the start of the experiment (i.e., for three months). Throughout this study, we therefore ensured to use a harvest and storage protocol similar for all cuttings in order to limit 113 potential biases related to harvest date, cutting size or differences in cutting location along 114 the parent shoot (by selecting cuttings only at the apex of the parent shoot). 115

116

117 *Cutting plantation*

After rehydrating cuttings by immersion under water for 24h to promote resprouting, each willow cutting was planted in a 30 L permeable bag filled with sand, with two-thirds of its length buried and at least three buds present on the aboveground part. Prior to planting, the initial diameter of each cutting measured. Cuttings were grown for three weeks at soil saturation and slightly fertilized with 500 mL of an NPK solution (20-20-20 kg.ha⁻¹) to reduce stress and mortality risk upon application of the soil moisture treatments.

125 Experimental design

A greenhouse split-plot experiment was conducted to determine the effect of drought, 126 soil saturation and intermittent flooding on the survival and growth (below- and 127 aboveground biomass, root length and root volume) of cuttings of the three willow species 128 studied. Soil moisture treatments were applied to main plots corresponding to plastic tanks 129 (110 x 72 x 100 cm) arranged into six blocks for a total of 18 experimental units. Willow 130 131 species were applied to subplots corresponding to the 30 L bags. One cutting was planted 132 in each bag, for a total of six subplots: i.e. two willow cuttings per species and per tank 133 (Figure S1).

134 The three soil moisture treatments were applied by using different watering frequency and volume. The drought treatment was obtained by irrigating cuttings once a week with 135 1-2 L of water per 30 L bag, a water availability ranging between wilting point and 136 optimum for plant growth. For the soil saturation treatment, cuttings were irrigated twice a 137 week with 3-4 L of water per 30 L bag, which corresponded to field capacity, i.e. the 138 139 amount of water retained in the soil after the excess water has drained away and the rate of downward movement has decreased (Veihmeyer and Hendrickson 1931). Under the 140 intermittent flooding treatment, water level was maintained at 5 cm above the substrate 141 142 surface for two weeks, then drained away using a faucet installed at the bottom of each tank, and soil kept at water saturation for one week; this three-week cycle was repeated 143 144 four times throughout the experiment. Soil water content was further monitored every two 145 days using a time-domain-reflectometry moisture sensor in order to maintain the desired water availability. 146

Greenhouse temperature, relative humidity and daily light integral respectively varied between 17.0 and 28.0 °C (mean: 23.5 °C), 35 and 75% (mean: 57.8%), and 6 and 25 mol.m⁻

².day⁻¹ (mean: 22 mol.m⁻².day⁻¹), during the three months of the experiment (March-May
2018), excluding the three-week acclimation phase.

151

152 *Growth measurements*

At the end of the experiment, cuttings were carefully removed from the substrate. Roots 153 154 were first separated from the aboveground parts (leaves and stem), cleaned with water, coloured with a red dye solution, and the complete root system of each plant scanned with 155 an image analysis system (WinRHIZO, Regent Instruments) to determine total root length 156 157 as well as the volume of three root types based on a preliminary experiment, i.e. fine (diameter: 0.5-1.5 mm), medium (1.5-2.0 mm) and coarse (2.0-2.5 mm). Roots, leaves and 158 stem were then dried at 105°C for 48h and weighed to measure newly produced 159 160 aboveground (leaf + stem) and belowground (root) biomass. Biomass allocation was then calculated as the ratio of aboveground biomass over belowground biomass. Cuttings were 161 excluded from both biomass and root measurements given that we aimed to evaluate the 162 resprouting ability of the studied species under various soil moisture treatments. 163

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165 *Statistical analyses*

Linear Mixed Models (LMMs) followed by LSD (Fisher's Least Significant Difference) were used to assess the effects of species and soil moisture on the five plant growth metrics, namely above- and belowground biomass, biomass allocation, root length and volume. Initial cutting diameter was included as a covariable while block and source population were included as random effects in these LMMs investigating changes in above- and belowground biomass allocation. For root volume, the effect of root type (i.e.,

172	fine, medium or coarse root) was also added to the model in interaction with species and
173	soil moisture. Data were log- or square root-transformed when needed to meet residual
174	normality and homoscedasticity, and back-transformed for results presentation. Analyses
175	were conducted using PROC MIXED on SAS 9.4 (SAS Institute, Cary, NC, USA).
176	
177	Results
178	Survival
179	High cutting survival was observed for all three species and soil moisture treatments at
180	the end of the experiment. All Salix eriocephala cuttings survived. Survival varied from
181	89% (soil saturation) to 92% (drought) and 94% (intermittent flooding) for S. discolor, and
182	from 97% (drought and soil saturation) to 100% (intermittent flooding) for S. interior.
183	
184	Biomass production
185	Biomass production was independent of soil moisture treatment, but strongly varied
186	between species for all biomass components investigated (Table 1). S. eriocephala
187	produced the highest above ground biomass, namely 3.9 and 1.6 times more than for S.
188	interior and S. discolor, respectively (Fig.1). Aboveground biomass production was almost
189	equally distributed between leaves and (new) stems for S. eriocephala (respectively 55%
190	and 45%) while leaf biomass was approximately twice that of stem biomass for the two
191	other species studied ($p = 0.0027$ for species effect on leaves biomass and $p < 0.0001$ for
192	species effect on stem biomass, all species being significantly different from each other for

biomass was also maximal for *S. eriocephala*, with 2.8 and 2.3 times more root biomass

these two biomass metrics according to *post-hoc* multiple comparisons). Belowground

195	produced relative to S. discolor and S. interior, respectively (Fig. 1). Finally, biomass
196	allocation differed between the three species: aboveground biomass was 4.4 times higher
197	than belowground for S. interior, 2.6 times higher for S. eriocephala and 1.3 times higher
198	for S. discolor (Fig. 1).
199	
200	Root length and volume
201	Soil moisture influenced root length differently for each species (significant interaction;
202	Table 2), though on average, root length was maximal for S. eriocephala and minimal for
203	S. interior. Root length increased at soil saturation compared to intermittent flooding for S.
204	eriocephala, while the reverse was observed for S. interior. For S. discolor, root length was
205	independent of soil moisture, with length similar to S. interior under intermittent flooding,
206	and similar to <i>S. eriocephala</i> at soil saturation (Fig. 2).
207	Root volume varied between species, independently of soil moisture (Table 3). The root
208	volume of S. eriocephala cuttings was indeed almost twice that of S. discolor and S.
209	interior (Fig. 3). Yet, for all species, root volume was mostly accounted for by fine roots
210	(66%), while medium and coarse roots respectively contributed to 26% and 8% of the total
211	root volume (Table 3; Fig. 3).
212	

213 **Discussion**

This study provides a greater understanding of the establishment and growth potential of willow cuttings from *Salix discolor*, *S. eriocephala*, and *S. interior*, under various water stress levels. Among the three growth parameters studied here, only root length was significantly influenced by soil moisture, with distinct responses among species. *S.*

eriocephala produced the longest roots under all soil moisture treatments, despite reduced 218 length under intermittent flooding. S. interior had the shortest roots of the three species, 219 and produced longer roots under intermittent flooding. The contrasting effect of soil 220 moisture on S. eriocephala and S. interior concurs with previous studies demonstrating a 221 high plasticity of willow root systems in response to drought and flooding (Pezeshki et al. 222 223 1998; Wikberg and Ögren 2007; Parent et al. 2008). Root length was however independent of soil moisture for S. discolor. These findings partly support our hypotheses: only S. 224 interior, which is usually found on lower banks, performed better under intermittent 225 226 flooding. Conversely, S. eriocephala showed a reduced tolerance to intermittent flooding despite being a generalist species distributed both on lower and upper banks. Although 227 Amlin and Rood (2001) found that S. discolor root length decreased with increasing water 228 depths in a five-month experiment, no difference in root length was detected here under 229 drought compared to soil saturation. Our results suggest that the two other species studied 230 may be as well adapted to drought as S. discolor, even if this latter species is more 231 frequently found on upper banks. Factors other than soil moisture (e.g., soil nutrient 232 resources, interspecific competition) may explain the distribution of our willow species 233 234 under natural conditions. Further investigations are therefore required to determine these 235 limiting factors.

Interestingly, the two other growth parameters studied only differed between species, independently of soil moisture. Biomass production (both above- and belowground) and root volume were higher for *S. eriocephala* compared to *S. discolor* and *S. interior*. Higher rooting ability was also previously observed in *S. eriocephala* compared to *S. discolor* in highly disturbed coal mines (Mosseler et al. 2014). Differences in biomass allocation were

also evidenced between species: S. interior and S. eriocephala mostly invested resources 241 in aboveground biomass, while biomass was equally distributed in S. discolor. While 242 riparian plants are generally considered to invest resources firstly in anchoring to the soil 243 and secondly in developing aboveground parts, the three species studied here mostly 244 allocated resources to stems and leaves which could possibly be due to the absence of shear 245 246 stress and scouring in greenhouse. The absence of soil moisture effect on biomass allocation contrasts with previous studies reporting that willow root/shoot ratio increased 247 248 with drought and decreased with flooding (Kozlowzki 1997; Lavaine et al. 2015, Markus-249 Michalczyk et al. 2016). As suggested by Li et al. (2004), more prolonged or pronounced water stress might be required to observe differences in biomass allocation. Even though 250 251 we did not find differences in biomass production and allocation between soil moisture 252 treatments, we believe that the findings related to allocation to above ground biomass, which were higher for S. interior and lower for S. discolor are consistent with their relative 253 254 positions on riverbanks. S. interior on lower banks regularly experience anoxia and invest more in lateral spread through root suckering from an extensive lateral root system, hence 255 promoting higher aboveground biomass (Mosseler et al. 2014), whereas the other two 256 257 species do not share this ability. This ability might have promoted higher S. interior root length under intermittent flooding. S. discolor usually grows on the upper parts of the 258 259 bank, where it has greater access to unsaturated soil. A different root architecture would be 260 expected in plants in a lower topographic position, which also need to cope with shear 261 stress and scouring through anchoring.

The differential response of root length, root volume and biomass production to water stress suggests high physio-morphological adaptability of willow species to environmental

264 conditions in relation to complex trade-offs between plant traits (Kozlowski 1997).
265 Previous studies have shown that drought and flooding modulate leaf area, wood density,
266 stomatal conductance or xylem cavitation among some willow species (Wikberg and Ögren
267 2007; Savage and Cavender-Bares 2011, Doffo et al. 2017). Such physiological
268 adjustments may therefore help cuttings to maintain similar levels of biomass production
269 despite varying soil moisture. As shown here, investigating multiple plant traits is required
270 to fully characterize willow response to environmental stressors.

In a context of riverbank stabilization by soil bioengineering, our study suggests that S. 271 272 *eriocephala* should be preferred to ensure rapid erosion control through its higher biomass and tolerance to changing water availability. When drought and flooding are less frequent, 273 274 S. discolor also seems a good candidate species, as it produced similar root length to S. eriocephala at soil saturation. The higher investment of S. discolor in belowground 275 276 biomass relative to above ground biomass is also known to be a plant trait fostering soil stabilization (Gray and Sotir 1996). Introducing a mix of both S. eriocephala and S. 277 discolor cuttings could also be an interesting alternative strategy to provide higher 278 resilience to changing environmental conditions (such as climate-induced increases in 279 280 summer drought; Garssen et al. 2014; Bourgeois and González 2019) or optimized 281 ecosystem functions (such as biodiversity support; Fang et al., 2015), and hence promote 282 the success of bioengineering projects. While S. interior might appear less suitable for soil 283 bioengineering given its lower relative investment in belowground biomass, it may be of interest for vegetating the lower parts of the banks. Indeed, compared to the two other 284 285 species, its lower position on the bank seems to indicate higher tolerance to flooding. S. 286 *interior* also has notable regeneration abilities, including root suckering and short, flexible

multistems, suitable traits in a context of soil bioengineering (Gray and Sotir 1996). Longer 287 experiments including a larger number of *Salix* populations might however be required to 288 289 confirm these recommendations. Further investigations that would include additional species could also help expand the list of willow species suitable for riverbank stabilization 290 by soil bioengineering. Determining the response of willow species to additional flood- or 291 292 ice-induced disturbances such as resistance to shear stress and scouring (e.g., Kui and Stella 2016) should also be considered in future experiments to gain further insight into species 293 294 performance on riverbanks and improve soil bioengineering techniques.

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Table 1. Effect of soil moisture treatments (drought – soil saturation – intermittent flooding) and species (*Salix discolor – S. eriocephala – S. interior*) on the aboveground (leaf + stem) and belowground (root) biomass production and biomass allocation (ratio of aboveground biomass over belowground biomass) of willow plants obtained from cuttings, assessed by linear mixed models. P-values for initial cutting diameter used as a covariate were 0.9901 for aboveground biomass production, 0.0058 for belowground biomass production, and 0.0567 for biomass allocation. Significant p-values are indicated in bold.

			Abovegro	und biomass	Belowgro	ound biomass	Biomass	s allocation	
		df	F	p-value	F	p-value	F	p-value	
	Soil moisture	2	0.52	0.6091	0.85	0.4554	0.05	0.9522	
	Species	2	25.80	0.0011	20.68	< 0.0001	39.12	< 0.0001	
421	Soil moisture x Species	4	0.23	0.9121	1.24	0.3422	0.44	0.7765	
									-

Table 2. Effect of soil moisture treatments (drought – soil saturation – intermittent
flooding) and species (*Salix discolor – S. eriocephala – S. interior*) on the root length of
willow plants obtained from cuttings, assessed by a linear mixed model. The p-value for
initial cutting diameter used as a covariate was 0.9800. Significant p-values are indicated
in bold.

	df	F	p-value
Soil moisture	2	0.51	0.6174
Species	2	52.82	< 0.0001
Soil moisture x Species	4	3.20	0.0489

Table 3. Effect of soil moisture treatments (drought – soil saturation – intermittent
flooding), species (*Salix discolor – S. eriocephala – S. interior*) and root type (fine –
medium – coarse) on the root volume of willow plants obtained from cuttings, assessed by
a linear mixed model. The p-value for initial cutting diameter used as a covariate was
0.9735. Significant p-values are indicated in bold.

	df	F	p-value
Soil moisture	2	0.67	0.5320
Species	2	7.77	0.0006
Root type	2	190.40	< 0.0001
Soil moisture x Species	4	0.50	0.7358
Species x Root type	4	1.59	0.1796
Root type x Soil moisture	4	0.66	0.6203
Soil moisture x Species x Root type	8	0.63	0.7486

Fig. 1. Variations in aboveground biomass production, belowground biomass production,
and biomass allocation (ratio of aboveground biomass over belowground biomass)
between plants of three willow species obtained from cuttings (*Salix discolor – S. eriocephala – S. interior*; mean ± standard error; n = 36 cuttings per species). Letters
indicate significant differences obtained by LSD (Fisher's Least Significant Difference).



Fig. 2. Variations in root length (mean \pm standard error) between the three soil moisture treatments (drought – soil saturation – intermittent flooding) and the three willow species studied (*Salix discolor – S. eriocephala – S. interior*; n = 12 cuttings per species and soil moisture treatments). Lowercase letters indicate significant differences between soil moisture treatments for a given species, and uppercase letters indicate significant differences between species for a given soil moisture treatment, obtained by LSD (Fisher's Least Significant Difference).

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Fig. 3. Variations in root volume (mean \pm standard error) between the three willow species studied (*Salix discolor – S. eriocephala – S. interior*; n = 36 cuttings per species) and between the three categories of root size (all species pooled; n = 36 root subsample per category). Letters indicate significant differences obtained by LSD (Fisher's Least Significant Difference).

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Table S1. Location of the natural willow populations sampled for cutting collection. For
each species and site, figures indicate the number of cuttings harvested / of individuals
sampled.

		Species collected			
Location	Coordinates	S. discolor	S. eriocephala	S. interior	
Base de plein air de Sainte-Foy	46°47'03.9"N	12/4	15 / 5	0 / 2	
	71°20'20.2"W		12/4	15/5	9/3
Rivière Cap-Rouge	46°45'57.1"N	<i>c</i> 10	6 / 2		
	71°21'23.2"W	6/2			
Domaine Pointe-de-Saint-Vallier	46°54'29.5"N	10 / 4			
	70°47'27.6"W	12/4			
Trait-Carré	46°51'34.4"N	6 / 2	6 / 2		
	71°16'26.2"W				
Parc des Chutes-de-la-Chaudière	46°43'02.1"N		0.42	<i></i>	
	71°16'55.3"W		9/3	6/2	
Parc de Duberger	46°49'01.3"N			3 / 1	
Rivière Saint-Charles	46°49'54.9"N			18 / 6	

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Figure S1. Illustrations of the greenhouse split-plot experimental design. Cuttings were
planted into 30L bag (subplot) and grouped by six into plastic tanks (main plot) to which
soil moisture treatments were applied, for a total of two cuttings per species and per tank.

