The effects of *Solidago canadensis* water extracts on maize seedling growth in association with the biomass allocation pattern

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Abstract

Background. *Solidago canadensis* L. is an aggressive exotic plant species in China that has potential allelopathic effects on competing plant species. Hormetic effects are frequently observed in studies of allelopathy; however, the mechanisms of such effects need to be elucidated. Allelopathic compounds may affect the growth of recipient plants via alteration of biomass allocation patterns or photosynthetic capacity. The aim of this study was to determine how water extracts from *S. canadensis* affected the shoot and root growth of recipient plants and whether the underlying mechanism was related to the biomass allocation pattern or photosynthetic gas exchange capacity.

Methods. The water extracts from *S. canadensis* shoots at twelve different concentrations in the range of 0-0.25 g/ml were applied thrice in 9 days to maize seedlings cultivated in silica sand. The growth (shoot height, leaf length and area and root length) and biomass accumulation and allocation (specific leaf area (SLA), leaf area ratio (LAR) and leaf mass ratio (LMR)) were compared among maize seedlings exposed to different treatment concentrations. Gas exchange (photosynthetic light response curve) was measured and compared among maize seedlings exposed to three concentrations of water extract (0, 0.0125 and 0.2 g/ml) before and after the first application, and seedling growth was measured after the third and final application.

Results. The growth of seedlings (shoot height, leaf length and area and root length) was promoted at concentrations below 0.125 g/ml and inhibited at concentrations above this level ($P < 0.05$). The pattern of change in biomass accumulation and allocation was similar to that of

47   shoot growth, but biomass accumulation and allocation was not significantly affected by the

48   water extract treatments ($P > 0.05$). The water extract treatments did not significantly affect the

49   photosynthetic capacity ($P > 0.05$), but the dark respiration rate was higher in the low-dose

50   treatment than that in the high-dose treatment. Shoot height was positively correlated with the

51   biomass allocation indicators SLA and LAR ($P < 0.05$) but not with LMR ($P > 0.05$).

52   **Conclusions.** The results suggested that the effects of the water extracts from *S. canadensis* were

53   highly dependent on the concentration, with the growth of maize seedlings promoted at low

54   concentrations of water extracts. The effects of the water extracts on the growth of maize

55   seedlings were mainly due to the effects on the LAR, the allocation to leaf area growth, whereas

56   the effects of the water extracts on leaf gas exchange capacity can not explain variation of

57   seedling growth. Thus, the stimulation of plant growth was very likely due to increased biomass

58   allocation towards the shoot.

59

60   *Solidago canadensis* L. (Asteraceae), which originates from North America, has successfully

61   invaded southeastern China. This species usually forms large monocultures and causes

62   substantial yield loss of crop plants (Liu et al., 2010). Although how the invasiveness of this

63   species develops is unknown, the hypothesis that allelopathy may contribute to the success of the

64   species is supported by some existing evidence (Abhilasha et al., 2008; Yuan et al., 2012). The

65   rhizome extract of *S. canadensis* imposed hormetic effects on both the growth and physiological

66   activity of lettuce seedlings in a laboratory experiment (Zhang et al., 2012). Therefore, whether

67   the allelochemicals of *S. canadensis* increase or decrease crop yields may depend on their

68 concentration in soils, which should be considered when explaining the interaction of *S.*

69 *canadensis* with native species or crop plants.

70   Hormesis refers to the stimulation of organism performance that occurs at low levels of

71 exposure to agents that are harmful or toxic at high levels of exposure (Forbes, 2000; Calabrese

72 and Baldwin, 2001). The hormetic effects of herbicides on plant growth have been observed

73 many times (Cedergreen, 2008a), while more recently, the hormetic effects of phytotoxins have

74 received attention due to their close association with exotic plant invasion (Prithiviraj et al., 2007;

75 Zhang et al., 2012).

76   Many mechanisms to explain hormetic effects have been proposed (Prithiviraj et al., 2007;

77 Duke et al., 2006). The induction of defense mechanisms induced by free radicals of oxygen can

78 lead to increased growth at low doses of phytotoxic chemicals (Kovalchuk et al., 2003). For

79 example, a low dose of (±)-catechin, which is produced by the invasive weed *Centaurea*

80 *maculosa,* induced moderate increases in reactive oxygen species in meristems and much greater

81 biomass accumulation (Prithiviraj et al., 2006). Moreover, reactive oxygen species have proven

82 to be essential for cell elongation in plants (Rodríguez et al., 2002). Some chemicals that can

83 affect plant secondary metabolism are associated with the synthesis of cell wall fibers at low

84 doses (Duke et al., 2006). For example, glyphosate inhibits the shikimate pathway, the source of

85 lignin precursors, and might preferentially inhibit lignin synthesis at low, nonherbicidal doses,

86 making cell walls more elastic for longer periods during development (Duke et al., 2006). The

87 roles of photosynthetic capacity in explaining growth promotion effects by low-dose chemicals

88 have also been carefully examined. Compared with untreated barley plants (Cedergreen, 2008b),

89   when sprayed with low doses of glyphosate, barley plants had a higher relative growth rate (RGR)

90   that was partly attributed to the increased photosynthesis rate (Cedergreen and Olesen, 2010).

91   Increaded photosynthesis rate was also found in the promotion effects of cadmium, a heavy

92   metal, on the growth of several plant species (Jia et al., 2015; Pereira et al., 2016). Nevertheless,

93   enhanced photosynthesis was not observed when growth was stimulated in cucumber plants

94   treated with several herbicides (Wiedman and Appleby, 1972) or in rice plants treated with

95   microcystins (Liang and Wang, 2015) . These inconsistent results suggest that other critical

96   responses explain the dose effects on plant growth, such as biomass allocation patterns.

97   Considering that the plant RGR consists of a morphological component, the leaf area ratio

98   (LAR), and a physiological component, the net assimilation rate (NAR) (Poorter, 1990), an

99   increase in the RGR under a low dose of a hormetic substance is not necessarily caused by an

100 increase in the photosynthesis rate but can also be due to an increase in the allocation to leaf area.

101 Indeed, some hypotheses state that the stimulatory growth at low concentrations is due to altered

102 resource allocation between shoots and roots (Duke et al., 2006). Therefore, to best explain the

103 hormetic effect of growth stimulation, the physiological factor (assimilation capacity) and the

104 biomass allocation factor are both important to consider.

105   The objective of this study was to first test the effects of the shoot extract of *S. canadensis*

106 on the growth and biomass accumulation of maize seedlings and, second, to elucidate the

107 possible mechanisms underlying the promotion or inhibitory effects. Specifically, we

108 investigated how the extracts of *S. canadensis* affected the growth and biomass accumulation and

109 allocation patterns of treated maize seedlings. We correlated the maize seedling shoot height to

110 biomass allocation patterns (LAR, specific leaf area (SLA) and leaf mass ratio (LMR)) to

111 determine whether the biomass allocation pattern could explain the promotion or

112 inhibition observed. We also compared the photosynthetic capacity under the concentrations that

113 either promoted or inhibited growth to determine whether the variation in photosynthetic

114 capacity could explain the hormetic effects.

115

Materials and methods

Water extract preparation

118   In September 2017, when *S. canadensis* plants started to flower, the shoots of *S. canadensis*

119 plants were collected from fields and immediately transported to the laboratory, where the

120 inflorescence was removed. The shoots were collected during this period because in this stage, *S.*

121 *canadensis* reportedly accumulates the highest content of phenolics, which are assumed to be the

122 major allelopathic substances in this species (BaležEntienė, 2015). As shoots are proven to be

123 most allelopathic part of *S. canadensis* (BaležEntienė, 2015), only the allelopathic effects of

124 shoots were investigated in this study. The procedure for the water extraction of shoots followed

125 the modified methods from Meiners (2014). The shoots were cleaned with tap water and dried at

126 room temperature. Afterwards, the shoots were cut into 8 mm pieces. The water extracts were

127 made with a ratio of 1 g of shoot pieces:4 ml of distilled water in beakers. The extraction was

128 performed an incubation chamber at 30-31°C for 24 hr. Subsequently, the extraction solution was

129 filtered through 2 layers of cotton and stored in a refrigerator at 4°C until ready for use.

Maize seedling culture

131   We used maize plants as the target species, due to the frequent interaction of this crop with

132   *S. canadensis* and the large yield losses associated with *S. canadensis* invasion (Liu et al., 2010).

133   Commercially sold maize (*Zea mays* L.) seeds (var. Meiyu 8, Hainan Lvchuan Seeds Co., Ltd.,

134   China) were germinated in 9 mm Petri dishes, with thirty seeds placed in each dish. After

135   germination for 6 days, and when the first leaf was fully open, 72 seedlings with similar size

136   (plant height and leaf number) were transplanted into 180 ml pots containing 120 g of silica sand,

137   with one plant in each pot. For each treatment concentration, 6 replicate plants were used. The

138   maize seedlings were grown for another 4 days, and then, the first of the water extract

139   supplement treatments was applied. The seeds were germinated and the seedlings cultured in a

140   plant growth chamber, with a constant irradiance of 250 $\mu mol \cdot m^2 \cdot s^{-1}$ (photosynthetically active

141   radiation, PAR) above the shoots and an air temperature of 24°C for 12 hr during the day and

142   18°C for 12 hr at night.

143   **Experimental design and water extract supplement treatments**

144   To prepare the water extract concentration gradient, the original shoot water extract was

145   diluted with distilled water. The final concentrations were as follow: 0, 0.0125, 0.025, 0.05,

146   0.075, 0.1, 0.125, 0.15, 0.175, 0.2, 0.225 and 0.25 g shoot equivalent/ml (hereafter referred to as

147   g/ml). The seedlings were supplemented with the water extract from the top of the pots. Every 3

148   days for 9 days, each pot was treated with 100 ml of nutrient solution (1/4-strength Hoagland's

149   solution) and 4 ml of extract solution. For a total of 9 days, the water extract treatments

150   continued. The treatments were applied under the same growth chamber conditions as described

151   above.

152 **Gas exchange measurement**

153   The gas exchange measurements were performed on maize seedlings treated with three

154 concentrations of water extract: 0 (CK, control), 0.0125 g/ml (Low concentration) and 0.2 g/ml

155 (High concentration). The measurements were conducted on the day preceding the

156 commencement of treatments (0 day) and on the following 3 days. Net photosynthetic rates (Pn)

157 and respiration rates (Rd) were measured on the fourth fully expanded leaf with an open-type gas

158 exchange system (LI-6400, Li-Cor Inc., Lincoln, NE). Photosynthetic light response curves were

159 individually analyzed for the 6 replicated seedlings. The PAR for the light response curve was as

160 follows: 2500, 2000, 1500, 100, 500, 300, 100, 50 and 0 $\mu mol \cdot m^2 \cdot s^{-1}$, and the flow rate was 0.5

161 $l \cdot min^{-1}$. The stability waiting time in the light response curve autoprogram was set as 60~120 s.

162 Before each measurement, the leaves were light activated for 20 min at the PAR of 2500

163 $\mu mol \cdot m^2 \cdot s^{-1}$. Light-saturated net photosynthetic rate (P_{max}), apparent quantum yield (AQY) and

164 dark respiration (R_d) were determined by using the following model (Lewis, Olszyk and Tingey,

165 1999):

166     $$P = \frac{P_{max}PPFD}{K + PPFD} - R_d$$

167   where P is the simulated photosynthesis rate calculated with the above model, PPFD is the

168 photosynthetic photon flux density, and K is equal to the PPFD required to produce one-half of

169 the light-saturated photosynthetic rate.

170 **Growth measurement**

171   When the photosynthesis measurement was finished, the maize seedlings had developed

172 three to four true leaves. When the photosynthesis measurement was finished, the maize

173 seedlings have developed three to four true leaves. The maize seedlings were then harvested after

174 the third extract application. The height of each plant was measured with a ruler, while the roots

175 were washed with distilled water to remove any silica sand. The roots and leaves were then

176   separated from the plants and scanned with a Microteck Scanwizard 5 (Microtek International,

177   Inc., Taiwan). Next, the total root length and the total leaf length and area were analyzed with the

178   programs Winrhizo and Winfolia (Regent Instruments Inc., Canada), respectively. Plant

179   materials were then oven dried at 60°C for 72 hr, and the mass weight of the leaf, stem and root

180   for each seedling was measured. The SLA, LMR and LAR were calculated as follow: SLA =

181   total leaf area/total leaf weight; LMR = total leaf weight/whole plant weight; and LAR = total

182   leaf area/whole plant weight.

183   **Data analysis and statistics**

184   Compared with the controlled plants (water extract concentration = 0), the change in plant

185   height, total root length, total leaf length and area, SLA, LMR, LAR and biomass was calculated

186   as follows: (Growth of treated plants − growth of controlled plants)/growth of controlled plants

187   ×100%. The effects of the water extract concentration on plant growth were analyzed with one-

188   way ANOVA (analysis of variance). The gas exchange characteristics (light-saturated Pn, Rd

189   and AQY) were analyzed with two-way ANOVA with water extract concentration and treatment

190   time (days) as fixed factors. Linear regression analysis of biomass based on SLA, LMR and LAR

191   was performed with the data pairs of the plant height value and the SLA, LMR and LAR values

192   of each individual plant. All analyses were conducted in the SPSS 16.0 statistical software

193   package (SPSS 16.0, SPSS Inc., Chicago, IL).

194

195   # Results

196   The effect of *S. canadensis* water extracts on maize seedling growth and biomass

197   accumulation followed a hormetic pattern, i.e., seedling growth and biomass accumulation

198   increased at low concentrations (0.0125-0.125 g/ml) and decreased at high concentrations

199   (0.125-0.25 g/ml) (Figs. 1 and 2), with the most remarkable stimulatory effects at 0.0125 g/ml

200   (Figs. 1 and 2). The effects of water extracts on plant height, total leaf length, total leaf area and

201   total root length ($P < 0.05$, Table 1) were significant, whereas the effects on the biomass

202   accumulation of leaf, stem, root and whole plant and on the resource allocation indexes SLA,

203   LMR, LAR and root/shoot ratio were not significant ($P > 0.05$, Table 1).

204   Hormetic-like effects were also observed on SLA and LAR (Fig. 3), but the effect of

205   treatment concentration on these indexes was not significant (Table 1). The maximum

206   photosynthesis rate and apparent quantum efficiency were not significantly different among the

207   three different water extract treatments: CK (0 g/ml), low concentration (0.0125 g/ml) and high

208   concentration (0.2 g/ml) ($P > 0.05$, Table 2, Fig. 4). However, those plants that received the low

209   dose of water extract had higher respiration rates than those of the two other treatments ($P < 0.05$,

210   Fig. 4). Although SLA, LAR and LMR were not significantly affected by the water extract

211   treatments, the pattern of change in these morphological parameters was similar to that of plant

212   shoot height. The regression analysis indicated that plant shoot height was closely associated

213   with SLA and LAR ($P < 0.01$) but not with LMR ($P > 0.05$) (Fig. 5).

214

Discussion

216   We observed that the water extracts of *S. canadensis* shoots had hormetic-like effects on the

217   growth of maize seedlings, which is a result consistent with the findings of Sun et al. (2006) and

218 Zhang et al. (2012), suggesting that the potential allelopathic effects of the water extracts on

219 recipient plants were highly dependent on the concentration. In other studies, negative

220 allelopathic effects of *S. canadensis* are reported (Butcko and Jensen, 2002; Abhilasha et al.,

221 2010). The variation in the effects of water extracts on recipient plant growth may be due to the

222 tissues studied, methods used for preparation, concentration dose of water extract applied,

223 growth conditions and species of the recipient plant. Our study showed that identifying the

224 potential allelopathic compounds and determining their actual concentrations in the environment

225 are critical when regarding the allelopathic effects of *S. canadensis*.

226   We observed hormetic-like effects of the water extracts on the growth and biomass

227 accumulation of maize seedlings. The shoot and root growth was promoted significantly by the

228 low-dose water extract, but maize seedling biomass accumulation was not significantly promoted.

229 The lack of significant effects on biomass accumulation was possibly due to the relatively low

230 light availability (250 μmol·m^2·s^{-1}) and low CO_2 concentration (ambient CO_2 concentration,

231 approximately 380 ppm) applied. Cedergreen and Olesen (2010) showed that the promotion

232 effects on barley plant growth with low-dose glyphosate application were absent or much weaker

233 at relatively low light availability or CO_2 concentrations. We expected that an increase in the

234 photosynthesis rate would explain the enhanced growth; however, no significant effects on the

235 photosynthetic capacity of maize seedlings were observed (Fig. 3), although the respiration rate

236 was indeed higher for the low water extract concentration of 0.0125 g/ml than that of the control

237 and the 0.2 g/ml treatment. Simijlar to our results, application of low concentration microcystins,

238 a group of cyanotoxins produced by cyanobacteria, also stimulated the growth (plant height and

239 biomass accumulation) in rice seedlings, but did not stimulate photosynthesis rate of the plants

240 (Liang and Wang, 2015).

241 Two explanations are possible for the lack of significant effects on the photosynthetic

242 capacity. First, unlike glyphosate, the shoot water extract of *S. canadensis* is a mixture of diverse

243 compounds that includes small to large molecules with differential dose-effect curves or that

244 even cause effects in contrasting directions. Therefore, the integrated action of these compounds

245 may lead to less pronounced effects compared with the unique effects of glyphosate (Duke et al.,

246 2006). These compounds in *S. canadensis* have been categorized as phenolics, flavones and

247 saponins (Yuan et al, 2013; BaležEntienė, 2015). The other explanation is that the activity of

248 Rubisco, RuBP regeneration or the use rate of triose phosphate was not enhanced in the maize

249 leaves due to the similar leaf N content. The leaf photosynthesis rate under ambient air conditions

250 is most limited by Rubisco activity and leaf nitrogen content (Sinclair and Horie, 1989; Makino,

251 2003). Thus, the photosynthesis rate in our study was not affected because the water extract

252 treatment may not have increased the leaf nitrogen content..

253 The increase in the dark respiration rate of maize seedlings at the low concentration of

254 water extract, which is similar to that in barley plants treated with a low dose of glyphosate

255 (Cedergreen and Olesen, 2010), may explain the increase in maize plant height, leaf area and

256 length and root length. In hormesis, the increase in root and shoot growth is interpreted as an

257 adaptive mechanism of escape from stressful conditions (Duke et al, 2006). The increase in

258 respiration rate indicated increased metabolic activity in response to the toxic water extract,

259 which   may   enable   the   recipient   plant   to   activate   detoxification,   inactivation   or

260 compartmentalization processes (Cedergreen and Olesen, 2010). In addition, we observed a

261 pattern of allocating more resources towards aboveground growth at low water extract

262 concentrations, which could be a strategy to escape from the harmful underground conditions,

263 even though root growth was also promoted at low water extract concentrations. Other

264 environmental factors, such as mineral nutrient supplements, play important roles in growth

265 stimulation by increasing the aboveground biomass allocation parameters, such as SLA and LAR

266 (Poorter and Nagel, 2000). The increases in SLA and LAR suggested greater allocation to shoot

267 and leaf growth, which can increase the photosynthetic area relative to other nonphotosynthetic

268 organs. The concentration range that stimulated shoot growth overlapped with the range that

269 stimulated SLA and LAR (Figs. 1, 2 and 3). Furthermore, the positive correlations between SLA

270 and LAR and plant shoot height suggested that the promotion of growth with the low-dose water

271 extract was due more to the increase in assimilation area than to the increase in assimilation

272 capacity (per unit leaf area). The increase in SLA may be explained by either a moderate

273 increase in reactive oxygen species (Prithiviraj et al., 2006) or an inhibition of lignin synthesis

274 (Duke et al., 2006), which both occur at low-dose treatments. In another study on the hormetic-

275 like effects of *S. canadensis* extracts, the ability of the recipient plant to cope with stress, as

276 indicated by the activities of SOD (Superoxide dismutase) and other enzymes, was stimulated at

277 low extract concentrations but was inhibited at high concentrations (Zhang et al, 2012),

278 suggesting that the mechanisms also act at the physiological level.

279   Although whether a stimulatory effect occurs in fields where *S. canadensis* invades is not

280 clear, fast growth together with high SLA and LAR could have significant ecological

281   consequences for those plants that are affected by low-dose phytotoxins because these plants

282   with relatively fast growth rates may have increased vulnerability to mechanical stress or

283   herbivory (Belz et al., 2011). These secondary consequences should also be considered when

284   explaining crop yield loss caused by exotic plant invasion.

285   In summary, the water extract of *S. canadensis* had significant effects on maize seedling

286   growth, suggesting that the interactions of *S. canadensis* with crops or native species in fields

287   could be affected. The effects were highly dependent on the concentration; the stimulated growth

288   caused by the low-concentration water extract of *S. canadensis* shoots on maize seedlings growth

289   could be explained mostly by the biomass allocation patterns (leaf SLA and LAR) but not by the

290   gas exchange capacity. Therefore, the investigation of the concentration of allelopathic

291   compounds of *S. canadensis* in the field is critical to the study of their possible effects on native

292   species.

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350

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Figure 1

Growth of the maize seedlings exposed to the different water extract concentration treatments

(A) Plant height, (B) Total leaf length, (C) Total leaf area and (D) Total root length. 0-12 on the horizontal axis corresponds to water extract concentration: 0, 0.0125, 0.025, 0.05, 0.075, 0.1, 0.125, 0.15, 0.175, 0.2, 0.225 and 0.25 g/ml, respectively. The points in the plot refer to mean ± standard error.

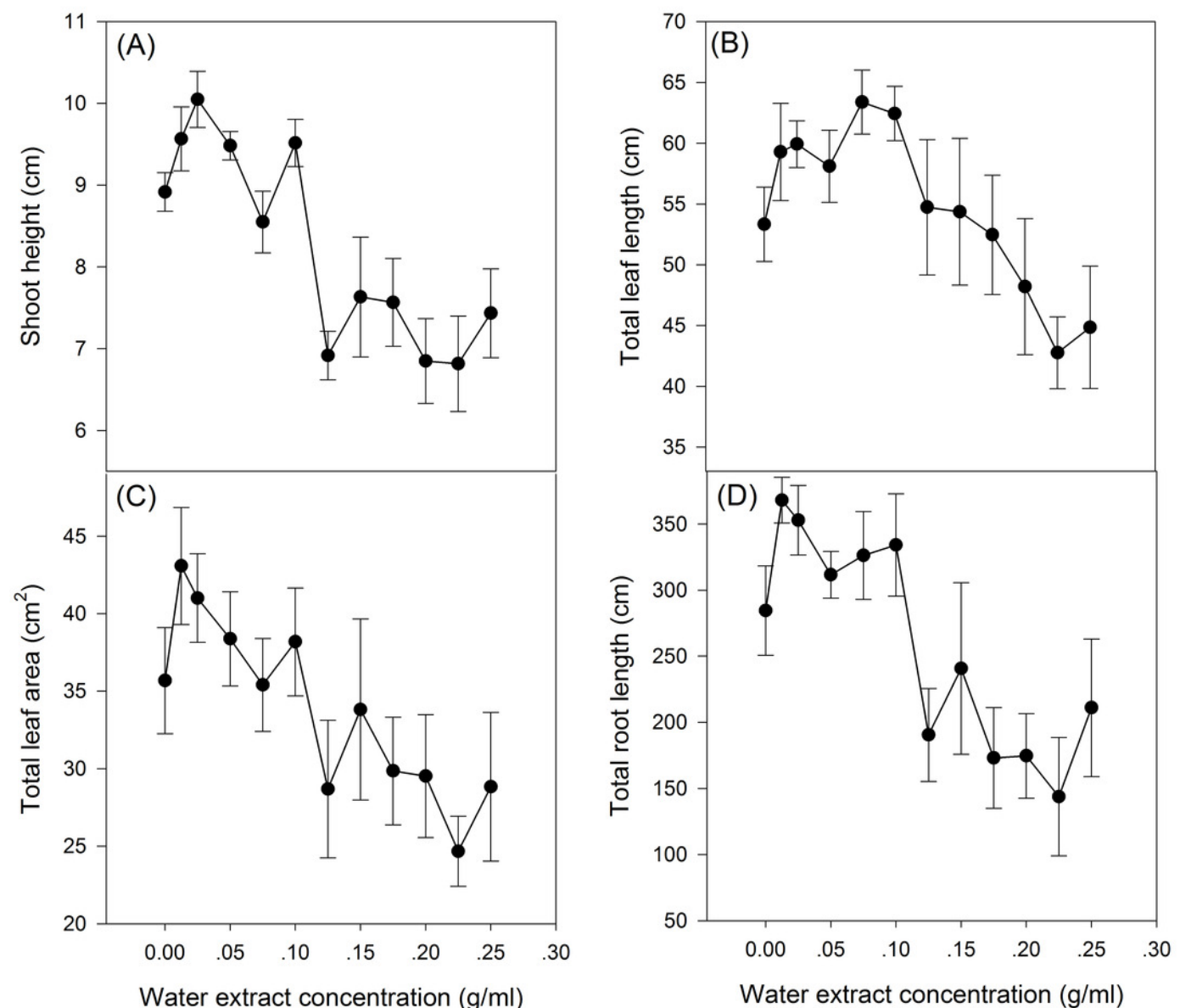



Figure 2

Biomass of the maize seedling treated with different concentrations of shoot water extract from *S. canadensis.*

Biomass of (A) Stem, (B) Leaf, (C) Root and (D) Whole plant of the maize seedlings.

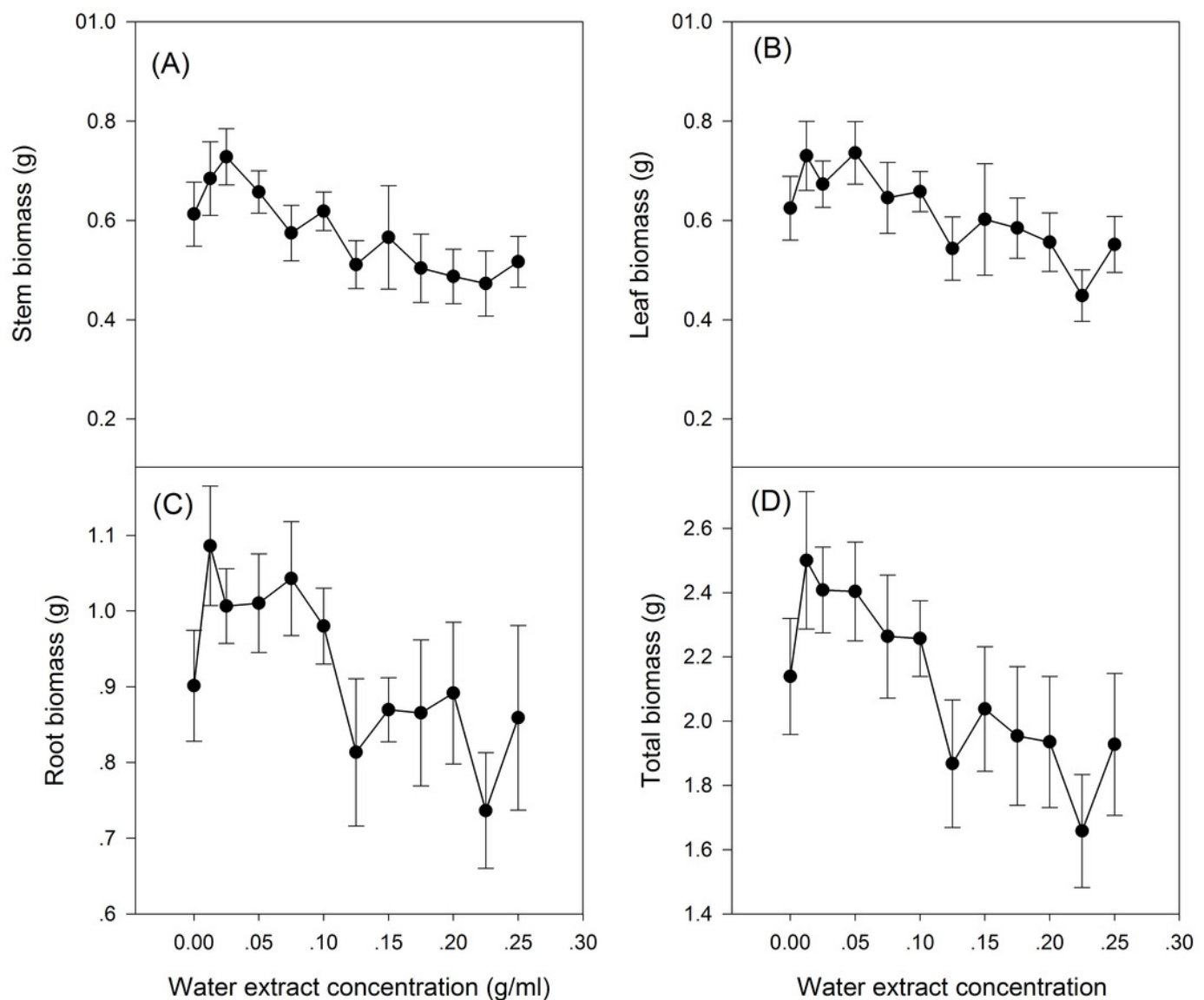



Figure 3

Biomass allocation to leaf of the maize seedlings treated with different concentrations of shoot water extract from *S. canadensis.*

(a) Specific leaf area (SLA), (b) Leaf mass ratio (LMR) and (c) Leaf area ratio (LAR). The points in the plot stand refer to mean ± standard error.

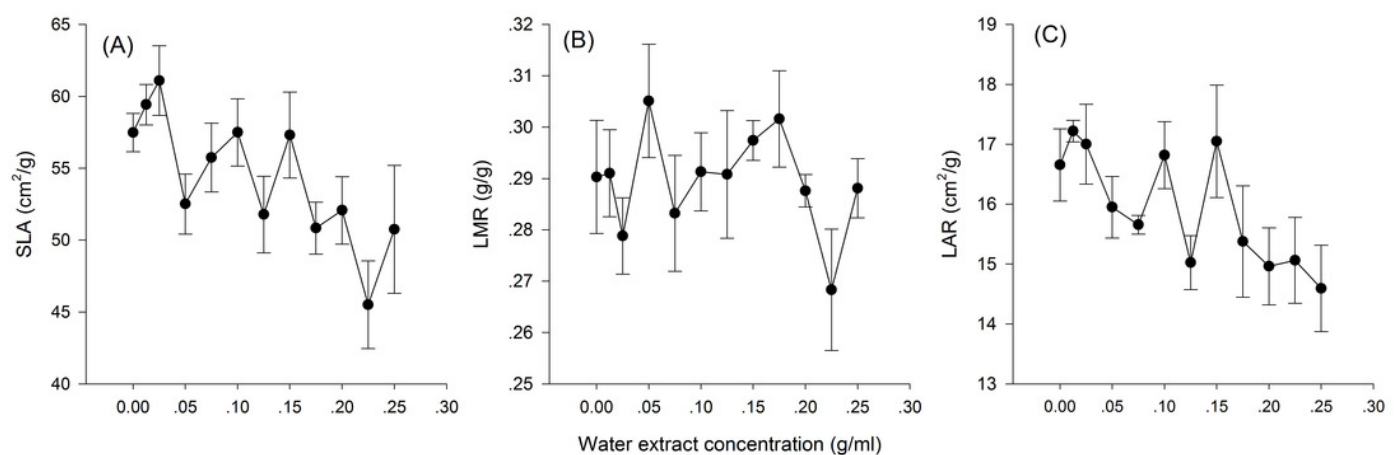



Figure 4

Gas exchange characteristics of the maize seedlings treated with the three shoot water extract concentrations from *S. canadensis.*

CK (control, 0.000 g/ml), Low concentration (0.0125 g/ml) and High concentration (0.2 g/ml). (A) P_{max} , light-saturated photosynthesis rate, (B) AQY, apparent quantum efficiency and (C) R_d, dark respiration rate. The points in the plot stand refer to mean ± standard error.

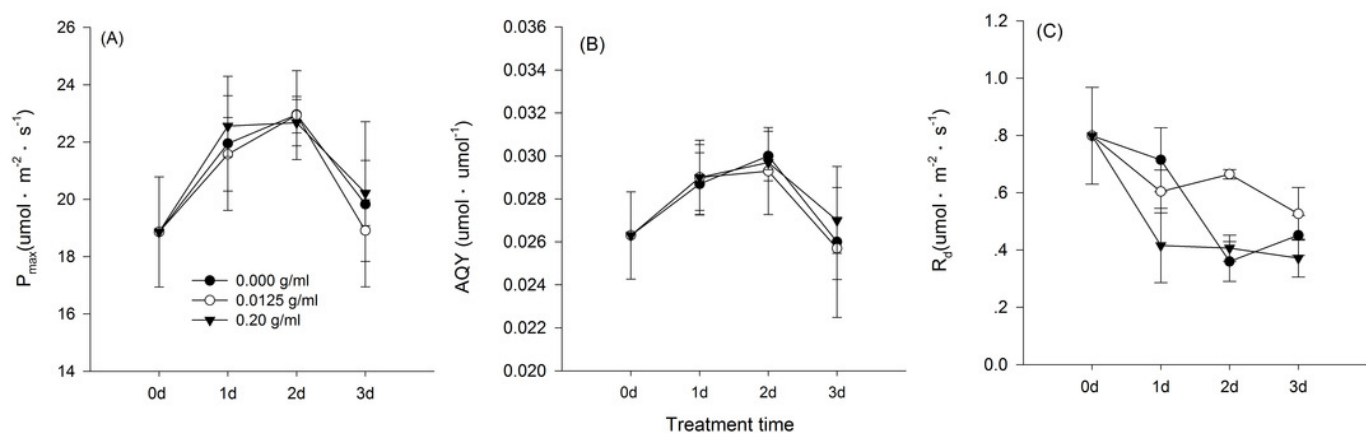
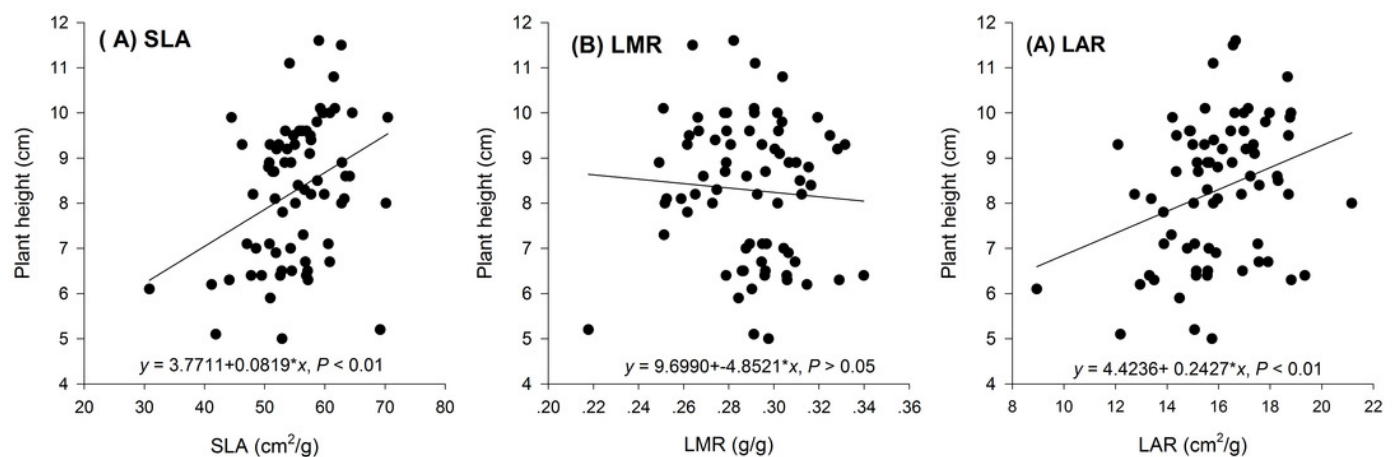



Figure 5

Regression of biomass allocation to leaf against the plant shoot of the maize seedlings treated with different concentrations of shoot water extract from *S. canadensis*.

(A) Specific leaf area (SLA), (B) Leaf mass ratio (LMR) and (C) Leaf area ratio (LAR) of the maize seedlings treated with different concentrations of shoot water extract from *S. canadensis*.

One-way ANOVA analysis for growth and biomass accumulation of the maize seedlings treated with different concentrations of water extracts from shoots of the *S. canadensis* plants

[z] *P* is the siginificance of the statistics. When *P* < 0.05, it is considered to be significant. [*]*P* < 0.05, [**], P< 0.01, [***] P < 0.001. When P > 0.05, it is considered to be not significant. [ns] indicates no significance.

3 **Table 1 One-way ANOVA analysis for growth and biomass accumulation of the maize seedlings treated with**

4 **different concentrations of water extracts from shoots of the *S. canadensis* plants**

Growth	*df*	F	P^Z	Growth	*df*	F	P^Z
Plant height	11,59	7.242	0.000^{***}	Stem mass	11,59	1.763	0.081^{ns}
Total leaf length	11,59	2.551	0.010^{*}	Leaf mass	11,59	1.597	0.123^{ns}
Total leaf area	11,59	2.204	0.026^{*}	Root mass	11,59	1.187	0.316^{ns}
Total root length	11,59	4.284	0.000^{***}	Whole plant mass	11,59	1.494	0.158^{ns}
LMR	11,59	1.173	0.325^{ns}	LAR	11,59	1.502	0.155^{ns}
SLA	11,59	1.891	0.059^{ns}	Root/shoot ratio	11,59	1.017	0.433^{ns}

Two-way ANOVA analysis for gas exchange characteristics of the maize seedlings treated with different concentrations of water extract from shoots of the *S. canadensis* plants.

CK (0.000 g/ml), Low concentration (0.0125 g/ml) and High concentration (0.2 g/ml); ^{z} P is the siginificance of the statistics. When $P < 0.05$, it is considered to be significant. $^*P < 0.05$, **, $P < 0.01$, $^{***}P < 0.001$. When $P > 0.05$, it is considered to be not significant, and ^{ns} indicates no significance.

2   **Table 2 Two-way ANOVA analysis for gas exchange characteristics of the maize seedlings treated with**

3   **different concentrations of water extract from shoots of the *S. canadensis* plants: CK (0.000 g/ml), Low**

4   **concentration (0.0125 g/ml) and High concentration (0.2 g/ml)**

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Variation source	df	F	P^Z
Light-saturated photosynthesis rate			
Treatment	2	0.095	0.91^{ns}
Day	3	3.859	0.022^*
Treatment ×day	6	0.055	0.999^{ns}
Apparent quantum efficiency			
Treatment	2	0.05	0.951^{ns}
Day	3	2.653	0.072^{ns}
Treatment× day	6	0.043	0.96^{ns}
Leaf dark respiration rate			
Treatment	2	5.856	0.004^{**}
Day	3	2.261	0.126^{ns}
Treatment ×day	6	0.968	0.467^{ns}