

1 **Effects of planting density on the growth and photosynthetic characteristics of *Alternanthera***
2 ***philoxeroides* under different nutrient conditions**

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23 **Abstract**

24 Density and nutrient level are important factors that might affect the growth of invasive
25 plants. To reveal the effects of plant density on the performance of invasive plant *Alternanthera*
26 *philoxeroides* under different nutrient conditions, a greenhouse experiment was conducted in
27 which *A. philoxeroides* was planted at three densities (low, medium and high) under three
28 nutrient levels (low, medium and high). The results showed that both planting density and
29 nutrient levels had significant effects on the growth of the plant. The biomass of individual plant
30 and all plants in one pot under medium nutrient level were the highest while the photosynthetic
31 rate and total chlorophyll content were the highest at the high nutrient level. Under different
32 nutrient levels, the photosynthetic rate was the highest at medium planting density. The biomass
33 of single plant decreased with the increase of population density, while the total biomass in the
34 whole pot increased with the increase of density. These characteristics might contribute to the
35 invasion of *A. philoxeroides* and help the plant to form monodominant community.

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37 *keywords: Alternanthera philoxeroides; Biomass; Nutrients; Population density; Photosynthesis.*

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45 Introduction

46 Biological invasion has far reaching impacts on ecological functions and the ecological
47 diversity of native environments [1-5]. The invasive species have high fecundity, and once the
48 invasion succeeds, it is easy to form the predominant population. The success of biological
49 invasion is not only determined by the physiological and genetic characteristics of invasive
50 species, but also by the factors such as population density and nutrient levels [6-10].

51 The nutrient is one of the important factors for plant growth. Previous studies have found
52 that traits associated with the resource used determine the invasion success of several invasive
53 species [11, 12]. Invasive plants generally show stronger photosynthesis and growth when
54 invading habitats with richer nutrients [12-15]. Therefore, the nutrient level is also associated
55 with the invasion success [9]. The research on the influence of nutrient on invasive plants plays
56 an important role in understanding the successful plant invasion.

57 The competition among plants is also an important factor affecting the spatial distribution,
58 dynamics and species diversity, promoting the succession of communities [16]. Invasive plants
59 can replace local plants through interspecific competition, accomplishing the process of
60 successful invasion [17]. However, when invasive plants spread to a certain extent, there is a
61 degree of intraspecific competition. In order to adapt to this change, plants tend to change their
62 own characteristics, such as plant height, biomass of branches and physiological characteristics
63 of leaves, etc [18, 19]. And this phenotypic plasticity allows invaders to allocate more nutrients
64 than their native counterparts to increase biomass [20, 21]. Several studies found that the
65 physiological indexes of invasive plant under high density are less than those under low
66 population density [8, 22]. Plant density determines the competitiveness of aquatic clonal plants

67 in complex habitats [23]. Therefore, we can analyze the growth mechanism by studying the
68 morphological changes of plant. At the same time, the effect of population density on invasive
69 plants is one of the core problems in the study of invasion ecology at present [24].

70 Aquatic species might have a fast response to nutrient enrichment, increasing their biomass
71 rapidly, which is particularly true in the aquatic invasive species [9, 25-27]. Therefore, aquatic
72 invasive species affects the productivity and management of land and water resources
73 worldwide [28]. *A. philoxeroides* is one of these aquatic invasive plants. It is a clone weed that is
74 native to South America and it is a stoloniferous and rhizomatous perennial herbaceous plant
75 [28-30], which propagates clonally and expands rapidly in both aquatic and terrestrial habitats
76 [31-34]. *A. philoxeroides* has experienced an invasion history of more than 80 years in China and
77 become one of the most harmful invasive species [34]. At present, there are many researches
78 focused on the physiological characteristics of *A. philoxeroides*, its response to natural
79 environmental factors, and biological and chemical control [10, 35-37]. Many studies have shown
80 that if the plant has a high photosynthetic rate, and it usually grows and propagate rapidly [38,
81 39]. Moreover, the invasive capacity of invasive plants is closely related to the ability of
82 photosynthesis, they often enhance its invasive ability by increasing the photosynthesis of
83 ramets [40, 41]. Thus, studying the photosynthetic capacity of *A. philoxeroides* is essential for
84 understanding the potential of invasive species and to develop appropriate control strategies.

85 Our previous studies have compared the growth of *A. philoxeroides* with native plants [10].
86 So in the present study, we conducted a greenhouse experiment which combined nutrient levels
87 with planting density to explore their effects on the growth and photosynthetic characteristic of
88 *A. philoxeroides*. We asked the following questions: (1) Will the increase of planting density

89 inhibit the growth of *A. philoxeroides* under various nutrient levels? (2) How do the nutrient level
90 and planting density affect the invasion of *A. philoxeroides*.

91

92 **Materials and methods**

93 **Ethics statement**

94 We collected plant material for our study with the official permission of the Environmental
95 Protection Bureau of Weishan County, and the Management Committee of the Weishan Lake
96 Constructed Wetland Park. We did not collect endangered or protected species.

97

98 **Plant material and experimental design**

99 The *A. philoxeroides* seedlings were collected from Weishan Lake Wetland Park, Shandong
100 province, in July 2017. The seedlings were cultured a week in the greenhouse of Fanggan
101 Research Station of Shandong University (36°26'N, 117°27'E). The method of sand culture was
102 used in the experiment, and the river sand was washed thoroughly before planting. The length of
103 the selected stem was about 11cm, and then was transplanted into a pot (h: 23.5cm; d: 22cm)
104 with 7 kg sand. Set up two factors in our experiment: the nutrient level of the sand and planting
105 density of *A. philoxeroides*. The nutrient treatments consisted of three levels (low, medium and
106 high; labeled as A, B and C) and three kinds of planting density (low, medium and high; 1, 2 and 4
107 seedlings per pot, respectively). In total, there were nine treatment combinations, each dealing
108 with five replicates. The nutrient levels and planting density settings in the experiment are
109 shown in Table 1.

110 **Table 1. Nutrient levels and planting density of *A. philoxeroides* at different treatment.**

Nutrient levels	TN (g kg ⁻¹ sand)	Amount of chemical fertilizer added (g kg ⁻¹ sand)	planting density	planting number (plant pot ⁻¹)
A	0.5	2.5	1	1
			2	2
			4	4
B	0.7	3.5	1	1
			2	2
			4	4
C	2.1	10.5	1	1
			2	2
			4	4

111 *A, B, and C: low, medium and high nutrient levels.

112 In the experiment, the compound fertilizer with the ratio of nitrogen and phosphorus (N: P
113 = 4: 1) similar to Nansi Lake was used as the nutrient source. According to our previous
114 experiments, the medium nutrient gradient in this experiment is the most suitable for the
115 growth of *A. philoxeroides* [37]. Water 200 mL every day, in order to ensure the normal growth
116 of *A. philoxeroides*, and would not lead to the loss of fertilizers in the pot. At the time of
117 fertilization, grounding the fertilizer into powder, then half dissolved in 200 mL of water each
118 time, added for two days, to prevent once adding cause damage to plants. At the time of
119 experiment, the low nutrient level was added the fertilizer only in the first week; medium and
120 high nutrient levels were added every two weeks during the experiment. The time of the

121 experiment was from the July 24, 2017 to September 20, 2017.

122

123 **Determination of photosynthetic rate and light response**

124 **curve**

125 The photosynthetic characteristics of each group were measured by a Portable
126 Photosynthesis System (*LI-COR 6800*, USA) using PAR of 1000 $\mu\text{molm}^{-2}\text{s}^{-1}$. Leaves were measured
127 under ambient CO_2 concentration [$385 \mu\text{molmol}^{-1}$] [42]. The light response curves were
128 measured under the PAR of 1600, 1200, 1000, 800, 600, 400, 200, 100, and 0 $\mu\text{molm}^{-2}\text{s}^{-1}$ [42].
129 The fitting of the light response curve adopts a non - right - angle hyperbolic model, and the
130 model formula is:

$$131 \quad Pn = \frac{\alpha I + Pn_{\max} - \sqrt{(\alpha I + Pn_{\max})^2 - 4\theta\alpha I Pn_{\max}}}{2\theta} - Rd$$

132 In this formula, α is the apparent quantum rate; I is the light quantum flux density; Pn_{\max}
133 is the maximum photosynthetic rate; Rd is the dark respiration rate; θ is the angle parameter
134 that reflects the degree of bending of the light response curve, and the range of values is $0 \leq$
135 $\theta \leq 1$ [43]. According to the light response curve, we calculated the light compensation point
136 (LCP) and the light saturation point (LSP).

137

138 **Determination of chlorophyll content**

139 In each treatment, using a volume fraction of 95% ethanol extract chlorophyll, then the
140 spectrophotometer was used to measure the absorbance values at 649nm and 665nm
141 wavelength [44]. The concentration of chlorophyll a, chlorophyll b and total chlorophyll were
142 calculated according to the formula:

$$Ca = 13.95A_{665} - 6.88A_{649}$$

$$Cb = 24.96A_{649} - 7.32A_{665}$$

143 $Cr = Ca + Cb = 18.08A_{649} - 6.63A_{665}$

144 In the formula, Ca, Cb and Cr represent the concentrations of chlorophyll a, chlorophyll b and
145 total chlorophyll respectively, [mg cm⁻²]; A₆₄₉ and A₆₆₅ represent the absorbance at the
146 wavelengths of 649 nm and 665 nm respectively [45].

147

148 **Determination of specific leaf area (SLA) of *A. philoxeroides***

149 Before harvest, randomly selected 20 mature leaves of each treatment, wiped clean and
150 flattened on the scanner. The determination of leaf area using Photoshop software.

151 Leaf area = the percentage of leaf pixels / background pixels · background paper area [46-48].

152 SLA = leaf area / leaf dry weight.

153

154 **Determination of morphological indexes of *A. philoxeroides***

155 We measured the length of stolon and recorded the number of internode before harvest.

156 The internode length of *A. philoxeroides* under different treatments was calculated.

157

158 **Determination of biomass index of *A. philoxeroides***

159 At the end of the experiment, the roots of *A. philoxeroides* were washed thoroughly, and

160 the leaves, stems and roots of each treatment were respectively put into the envelopes,

161 numbered and then dried up to constant weight in an oven which the temperature was 80 °C,

162 recorded the dry weight of each part.

163

164 **Statistical analysis**

165 The date of different variables, such as biomass, photosynthetic rate, SLA and total
166 chlorophyll content was analyzed by two-way ANOVA with SPSS 21.0 software (Table 2). The
167 significance test in all tests was performed at a level of $P < 0.05$. Use Origin 8.5 software to draw
168 charts.

169 **Results**

170 **Table 2. The two-way ANOVA of the effects of the independent variable nutrient level and**
171 **plant density, and their combination on studied parameters of species *A. philoxeroides* in**
172 **the experiment.**

Indices	Source	df	F	p
Single leaf biomass	Density	2	56.564	<0.001
	Nutrient	2	114.140	<0.001
	Nutrient × Density	4	7.131	<0.001
Single biomass	Density	2	201.859	<0.001
	Nutrient	2	97.273	<0.001
	Nutrient × Density	4	17.055	<0.001
Total leaf biomass	Density	2	25.660	<0.001
	Nutrient	2	108.667	<0.001
	Nutrient × Density	4	5.568	0.001
Total biomass	Density	2	28.790	<0.001
	Nutrient	2	68.308	<0.001
	Nutrient × Density	4	3.485	0.017

Internode length	Density	2	77.514	<0.001
	Nutrient	2	4.017	0.027
	Nutrient × Density	4	2.251	0.083
SLA	Density	2	49.876	<0.001
	Nutrient	2	195.844	<0.001
	Nutrient × Density	4	1.751	0.160
Photosynthetic rate	Density	2	35.230	<0.001
	Nutrient	2	42.370	<0.001
	Nutrient × Density	4	3.346	0.020
Total chlorophyll content	Density	2	10.451	<0.001
	Nutrient	2	156.668	<0.001
	Nutrient × Density	4	0.502	0.735

173

174 **Effects of density on Plant Biomass Index and Morphology**

175 **Index under different nutrient gradients**

176 Results showed that the interaction between nutrient level and plant density significantly
 177 affect the leaf biomass of per plant, single plant biomass, total leaf biomass and total biomass of
 178 a whole pot (Table 2).

179 Under three nutrient levels, the leaf biomass of single plant and the biomass of single plant all
 180 decreased significantly with the increase of planting density (Table 3). Among various nutrient
 181 levels, under three planting density, the reduction rate of leaf dry weight per plant was 47.9%,
 182 53.9%, 62.5%; the reduction rate of biomass per plant was 57.2%, 64.4%, 63.4% (Table 3). At

183 different nutrient levels, the difference in the leaf biomass of per plant between low density (1)
184 and medium density (2) was slightly greater than the difference between medium density (2) and
185 high density (4) (Table 3). At every nutrient levels, there was a significant difference in the
186 biomass of single plant among all three planting densities (Table 3). In low nutrient level (A), the
187 difference between medium planting density (2) and high planting density (4) is slightly larger
188 than that between low planting density (1) and medium planting density (2) (Table 3). Under
189 medium nutrient (B) and high nutrient (C), the gap between low density (1) and medium planting
190 density (2) is slightly larger than medium planting density (2) and high planting density (4) (Table
191 3).

192 At the three nutrient levels, the total leaf biomass and the total biomass of a pot all
193 increased significantly with the increase of planting density (Table 3). To total leaf biomass of *A.*
194 *philoxeroides*, there was no significant difference between low planting density (1) and medium
195 planting density (2) under the treatment of low (A) and medium (B) nutrient levels and the
196 difference among the three planting densities was not significant under the high nutrient level (C)
197 treatment (Table 3). For total biomass of a pot, at low nutrient level (A), the difference between
198 medium planting density (2) and high planting density (3) is significantly smaller than that
199 between low planting density (1) and medium planting density (2), besides there is no significant
200 difference between low planting density (1) and medium planting density (2) at medium (B) and
201 high (C) nutrient levels (Table 3).

202 According to the two-way ANOVA analysis (Table 2), there were have obvious interaction
203 between nutrient level and plant density on internode length of *A. philoxeroides*.

204 With the increase of planting density, the average internode length of *A. philoxeroides*

205 decreased in varying degrees, and the internode length was the longest at the treatment of low
 206 planting density (1) (Table 3). At the treatment of three nutrient levels, the average internode
 207 length of medium nutrient level (B) was the highest, is 5.6 cm (Table 3).

208 **Table 3. Different nutrient levels and different planting densities of *A. philoxeroides* biomass**
 209 **and morphological index.**

Treatments	Single leaf biomass (g)	Total leaf biomass (g)	Single biomass (g)	Total biomass (g)	Internode length (cm)
A1	2.90±0.56d	2.90±0.56e	22.83±3.35b	22.83±3.35d	5.66±0.28ab
A2	1.97±0.43e	3.94±0.88e	19.32±0.91c	38.64±1.83b	5.65±0.35b
A4	1.51±0.33e	5.80±1.30d	9.76±2.06de	39.03±8.25b	4.29±0.20d
B1	11.61±1.05a	11.61±1.05bc	40.52±3.03a	40.52±3.03b	6.60±0.61a
B2	7.21±2.13bc	14.42±4.25b	22.08±3.18b	44.16±6.36b	5.56±0.19c
B4	5.35±0.92c	21.38±3.66a	14.41±2.14cd	57.65±8.56a	4.65±0.50cd
C1	7.49±1.53b	7.49±1.53cd	21.38±2.60b	21.38±2.60d	6.05±0.40ab
C2	5.06±0.63c	10.11±1.26c	11.91±2.13d	23.83±4.26d	5.57±0.27c
C4	2.81±0.77de	11.25±3.07bc	7.83±0.91e	31.30±3.64c	4.55±0.06d

210 *A, B, and C: low, medium and high nutrient levels; 1, 2, and 4: the number of seedlings per pot.

211 Values are presented as means ±SD. Different letters indicate significant differences (p<0.05)

212

213 **Effects of plant density on SLA of *A. philoxeroides* under**
 214 **different nutrient levels**

215 According to the two-way ANOVA analysis (Table 2), there is no interaction between effects of
216 nutrient level and plant density on SLA of *A. philoxeroides*.

217 The SLA of *A. philoxeroides* increased significantly with the increase of nutrient level (Fig 1).

218 Different planting density had certain effects on the SLA of *A. philoxeroides*, which was the
219 highest under medium planting density (2) and the lowest under high planting density (4), and
220 both have significant differences (Fig 1).

221 **Fig 1. The SLA of *A. philoxeroides* at different nutrient level and plant density.** A, B, and
222 C: low, medium and high nutrient levels; 1, 2, and 4: the seedlings per pot. Values are
223 presented as means \pm SD. Different letters indicate significant differences ($p < 0.05$).

224

225 **Effects of density on photosynthetic rate and total chlorophyll** 226 **content of *A. philoxeroides* under different nutrient levels.**

227 We found that nutrient levels and planting densities on the photosynthetic rate of *A.*
228 *philoxeroides* has a obvious interaction, and for the total chlorophyll content, they had no
229 significant interaction to it (Table 2).

230 The analysis of photosynthetic rate and total chlorophyll content of *A. philoxeroides* under
231 different treatments showed that the change trend of the two indexes are basically the same,
232 and both of them increased with the increasing nutrient level (Fig 2). The photosynthetic rate of
233 medium planting density (2) of the three nutrient levels were the highest and had significant
234 differences, and they were the lowest under the treatment of high density (3) (Fig 2-A). The total
235 chlorophyll content of the medium nutrient (B) and high nutrient (C) had obvious differences (Fig
236 2-B). The total chlorophyll content of *A. philoxeroides* reached the maximum under high nutrient

237 level (C), and for the planting density, when the planting density was medium (2), the total

238 chlorophyll content of *A. philoxeroides* reached the maximum (Fig 2-B).

239 **Fig 2. The photosynthetic rate and chlorophyll content of *A. philoxeroides* at different**
240 **nutrient levels and plant densities.** A, B, and C: low, medium and high nutrient levels; 1, 2,
241 and 4: the number of seedlings per pot. Values are presented as means \pm SD. Different letters
242 indicate significant differences ($p < 0.05$).

243

244 **Effects of density on light response curve of *A. philoxeroides*** 245 **under different nutrient levels.**

246 The data were analyzed and fitted by SPSS software. The fitting coefficients (R^2) of the light
247 response curve of each group were all greater than 0.9, which showed that the curve fitting
248 degree was better and the photosynthetic characteristic of *A. philoxeroides* could be more
249 accurately reflected.

250 With the increase of the nutrient level, the maximum photosynthetic rate (Pn_{max}) of *A.*
251 *philoxeroides* increased in different degrees, so the Pn_{max} at the high nutrient level (C) were the
252 largest (Table 4). Among different planting density the Pn_{max} of *A. philoxeroides* were the largest
253 at the treatments of medium planting density (2), and the Pn_{max} of *A. philoxeroides* was minimal
254 under the high planting density (4) (Table 4). Besides, under the same nutrient level treatment,
255 there were significant differences among the three different planting densities on the Pn_{max} of *A.*
256 *philoxeroides* (Table 4).

257 The light compensation point (LCP) and light saturation point (LSP) of *A. philoxeroides* under
258 different nutrient treatments were the biggest when planting density was medium (2), and when
259 the planting density was high level (4), the value of LCP and LSP were the smallest (Table 4). At
260 the same planting density, both LCP and LSP increased with increasing nutrient levels, among
261 them, there was a larger gap between medium nutrient (B) and high nutrient (C) (Table 4). Under

262 the same nutrient level, at the difference of the value of LCP and LSP between medium planting
263 density (2) and high planting density (4) was larger than that between medium planting density
264 (2) and low planting density (1) (Table 4).

265 **Table 4. Light response curve parameters of *A. philoxeroides* at different nutrient levels and**
266 **planting densities.**

Treatments	Pn _{max}	LCP	LSP
A1	4.79 ± 0.30g	51.54 ± 4.60fg	250.21 ± 14.90e
A2	6.08 ± 0.28f	56.39 ± 4.46f	283.08 ± 9.79d
A4	3.77 ± 0.25h	40.68 ± 3.92h	205.30 ± 16.82f
B1	7.55 ± 0.34e	65.48 ± 3.67e	307.15 ± 8.56c
B2	8.34 ± 0.50d	72.2 ± 2.951d	341.17 ± 13.12b
B4	6.25 ± 0.18f	45.86 ± 1.42g	238.56 ± 4.46e
C1	11.31 ± 0.43b	91.21 ± 4.79b	377.10 ± 30.20ab
C2	13.40 ± 0.56a	117.73 ± 2.47a	392.55 ± 6.47a
C4	10.00 ± 0.82c	84.09 ± 4.33c	355.47 ± 21.62b

267 *A, B, and C: low, medium and high nutrient levels; 1, 2, and 4: the number of seedlings per
268 pot. Values are presented as means ±SD. Different letters indicate significant differences (p<0.05)

269

270 Discussion

271 In our experiment, nutrient and planting density had significant interaction effects on the
272 biomass accumulation of *A. philoxeroides*. Under the same planting density, the biomass
273 accumulation of *A. philoxeroides* could be promoted by increasing nutrients [49-51]. And our

274 previous studies concluded that compared with native plants, the *A. philoxeroides* had better
275 environmental adaptability and higher biomass and ratio of leaf area under different nutrient
276 conditions [10, 37]. At the treatment of medium nutrient level, the whole pot biomass of *A.*
277 *philoxeroides* among three different planting densities was the highest, indicating that too high
278 nutrient levels could be harmful for *A. philoxeroides* at the initial stage. At medium nutrient level,
279 the increase of planting density had the most obvious effects on the single plant biomass of *A.*
280 *philoxeroides* and the effects will be weakened at low nutrient. Therefore, we conclude that
281 under appropriate nutrient level, the effects of planting density on the growth of *A. philoxeroides*
282 were nutrient dependent. Some studies have shown that at same nutrient condition, the
283 biomass of invasive plants increased more than that of native plants [52]. So in our experiments,
284 under the same nutrient level, although the biomass of single plant was reduced with the
285 increase of planting density, the total biomass of the plant in whole pot was increased, especially
286 at low nutrient. That would enhance the invasive ability of *A. philoxeroides*.

287 In addition, according to the leaf biomass of *A. philoxeroides*, we analyzed the SLA of *A.*
288 *philoxeroides*. In our study, with the increase of nutrient level, the SLA of *A. philoxeroides*
289 increased, which is consistent with the studies on SLA of other plants [53-55]. Similarly, the
290 increase of planting density has different influences on the SLA of *A. philoxeroides*. In this study,
291 the SLA of *A. philoxeroides* was the highest under medium planting density treatment. SLA is one
292 of the important plant leaf traits and closely related to plant growth and survival strategy. Its
293 value can reflect the ability of plant leaves to intercept light and self-protection in bright light
294 [56]. It is closely related to the photosynthesis and respiration of plants [57]. We therefore
295 concluded that at the medium planting density, the leaf of *A. philoxeroides* had a higher net

296 photosynthetic rate. So we then analyzed the photosynthetic rate of rate of each treatments to
297 confirm our conclusion.

298 In this study, photosynthetic rate had increase with the increasing nutrient levels that is
299 consistent with previous studies [58-60]. Among the three kinds of plant density treatment, the
300 photosynthetic rate in medium planting density was the highest, and the difference with high
301 planting density was obvious. Chlorophyll is the main pigment of photosynthesis in plants, which
302 reflects the size of photosynthesis in plants [44]. By this experiment, we found that the content
303 of the total chlorophyll of *A. philoxeroides* had the same trend, indicating that under medium
304 planting density, plants can capture resources better [61].

305 In order to better understand the effects of planting density on the photosynthetic
306 characteristics of *A. philoxeroides* under different nutrient conditions, we studied the light
307 response curve parameters of *A. philoxeroides*. Photosynthetic parameters, such as maximum
308 photosynthetic rate (Pn_{max}), light compensation point (LCP) and light saturation point (LSP), are
309 important scientific basis for rapid growth of plants [62-64]. Light saturation point (LSP) can
310 reflected the adaptability of plants to strong light; the lower the light compensation point (LCP) is,
311 the better the normal photosynthesis is under the weak light and the maximum net
312 photosynthetic rate (Pn_{max}) reflects the utilization ability of *A. philoxeroides* to strong light under
313 different treatments. In our study, among the three kinds of nutrient, the Pn_{max} , LCP and LSP of
314 the *A. philoxeroides* seedlings in medium planting density were the largest, indicating that under
315 this treatment, *A. philoxeroides* had the strongest utilization ability and adaptability to glare, and
316 under high planting density, *A. philoxeroides* has better capability to utilize weak light. Moreover,
317 the photosynthetic parameters of the plant increased with the increasing nutrient levels. That is

318 similar to previous studies [65, 66]. It shows that the increase of nutrient will enhance the
319 utilization ability of *A. philoxeroides* to strong light. This suggests that at higher nutrient levels,
320 higher light intensities are required to produce more biomass, may be that is why the *A.*
321 *philoxeroides* has higher photosynthetic rate but the biomass is lower than the medium nutrient
322 level. Under the same nutrient level, the increase of planting density resulted in the decrease of
323 Pn_{max} , LCP and LSP and there were significant differences among the three planting densities. The
324 results suggested that the increase of planting density decreased the Pn_{max} of *A. philoxeroides*
325 and its ability to use strong light and its adaptability. Under the low nutrient level, there was no
326 obvious difference in the LCP between the medium and low planting density, which indicated
327 that under the low nutrient level, the high planting density *A. philoxeroides* had more obvious
328 photosynthetic ability at low light. But at the medium and high nutrient levels, the planting
329 density had more obvious influence on the LCP of *A. philoxeroides*, and the effects became more
330 obvious with the increase of nutrient level.

331 In conclusion, our study showed that at the three nutrient levels, the SLA, photosynthetic
332 rate and total chlorophyll content of *A. philoxeroides* at medium planting density were the
333 highest. What's more, although the biomass of single plant, SLA, photosynthetic rate and the
334 content of Chlorophyll reduced with the increase of planting density, the biomass of whole pot
335 tended to increase. These attributes may increase the competitive dominance of *A. philoxeroides*
336 and could help the *A. philoxeroides* population develop into a monodominant community.

337

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