Effect of different light conditions on the growth response of sugar beet to NaCl

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Abstract

It is known that sugar beet, derived from a halophytic wild ancestor, is highly salt-tolerant and that moderate concentrations of NaCl enhance its growth. However, the mechanisms of this improved growth performance by NaCl are not fully understood. In this study, we investigated the effects of NaCl on sugar beet growth under different light conditions and examined the relationship between light-induced oxidative stress and the beneficial effects of NaCl. Sugar beet seedlings in pots filled with fertilized soil were grown with different light intensities (low: 150–250 μmol $m^{-2}s^{-1}$ or high: 600–1,000 μmol $m^{-2}s^{-1}$) and NaCl treatments (irrigation with water with or without 50 mM NaCl) for 10 days. The enhanced sugar beet growth by NaCl application was only observed in plants with high light intensity treatments. Moreover, high light intensity treatment increased the shoot concentration of malondialdehyde, an indicator of oxidative stress, while NaCl application decreased it. While there was a positive correlation between Na concentration and the compatible solute glycine betaine in the shoots and roots under both light intensities, a significant negative correlation between the concentrations of glycine betaine and malondialdehyde was found only in the shoots under high light intensity. Because it is known that glycine betaine activates antioxidant enzyme activities and reduces oxidative stress responses, glycine betaine synthesized in response to NaCl accumulation may have reduced the oxidative stress caused by high light intensity in the shoots, which may have caused the enhanced growth

in sugar beet. Furthermore, the growth promotion by NaCl accumulation was accompanied by a significant decrease in NO_3–N concentration, which suggested that NaCl application affects nitrogen metabolism in sugar beet.

Keywords:

Beta vulgaris L. subsp. vulgaris; glycine betaine; light intensity; sodium chloride; oxidative stress

1. Introduction

Saline soils adversely affect crop growth, resulting in a reduction in crop production. It is estimated that soil salinity already occurs in 20% of the total cultivated and 33% of the irrigated agricultural land worldwide (Shrivastava and Kumar 2015). Saline soils consist of various salts, with NaCl being the predominant salt (Munns and Tester 2008; Tavakkoli et al. 2010). Excessive salt induces ionic and osmotic stress, which causes a water deficit, ion disequilibrium, and oxidative stress that adversely affects the plant's basic metabolic and physiological functions (Hasegawa 2013; Pang and Wang 2008). Plants that are adversely affected by salt stress are known as glycophytes and make up the majority of agricultural crops. In contrast, halophytes are salt-tolerant plants that have the ability to complete their life cycle under high salinity conditions (Tran et al. 2020), such as ice-plants (*Mesembryanthemum crystallinum*) and glasswort (*Salicornia*

53 *europaea*). In crops, sugar beet (*Beta vulgaris* L. subsp. vulgaris), which originated from a
54 halophytic wild ancestor, sea beet (*Beta vulgaris* L. subsp. maritima), is also highly tolerant to
55 salt stress and is often used to study the mechanisms of salt tolerance (Hossain et al. 2017).
56 Halophytes have been shown to cope with water stress by accumulating compatible solutes such
57 as glycine betaine (GB) and proline in their tissues under salt stress conditions (Singh et al. 2015).
58 In addition, GB plays an important role in plants under oxidative stress that are induced by
59 environmental stress, such as intense light and high temperatures (Sharma et al. 2019; Yang et al.
60 2005). In plants, oxidative stress is induced by various stresses, many of which are directly or
61 indirectly associated with photosynthesis (Foyer and Shigeoka 2010). For instance, excess energy
62 causes oxygen to be converted into reactive oxygen species (ROS) under high light conditions.
63 Moreover, salt stress also induces oxidative stress (AbdElgawad et al. 2016). Plants have
64 antioxidant mechanisms such as enhanced superoxide dismutase and catalase activities to
65 detoxify ROS (Tewari et al. 2004). However, insufficient function of the antioxidant mechanisms
66 could lead to induction of physiological disorders, such as a rapid decrease in photosystem II
67 activity, by oxidative stress (Murata et al. 2007).
68 Some halophytes and salt-tolerant plants grow better under mild NaCl conditions. For example,
69 it has been reported that the growth of ice-plants and sugar beets can be enhanced by 50–100 mM
70 NaCl (Kaburagi et al. 2014; Tran et al. 2020). Although Na might be required in the photosynthetic

71 pathways of C4 and CAM plants (Gorham 2006), plant species whose growth is promoted by
72 NaCl are often not C4 or CAM plants. The involvement of N nutrition has also been discussed,
73 as NaCl-induced growth enhancement in halophytes has been reported to be accompanied by
74 increased nitrate reductase activity and N concentration in the plant (Kaburagi et al. 2014; Ohta
75 et al. 1989; Tran et al. 2020). Interestingly, the activation of the antioxidative stress response by
76 NaCl is often accompanied by growth promotion (Reginato et al. 2014); however, its significance
77 in the beneficial effects of NaCl, rather than NaCl tolerance, has not been well studied.
78 Based on the above, we hypothesized that in some halophytes and salt-tolerant plants, the
79 activation of a NaCl-specific antioxidative stress response also reduces the damage caused by
80 oxidative stress from other factors, which results in improved growth. To evaluate this hypothesis,
81 we focused on light stress as an oxidative stress factor because excess light energy can be a factor
82 in ROS production. In this study, the effect of NaCl application under different light conditions
83 was investigated in sugar beet.
84
85 ## 2. Materials and Methods
86 ### *2.1. Plant cultivation and treatment*
87 Seeds of sugar beet (*Beta vulgaris* L. subsp. vulgaris cv. “Yukimaru”), kindly provided by
88 Nippon Beet Sugar Manufacturing Co., Ltd., were sown in vermiculite and germinated in a

89 growth chamber at 25°C. After germination, the seedlings were grown in a greenhouse at
90 Hokkaido University for two weeks. The seedlings were then transplanted into pots (7.5 cm in
91 diameter × 6.5 cm in height, one plant per pot) filled with commercial horticultural soil that was
92 fertilized with 340 mg of N, 590 mg of P, 180 mg of K, and 90 mg of Mg per liter of soil (Hokusan
93 Co., Ltd., Japan). The pots were irrigated with 60 mL of deionized water every two days from the
94 top of the pots. Fourteen days after transplanting, the pots were moved to a cultivation room with
95 a temperature of 23°C–25°C and a humidity of 50%–60%, and the light intensity and NaCl
96 treatments were conducted for 10 days. A factorial design of two light levels and two NaCl levels
97 was used in this study. For Na treatment, the plants were irrigated daily with 60 mL of
98 demineralized water (Control) or 50 mM NaCl solution from the top of the pot, as described above.
99 The Na concentration in the soil after each Na treatment is presented in the Supplementary Data
100 (Table S1). Light treatment was provided by an LED for plant cultivation (WAKYME, Shenzhen,
101 China) with either a low (150–250 μmol $m^{-2}s^{-1}$) or high (600–1,000 μmol $m^{-2}s^{-1}$) light intensity.
102
103 ***2.2. Sampling***
104 Sampling was conducted every two days, with triplicates. The plants were washed with
105 deionized water and divided into shoots and roots. The fresh weight (FW) of the shoots and roots
106 and the leaf area were measured. Samples were frozen in liquid nitrogen and stored at −80°C.

After lyophilization, the dry weight (DW) of the shoots and roots was measured. For the determination of malondialdehyde (MDA) concentration, samples stored in liquid nitrogen were used.

2.3. Lipid peroxidation

MDA concentration, an index of lipid peroxidation, was measured as previously described by Hodges et al. (1999), with minor modifications. Approximately 50 mg of shoot and root samples that were stored in liquid nitrogen were homogenized with 1 mL of 5% trichloroacetic acid (TCA). The homogenate was centrifuged for 10 min at 13,000 ×*g*. The supernatant was transferred to another tube. Then, 1 mL of 5% TCA was added to the precipitate. Extraction was performed via ultrasonication for 10 min in ice water, and the homogenate was centrifuged for 10 min at 13,000 ×*g*. The supernatant was collected and combined with the former supernatant. The combined supernatant was centrifuged at 13,000 ×*g* for 10 min. Then, 650 µL of the supernatant was mixed with 650 µL of +thiobarbituric acid (TBA) solution containing 20% TCA, 0.01% butylated hydroxyl toluene (BHT), and 0.65% TBA or –TBA solution containing 20% TCA and 0.01% BHT. The mixture was incubated at 95°C for 30 min, and the absorbance at 532 nm and 600 nm were measured. The MDA concentration was calculated using the following equation:

$$\mu\text{mol MDA/g FW} = \frac{(A_{532} - B_{532}) - (A_{600} - B_{600})}{155} \times 2 \times \frac{2}{1000} \times \frac{1000}{W}$$

where A is the absorbance of the sample with +TBA solution, B is the absorbance of a sample with –TBA solution, and W is the weight of the sample (mg).

2.4. Mineral analysis

Each 5–10 mg of plant sample was digested in 2 mL of 61% (w/v) HNO_3 (EL grade; Kanto Chemical, Tokyo, Japan) at 110°C in a DigiPREP apparatus (SCP Science, Montreal, Canada) for approximately 2 h until the solution had almost completely evaporated. After the samples had cooled, 0.5 mL of H_2O_2 (semiconductor grade; Santoku Chemical, Tokyo, Japan) was added, and the samples were heated to 110°C for an additional 20 min. Once digestion was complete, the tubes were cooled, and the samples were reconstituted to a volume of 5 or 10 mL by adding 2% (w/v) HNO_3 in Milli-Q water. To extract the water-soluble mineral elements in the soil, 12.5 mL of ultrapure water was added to 5 g of air-dried soil in a tube. The tubes were shaken for 30 min, centrifuged at 1,500 ×*g* for 10 min, and the supernatants were filtered through filter paper (No. 6, Advantec, Japan). The mineral concentrations in the samples were analyzed by inductively coupled plasma mass spectrometry (ELAN, DRC-e; Perkin-Elmer, Waltham, MA, USA).

To analyze nitrate (NO_3^-), 1.8 mL of ultrapure water was added to 5 mg of lyophilized plant sample and incubated for 20 min at 80℃. After centrifugation at 13,000 ×*g* for 15 min at 4°C, the supernatant was collected and stored at −20°C. Just before measurement, the sample solution was

143 filtered through a 0.45-μm membrane filter (Advantec). The NO_3^- concentration was determined
144 by capillary electrophoresis (Quanta 4000 CE, Waters, Milford, MA, USA). The measurement
145 conditions were as follows: electrolyte = 1.25% CIA-PaK™ OFM anion-BT (Waters), 5 mM
146 sodium chromate; capillary = fused silica (75 μm × 60 cm); run voltage = 20 kV (negative power
147 supply); and detection = 254 nm.
148 To determine the plant N concentration, each 25 mg sample was digested with 1.25 mL of
149 concentrated H_2SO_4 in a test tube at 200°C. At 30 min intervals, 0.3 mL of H_2O_2 was added to
150 each tube for a total of eight times, following which the N concentration in the digests was
151 determined using the micro-Kjeldahl method.
152
153 ***2.5. Glycine betaine analysis***
154 GB concentration was measured as previously described by Nishimura et al. (2001), with minor
155 modifications. The water extract for the plant NO_3^- analysis was also used for GB analysis. To
156 determine the GB concentration in the plant, 0.2 mL of the water extract was combined with 0.1
157 mL of buffer solution (100 mM $KHCO_3$:100 mM KH_2PO_4:acetonitrile at a ratio of 1:1:4) and 0.6
158 mL of p-bromophenacyl bromide (20 mg mL^{-1} acetonitrile solution) and incubated for 75 min at
159 80°C. After cooling to room temperature (25°C), the mixture was filtered through a 0.45-μm
160 membrane filter (Advantec). The measurement was performed via capillary electrophoresis

(Quanta 4000 CE, Waters). The measurement conditions were as follows: electrolyte = 50 mM Na_2PO_4 (pH 3.5); capillary = fused silica (75 μm × 60 cm); run voltage = 15 kV (positive power supply); and detection = 254 nm.

2.6. Statistical analysis

Data were subjected to analysis of variance (ANOVA) to evaluate the differences among treatments. Multiple comparisons after ANOVA were performed with Tukey's multiple comparison test. Pearson's correlation analyses were used to evaluate the relations between GB concentration and other parameters. All statistical analyses were performed using Sigmaplot 14.5 (Systat Software, Inc., San Jose, CA, USA) and Excel 2013 (Microsoft, Redmond, WA, USA).

3. Results

3.1. Plant growth

The changes in DW with time after the start of the treatment are shown in Fig. 1, and photographs of the growth at day 10 for each light treatment are shown in Fig. S1. The effect of the treatment was apparent from day 6 after the start of the treatment. For the light treatments, the growth under the low light treatment was less than under the high light treatment. While no effect of NaCl treatment was observed under the low light treatment, the growth of both shoots and roots under

179 the high light treatment was significantly higher in the 50 mM NaCl treatment than in the Control
180 treatment after 6 days of treatment.
181
182 ***3.2. Lipid peroxidation***
183 As an index of lipid peroxidation, the MDA concentration was determined. The MDA
184 concentration in the shoots was relatively high on day 2, immediately after the plants were
185 transferred from the greenhouse, but temporarily decreased on day 4 and increased under high
186 light conditions from day 6 (Fig. 2). The shoot MDA concentration was reduced by the 50 mM
187 NaCl application on days 8 and 10. However, the effects of light intensity and NaCl application
188 on the root MDA concentration were unclear (Fig. 2).
189
190 ***3.3. Mineral concentration***
191 Na concentrations in the shoots and roots were significantly increased by NaCl treatment under
192 both light intensity treatments; however, the increase was smaller under low light conditions (Fig.
193 S2). K concentration was not significantly affected by NaCl application under low light intensity
194 in both the shoots and roots and exhibited little variation during the treatment period (Fig. S3).
195 However, under high light intensities, the K concentration tended to decrease with plant growth,
196 especially in the NaCl treatment (Fig. S3). Ca and Mg concentrations were little affected by the

197 treatment duration or NaCl treatment (Figs. S4 and S5). Similarly, shoot N concentration was not
198 affected by either treatment duration or NaCl treatment (Fig. S6). However, the NO_3–N
199 concentration was significantly reduced by NaCl treatment after day 6 of treatment under high
200 light intensity in the shoots and roots (Fig. 3).
201
202 ***3.4. Glycine betaine concentration***
203 Leaf and root GB concentrations tended to increase with NaCl application, especially under high
204 light intensity conditions (Fig. 4). There was a significantly positive correlation between the
205 concentration of GB and NaCl in both the shoots and roots and under both low and high light
206 intensity conditions (Fig. 5). In contrast, there was a significantly negative correlation between
207 the concentration of GB and MDA in only the shoots under high light intensity (Fig. 5). GB
208 concentration also exhibited a significant negative correlation with NO_3–N concentration, except
209 in the roots under low light intensity (Fig. 5).
210
211 **4. Discussion**
212 Na encompasses toxic and beneficial aspects to plant growth (Marschner 2012). As a toxic
213 element, excess Na in the medium or soil causes osmotic stress, ionic stress, and oxidative stress,
214 which inhibit plant growth (Parida and Das 2005). Of these, oxidative stress is caused by various

215 factors other than Na. Although light is essential for photosynthesis and plant growth, excess light
216 energy causes oxidative stress (Mittler 2002). This study focused on light intensity as another
217 source of oxidative stress and examined the involvement of antioxidative response in the
218 beneficial effects of NaCl in sugar beet. Sugar beets were grown at two levels of light intensity,
219 and the effects of NaCl application were compared between the light treatments. While the DW
220 was higher under high light treatment, MDA, an indicator of oxidative stress, was also higher in
221 the shoots under high light treatment (Figs. 1 and 2). However, oxidative stress under high light
222 intensity was significantly reduced by NaCl application, and the DW increased (Fig. 1 and 2). No
223 significant effect of NaCl on DW and MDA was observed under low light intensity treatment with
224 low oxidative stress, which suggests that the enhanced growth by NaCl application under high
225 light treatment was due to the reduction of light-induced oxidative stress by NaCl.
226 GB, which accumulates at high concentrations as a compatible solute in salt-treated sugar beets,
227 has been shown to reduce the water potential in plants (Acosta-Motos et al. 2017). In addition, it
228 has been revealed to promote the activation of the oxidative stress response. GB has been
229 suggested to stabilize protein structure and induce specific genes that encode for enzymes
230 involved in ROS removal, thereby preventing the accumulation of ROS and enhancing the cell
231 membrane and photosynthetic systems (Alasvandyari et al. 2017; Chen and Murata 2011; Sofy et
232 al. 2020). Foliar application of GB to *Brassica juncea* has been reported to activate antioxidant

enzyme activities and reduce oxidative stress (Islam et al. 2021). In this study, the GB concentration in sugar beet shoots and roots increased with NaCl application under both light intensities, and this increase was more pronounced with longer treatment periods (Fig. 4). As there is a significant positive correlation between Na and GB concentrations, regardless of light intensity, in both the shoots and roots (Fig. 5), it is likely that Na accumulation induced GB synthesis. However, for the correlation between GB and MDA, a significantly negative correlation was found only in the shoots under high light intensity (Fig. 5). This strongly suggests that GB, whose synthesis was enhanced by NaCl application, also secondarily reduced the oxidative stress caused by high light treatment, which resulted in the NaCl-induced enhanced growth observed only under high light treatment.

Interestingly, where the NaCl treatment had no significant effect on the shoot N concentration throughout the treatment period (Fig. S6), NaCl application significantly reduced the NO_3–N concentration as the treatment period progressed in both the shoots and roots (Fig. 3). A significant negative correlation was found between the GB and NO_3–N concentrations in the shoots (Fig. 5). Because GB is an N-containing compound, it is possible that NO_3–N was used for GB synthesis. However, it was reported that GB synthesis was not affected by N nutrition in Durum wheat under increased salinity conditions (Carillo et al. 2008). In contrast, the addition of GB to the medium/soil reduced the NO_3–N concentration in lettuce (Jokinen et al. 2022). These results

suggest that the reduction of NO_3–N by NaCl addition in sugar beet cannot be explained simply by the increased N utilization for GB synthesis. It could also be possible that the reduction of NO_3–N by NaCl application is related to the activation of N assimilation, and overall N metabolism might be affected. Further studies on N nutrition and the NaCl response of sugar beets are required.

Although this study revealed that the reduction of oxidative stress by GB, which is increased by NaCl, is one of the factors that promote growth with NaCl application under high light intensity, there remains a possibility for involvement of factors other than GB. In this study, high light intensity treatment significantly reduced K concentration in shoots and roots (Fig. S3). Thorne and Maathuis (2022) suggested that Na can substitute for some functions of K, and it is possible that the accumulation of high concentrations of Na might have alleviated K deficiency in sugar beet under high light intensity. An integrated understanding of the complexity of these NaCl-induced growth enhancements needs to be developed in the future.

5. Conclusion

In conclusion, this study suggested that GB, a compatible solute that accumulates in response to NaCl application, alleviated NaCl-induced stress and light-induced oxidative stress. The maximum photosynthetically active radiation in Hokkaido, where sugar beets are cultivated,

reached 1,600 μmol $m^{-2}s^{-1}$ on a sunny day (Kitao et al. 2000), which is higher than the high light treatment used in this experiment. Therefore, this secondary effect of GB may be one of the growth-promoting factors of NaCl application in sugar beet cultivation. Similarly, when toxic elements other than Na act as beneficial elements, they are often accompanied by the activation of antioxidative activity and reduction of oxidative stress; e.g., aluminum in tea plants (Hajiboland et al. 2013) and arsenic in *Pteris vittata* (Cao et al. 2004). These results imply that toxic elements, when act as beneficial elements, are generally related to common phenomena, i.e., the toxic element may act as a specific stimulant of antioxidative stress activity in some plant species that are highly tolerant to the element, thereby reducing the oxidative stress caused by other environmental factors and improving growth.

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Disclosure statement

No conflicts of interest declared.

286

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Figure captions

Figure 1. Shoot and root dry weight of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference ($P < 0.05$) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA.

Figure 2. The concentration of malondialdehyde (MDA) in the shoots and roots of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference ($P < 0.05$) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA. Root data on day 2 could not be obtained because of the low sample amount.

Figure 3. Shoot and root NO_3–N concentration of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference ($P < 0.05$) at

each sampling day using Tukey's multiple comparison test following a one-way ANOVA. Since the results in the root with high light/NaCl treatment on days 6, 8, and 10 were below the detection limit of the instrument (< 0.05 mg g^{-1}, shown as ND), statistical analysis was performed excluding this treatment.

Figure 4. Shoot and root glycine betaine (GB) concentration of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference (P < 0.05) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA.

Figure 5. Correlation graphs of glycine betaine (GB) concentration with malondialdehyde (MDA), Na, and NO_3–N in sugar beet shoots and roots under different light intensities. The numbers in the graph indicate Pearson's correlation coefficient. *, **, and *** indicate a significant difference at P < 0.05, 0.01, and 0.001, respectively.

Supplemental Materials

Figure S1. Photographs of the sugar beet at day 10 with NaCl treatment under each light treatment.

Figure S2. Shoot and root Na concentration of sugar beet grown with or without NaCl application

under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference ($P < 0.05$) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA.

Figure S3. Shoot and root K concentration of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference ($P < 0.05$) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA.

Figure S4. Shoot and root Ca concentration of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference ($P < 0.05$) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA.

Figure S5. Shoot and root Mg concentration of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error. Different letters indicate a statistically significant difference ($P < 0.05$) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA.

Figure S6. Shoot N concentration of sugar beet grown with or without NaCl application under different light intensities. Values are the means of triplicates. Range indicates ± standard error.

Different letters indicate a statistically significant difference ($P < 0.05$) at each sampling day using Tukey's multiple comparison test following a one-way ANOVA.

Table S1. Na concentration in the soil after each NaCl treatment for 10 days.

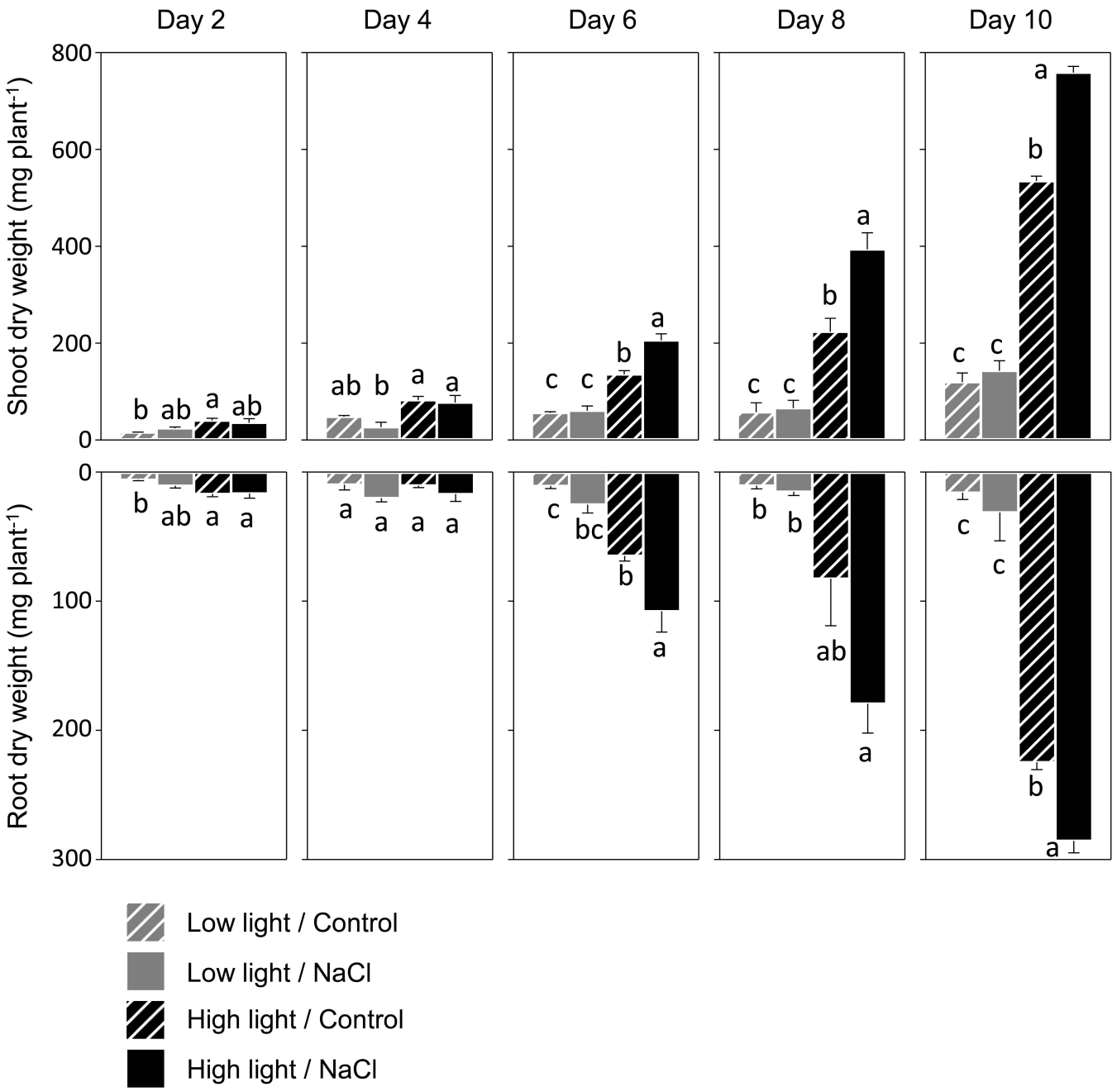
Day 2
Day 4
Day 6
Day 8
Day 10
Shoot dry weight (mg plant-1)
800
600
400
200
0
b ab a ab
ab b a a
c c b a
c c b a
c c b a
Root dry weight (mg plant-1)
0
100
200
300
b ab a a
a a a a
c bc b a
b b ab a
c c b a
Low light / Control
Low light / NaCl
High light / Control
High light / NaCl

Figure 1.

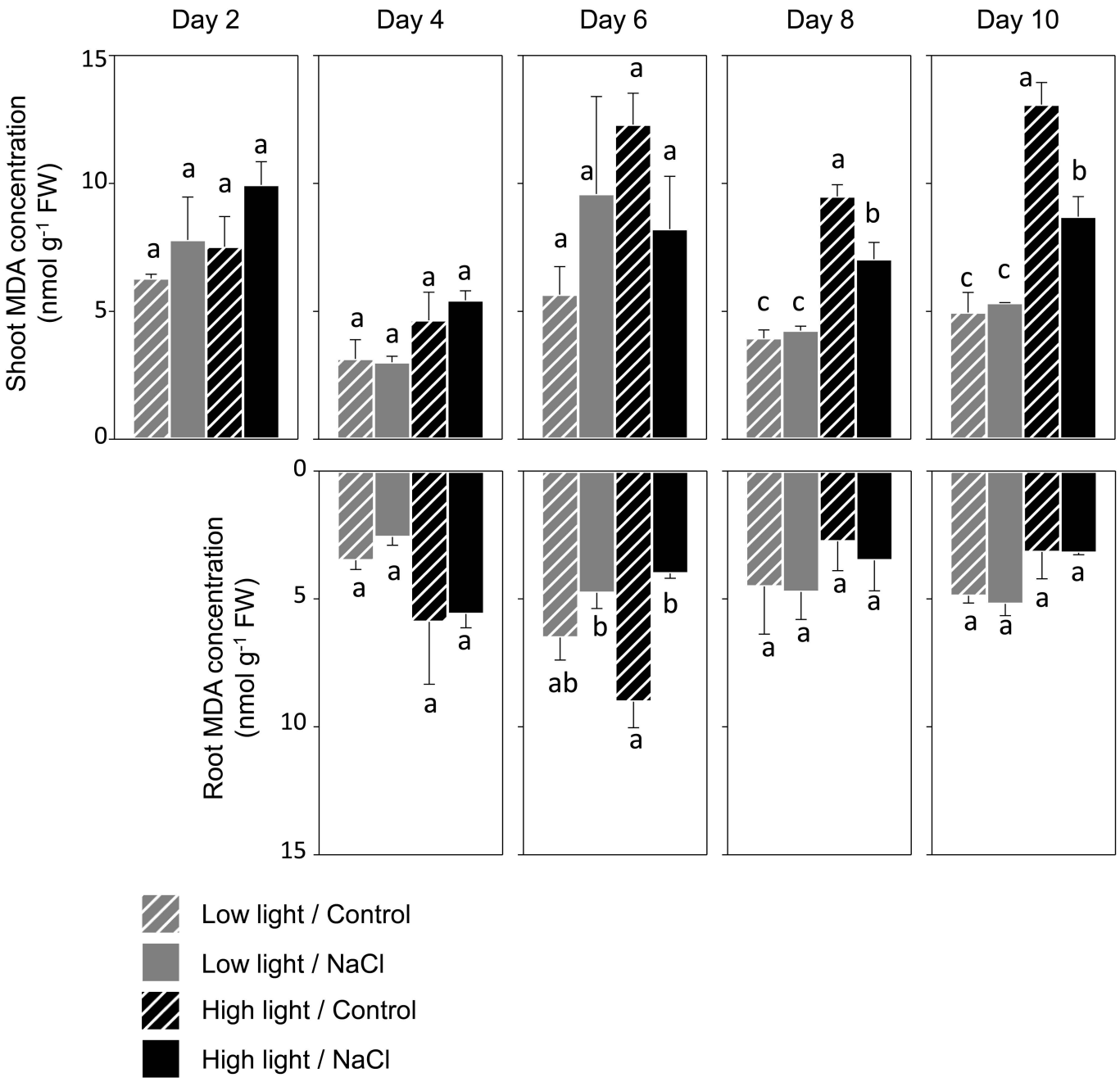
Day 2
Day 4
Day 6
Day 8
Day 10
Shoot MDA concentration (nmol g-1 FW)
Root MDA concentration (nmol g-1 FW)
Low light / Control
Low light / NaCl
High light / Control
High light / NaCl

Figure 2.

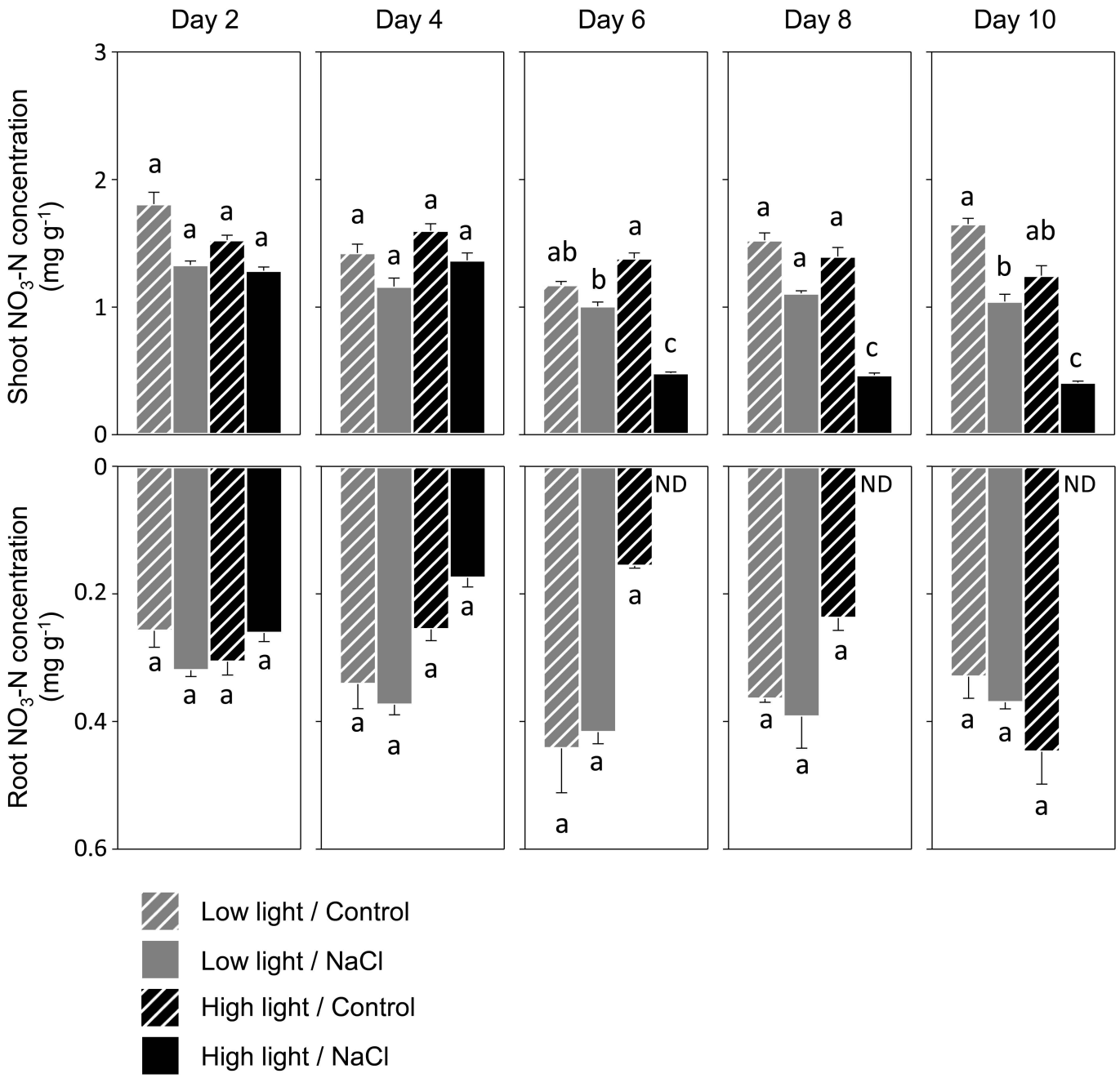
Day 2
Day 4
Day 6
Day 8
Day 10
Shoot NO_3-N concentration (mg g^{-1})
Root NO_3-N concentration (mg g^{-1})
ND
Low light / Control
Low light / NaCl
High light / Control
High light / NaCl

Figure 3.

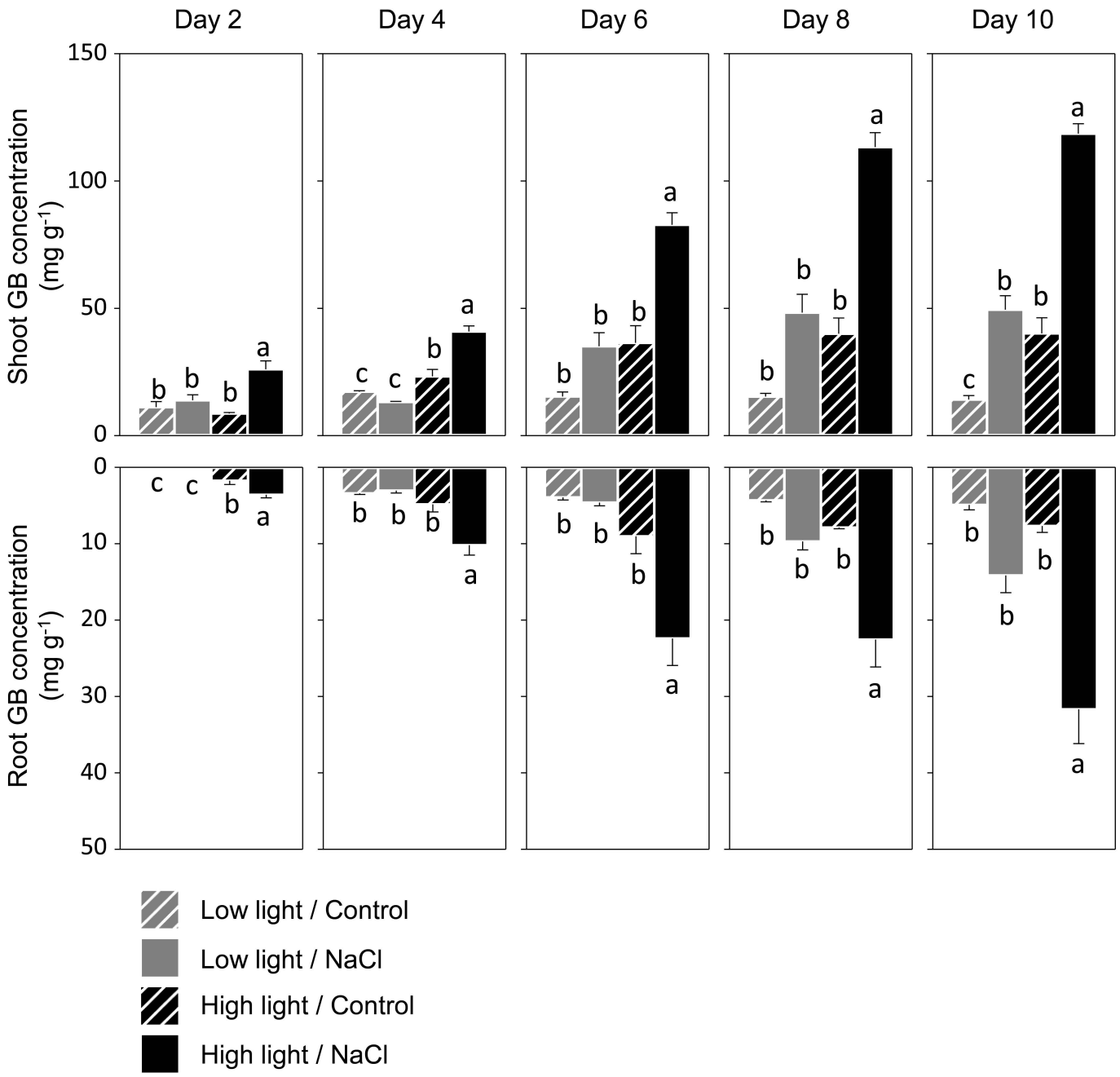
Day 2
Day 4
Day 6
Day 8
Day 10
Shoot GB concentration (mg g-1)
Root GB concentration (mg g-1)
150
100
50
0
0
10
20
30
40
50
Low light / Control
Low light / NaCl
High light / Control
High light / NaCl

Figure 4.

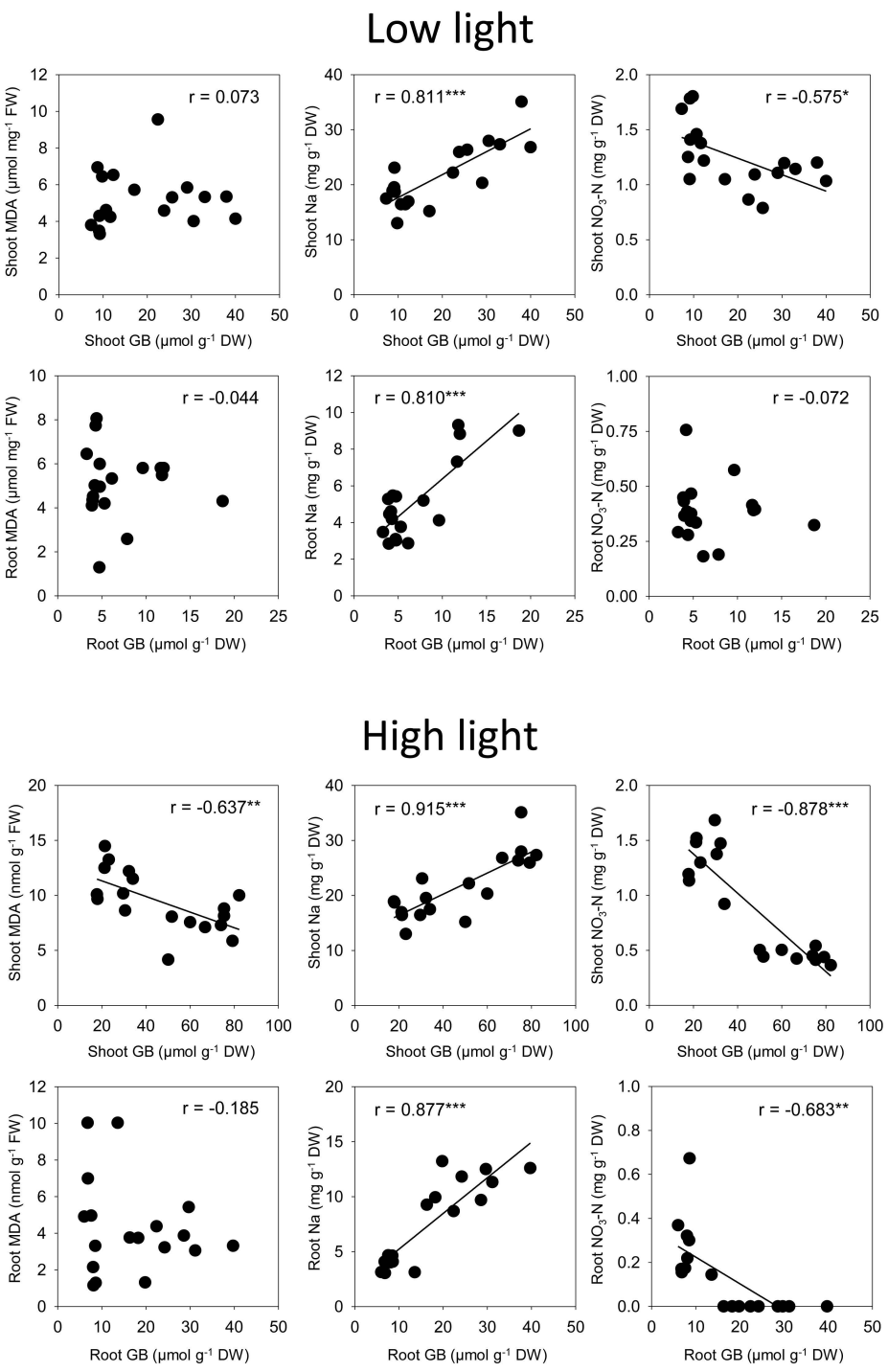
Low light
r = 0.073
Shoot MDA (μmol mg-1 FW)
Shoot GB (μmol g-1 DW)
r = 0.811***
Shoot Na (mg g-1 DW)
Shoot GB (μmol g-1 DW)
r = -0.575*
Shoot NO3-N (mg g-1 DW)
Shoot GB (μmol g-1 DW)
r = -0.044
Root MDA (μmol mg-1 FW)
Root GB (μmol g-1 DW)
r = 0.810***
Root Na (mg g-1 DW)
Root GB (μmol g-1 DW)
r = -0.072
Root NO3-N (mg g-1 DW)
Root GB (μmol g-1 DW)
High light
r = -0.637**
Shoot MDA (nmol g-1 FW)
Shoot GB (μmol g-1 DW)
r = 0.915***
Shoot Na (mg g-1 DW)
Shoot GB (μmol g-1 DW)
r = -0.878***
Shoot NO3-N (mg g-1 DW)
Shoot GB (μmol g-1 DW)
r = -0.185
Root MDA (nmol g-1 FW)
Root GB (μmol g-1 DW)
r = 0.877***
Root Na (mg g-1 DW)
Root GB (μmol g-1 DW)
r = -0.683**
Root NO3-N (mg g-1 DW)
Root GB (μmol g-1 DW)

Figure 5.