Journal of Agricultural Science; Vol. 10, No. 10; 2018
ISSN 1916-9752 E-ISSN 1916-9760
Published by Canadian Center of Science and Education

Cl^- More Detrimental Than Na^+ in Rice Under Long-Term Saline Conditions

Hanh Duy Dao[1] & Yoshihiko Hirai[1]

[1] Graduate School of Environmental and Life Science, Okayama University, Okayama, Japan

Correspondence: Yoshihiko Hirai, Graduate School of Environmental and Life Science, Okayama University, 1-1-1 Tsushima-Naka Kita-Ku Okayama 700-8530, Japan. Tel: 81-86-251-8316. E-mail: yhirai@okayama-u.ac.jp

Received: June 28, 2018 Accepted: July 30, 2018 Online Published: September 15, 2018

doi:10.5539/jas.v10n10p66 URL: https://doi.org/10.5539/jas.v10n10p66

Abstract

Rice is considered sensitive to salinity and hence, improving the salinity tolerance of rice is desired to increase productivity. Most research on salinity tolerance for the growth and grain yield of rice focuses on the toxicity of sodium (Na^+) and not chloride (Cl^-); the information on the negative effects of Cl^- on rice is still limited. To learn the difference in the long-term effects of Na^+ and Cl^- on the whole plant and grain productivities, three rice varieties differing in salinity tolerance were grown in pots irrigated by water with NaCl and KCl in the same molar concentration. The whole plant dry weight and grain yield in all varieties decreased to the same extent after NaCl and KCl treatments compared to the control during the full heading and maturity stages. However, Na^+ content in shoots of all varieties under NaCl treatment were higher at all stages than that under KCl treatment and the control. In the most cases, the Cl^- content in plants was similar in the NaCl and KCl treatment groups. There was a negative significant correlation between the relative dry weight and grain yield (treated/control) and the Cl^- content in the plants. From these results, it was suggested that plant dry weight and grain yield under long-term salinity conditions was reduced by Cl^- toxicity rather than Na^+ toxicity.

Keywords: chloride, ion toxicity, rice, salinity tolerance, sodium

1. Introduction

Soil salinity is one of the most severely limiting environmental factors for crop production. Globally, the total area of saline soils covers more than 800 million ha, and 45 million ha of irrigated land (19.5% of irrigated land) were salt-affected soils (FAO, 2018). Rice is a major staple food for hundreds of millions of people, but it is the most sensitive among cereal crops (Munns & Tester, 2008). As such, improving the salinity tolerance of rice is desired to increase productivity on salt-affected soil.

Plant growth responds to salinity in two phases: a rapid, osmotic phase that inhibits growth of young leaves, and a slower, ionic phase that accelerates senescence of mature leaves (Munns & Tester, 2008). The salinity tolerance of rice is thought to be closely related to Na^+ accumulation in shoots because there is overall a negative correlation between sodium content in plants and salinity tolerance in terms of survival (Flowers & Yeo, 1981; Yeo & Flowers, 1983), chlorophyll content (Yeo & Flowers, 1983), photosynthesis (Yeo, Caporn, & Flowers, 1985; Maegawa, Usii, Uchida, Yasud, & Yamaguchi, 1987), and plant growth (Akita & Cabuslay, 1990). There is a positive relationship between Na^+ and Cl^- in roots and leaves (Maegawa et al., 1987; Ammar et al., 2009; Teakle & Tyerman, 2010), so Cl^- content in plants also correlates to salinity tolerance (Flowers & Yeo, 1981). Several reports suggested that Na^+ toxicity is higher than Cl^- toxicity by analyzing the contribution of Na^+ and Cl^- (Kingsbury & Epstrin, 1986; Yamanouchi, 1989; Tsai, Hong, Liu, & Kao, 2004; Khare, Kumar, & Kishor, 2015). It is generally accepted that Na^+ appears to reach a toxic concentration before Cl^- does in most species (Munns & Tester, 2008). Because of this, most research on salinity tolerance in cereals focuses on the toxicity of Na^+ and not Cl^- (Teakle & Tyerman, 2010). As a result, the information on the effect of Cl^- on rice is still limited.

The contribution of Na^+ and Cl^- to plant growth was mainly investigated under short-term salinity stress (Lin & Kao, 2001; Tsai et al., 2004; Luo, Yu, & Liu, 2005). However, the ionic effect in plants under salinity stress appears when salt accumulates to toxic levels within the plant (Munns, Schachtman, & Condon, 1995). Therefore, the contribution of each ion to plant growth should be evaluated under long-term saline conditions. To separate the effects of Na^+ and Cl^- on plant growth, equimolar concentrations of Na^+ and Cl^- of various salts

were made and increasing particular counter-anions or counter-cations were avoided (Kingsbury & Epstein, 1986; Luo et al., 2005; Tavakkoli, Fatehi, Coventry, Rengasamy, & McDonald, 2011; Khare et al., 2015). However, the ameliorative and/or deteriorative effects of counter-anions and counter-cations may not be completely excluded in such experiments. On the other hand, potassium (K^+) is an essential macronutrient which exists in relatively high concentrations in plants (Leigh & Jones, 1984), and its toxicity in plant is lower than that of Na^+ (Lynch, Cramer & Lauchli, 1987; Martin & Koebner, 1995). Therefore, the use of KCl equivalent to NaCl concentration is possible to detect the harmful effects of Cl^- on the whole plant and grain productivities. We were to study the difference in the long-term effects of Na^+ and Cl^- on the whole plant and grain productivities in three rice varieties and to clarify the toxicity of Cl^- from its saline impact.

2. Materials and Methods

Three rice varieties—NSICRc106 (salt tolerant), Nipponbare (salt sensitive), and IR28 (salt sensitive)—were used. The experiment was conducted in a greenhouse at Okayama University. Pre-germinated seeds were seeded on 19 May, 2013 in nursery boxes (Minoru pot 448, Minoru Industrial Co. Ltd., Japan) with 448 holes (16 diameter, 25 mm depth). One seed was seeded in each hole. All holes were filled with nursery soil for rice seedlings (Kumiai Ube Ryu-joh Baido, Ube Industries, Ltd., Japan). The seedlings were transplanted manually at the 6-leaf stage on June 13 into 5 L plastic buckets of 135 pots filled with grey lowland soil. Slow-release compound (NPK 14-14-14) fertilizer was mixed with the soil (5 g per pot). Different salts, such as NaCl and KCl, were mixed with soil as salt treatments; soil without salt was considered as the control. The equimolar concentration (60 mM) of NaCl and KCl was applied by adding 12.0 and 15.31 g of the salt per pot, respectively. Tap water (3.4 L) was supplied, and plans were irrigated every day to keep a stable water level. The additional 5g of compound fertilizer (NPK 16-16-16) was supplied at 30 days after treatment (DAT) and at flowering stage. Pots were arranged randomly in the plastic covered house and the experimental design was completely random.

Five plants in each treatment group were harvested at three developmental stages: 30 DAT, the full heading stage (7 days after head emergence), and the maturity stage (45 days after head emergence). The dry weights of the leaf blades, stems (including the leaf sheath), and panicles during the three stages were measured after being dried in an oven at 80 °C for 72 hours. The grains were separated into ripened and immature grains by sinking them in a NaCl 1.06 specific gravity solution. Grain yield was divided into four components: panicle number, number of grains per panicle, percentage of ripened grain, and 1000 grain weight. The dried samples were extracted in a 1% HNO_3 solution at 80 °C for 24 h. The concentrations of Na^+ and K^+ in the samples were determined using a flame photometer (BWB XP, BWB technologies UK Ltd., UK). The concentration of Cl^- was determined using an ion meter (D-53, Horiba, Japan).

The visual salt damage of a panicle was scored on a 0 to 4 scale. A score of 0 indicates that deformed spikelets are not observed in the panicle. A score of 1 indicates that the percentage of deformed spikelets of the total number is under 10%. A score of 2 indicates that the percentage of deformed spikelets of the total number ranges from 10 to 25%. A score of 3 indicates that the percentage of deformed spikelets of the total number ranges from 25 to 50%. A score of 4 indicates that the percentage of deformed spikelets of the total number is over 50%.

The results were analyzed using JMP software version 9.0. The difference among treatments were determined by a one-way analysis of variance (ANOVA) based on Tukey's multiple range test ($p < 0.05$).

3. Results

3.1 Whole Plant Growth, Grain Production, and Yield Components

The heading dates in the control group were 4 August (52 DAT) in IR28, 8 August (56 DAT) in NSICRc106, and August 15 (63 DAT) in Nipponbare. Under NaCl and KCl treatments, the heading dates in IR28 and NSICRc106 were delayed by 3-5 days, but that in Nipponbare was almost same in control.

At 30 DAT, the whole plant dry weight of Nipponbare decreased by 44% in the NaCl treatment group and 24% in the KCl treatment group (Figure 1). At the full heading stage and maturity stage, the plant dry weight in the NaCl and KCl treatment groups decreased by around 30%; there was no difference between both treatments. The plant dry weight of IR28 and NSICRc106 in the NaCl and KCl treatment groups decreased by 21 to 43%, but there was no difference between both treatments. The reduction of grain weight in all varieties under NaCl and KCl treatments ranged from 58 to 87%, where there was no difference between NaCl and KCl treatments (Figure 2). Figure 2 shows that none of the varieties could be described as salinity-tolerant. Although IR28 had the highest relative grain yield (grain weight at salinity-stress/grain weight at control, as %) of 43%, NSICRc106 had maginally higher grain yield under NaCl (though not significant different), but a low relative grain yield of 30% (as it grew better than IR28 under good condition). The percentage of ripened grains was most affected by

NaCl and KCl treatments among the yield components, but there was no difference between both treatments in all varieties (Figure 3). The percentage of deformed spikelets caused by NaCl and KCl treatments was high in IR28 and low in Nipponbare. However, there was no difference between NaCl and KCl treatments with regards to the percentage of deformed spikelets in all varieties (Figure 4).

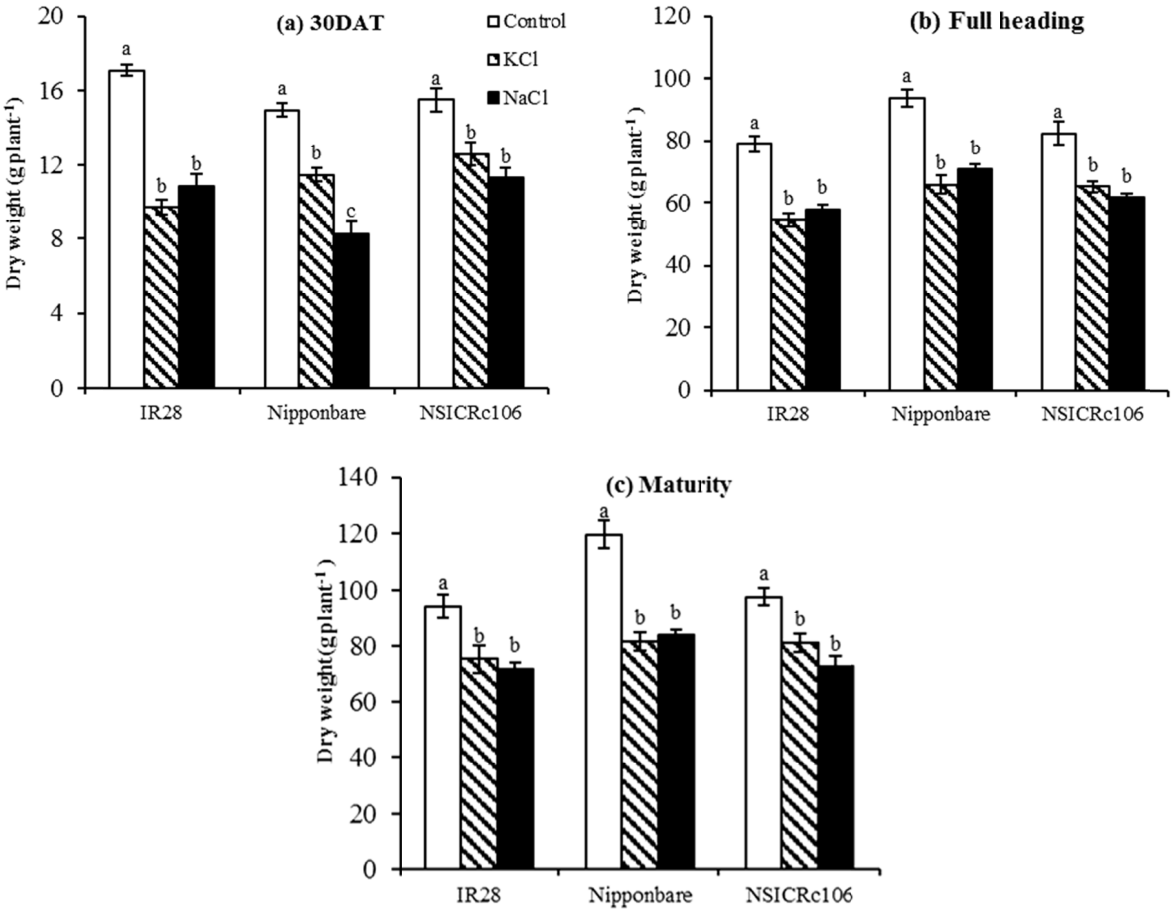

Figure 1. (a) The effect of salinity on plant dry weight at 30 DAT, (b) the full heading stage, and (c) the maturity stage. Bars show the average value ± SE (n = 5). Bars with the same letters within each variety indicate no significant difference between treatments related to plant dry weight based on Tukey's multiple-range test ($p < 0.05$)

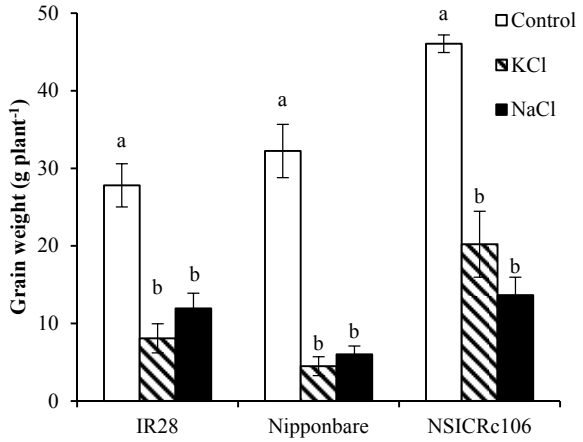

Figure 2. The effect of salinity on the grain weight of plants under salinity conditions. Bars show the average value ± SE (n = 5). Bars with the same letters within each variety indicate no significant difference among treatments related to grain weight based on Tukey's multiple-range test ($p < 0.05$)

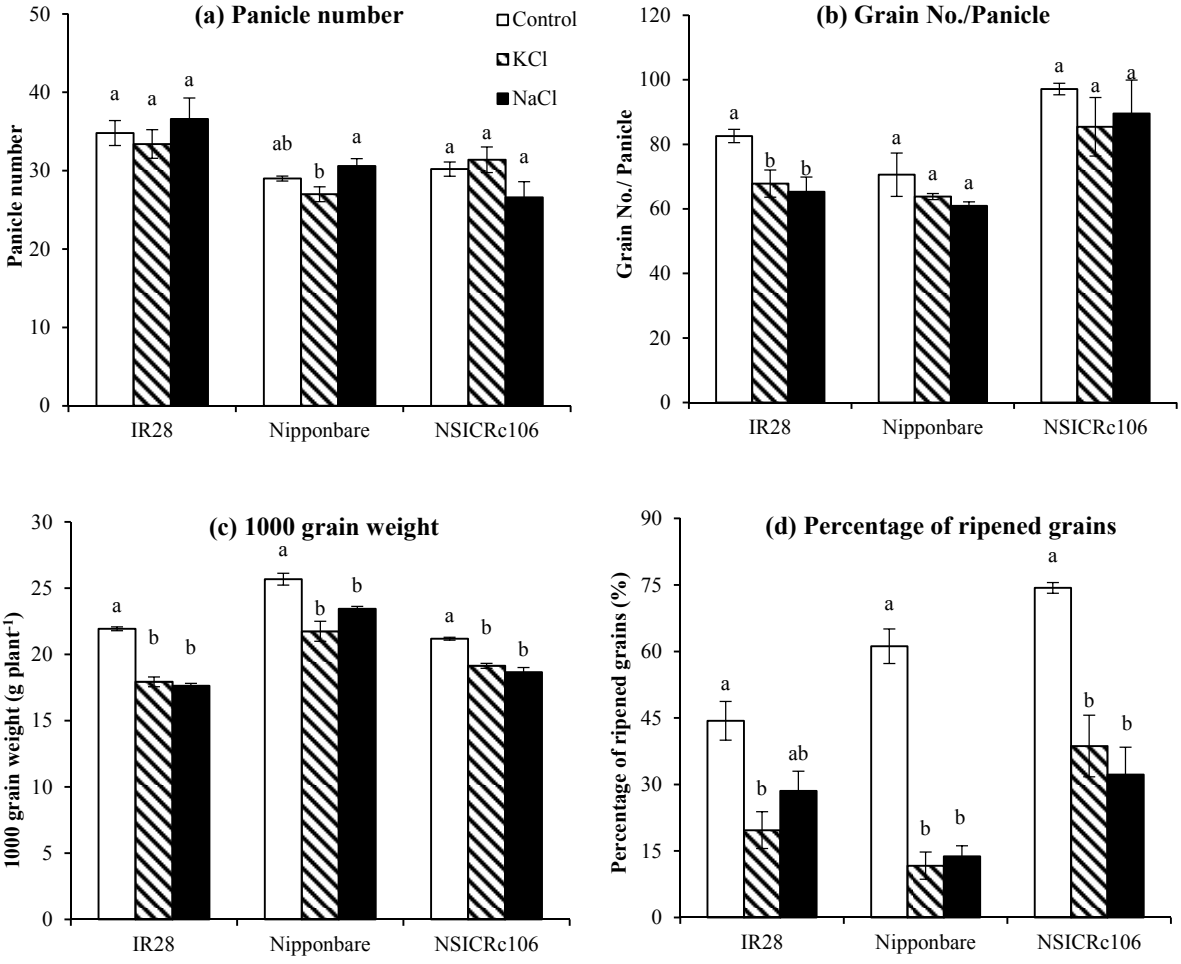

Figure 3. The effect of salinity on the yield components of plants under salinity conditions. Yield was divided into four components: (a) panicle number, (b) number of grains per panicle, (c) 1000 grain weight, and (d) the percentage of ripened grain. Bars show the average value ± SE (n = 5). Bars with the same letters within each variety indicate no significant difference among treatments based on Tukey's multiple-range test ($p < 0.05$)

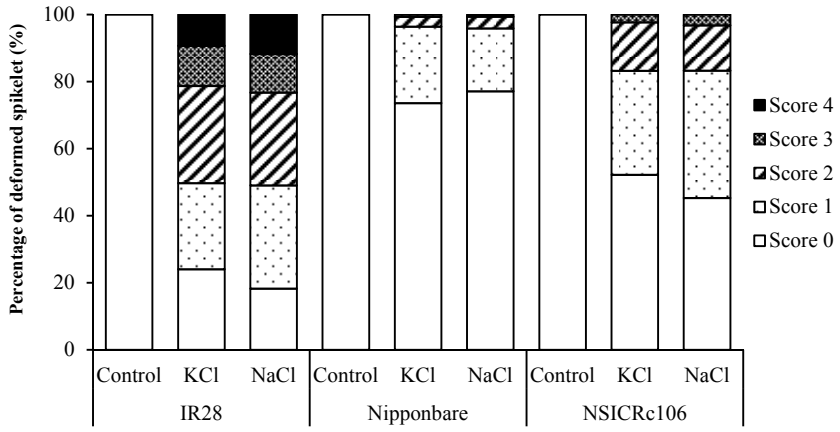

Figure 4. The effect of salinity on deformed spikelets of plants under salinity conditions. The visual salt damage of panicles was scored from 0 to 4. A score of 0 indicates that deformed spikelets are not observed in the panicle. A score of 1 indicates that the percentage of deformed spikelets of the total number is under 10%. A score of 2 indicates that the percentage of deformed spikelets of the total number ranges from 10 to 25%. A score of 3 indicates that the percentage of deformed spikelets of the total number ranges from 25 to 50%. A score of 4 indicates that the percentage of deformed spikelets of the total number is over 50%.

3.2 Ion Content in Plants

The Na^+ content in shoots of all varieties in the NaCl treatment group at all stages was higher than that in the KCl treatment and control groups (Figures 5a, 5d, and 5g). The K^+ contents in shoots of all varieties at all stages in the NaCl treatment group was lower than that in the KCl treatment and control groups (Figures 5b, 5e, and 5h). There was no difference in the K^+ content in shoots of all varieties between the KCl treatment and control groups at 30 DAT (Figure 5b); after that, the K^+ content in shoots in the KCl treatment group was higher or the same as the control (Figures 5e and 5h). The Cl^- content in shoots of all varieties in the NaCl and KCl treatment groups at all stages was higher than that in the control group (Figures 5c, 5f, and 5i). The Cl^- content in shoots of IR28 in the KCl treatment group at 30 DAT and at the full heading stage was higher than that in the NaCl treatment group (Figures 5c and 5f). The Cl^- content in shoots of NSICRc106 in the KCl treatment group at 30 DAT was also higher than that in the NaCl treatment group (Figure 5c). There was no difference in the Cl^- content in shoots of Nipponbare between the NaCl and KCl treatment groups (Figures 5c, 5f, and 5i).

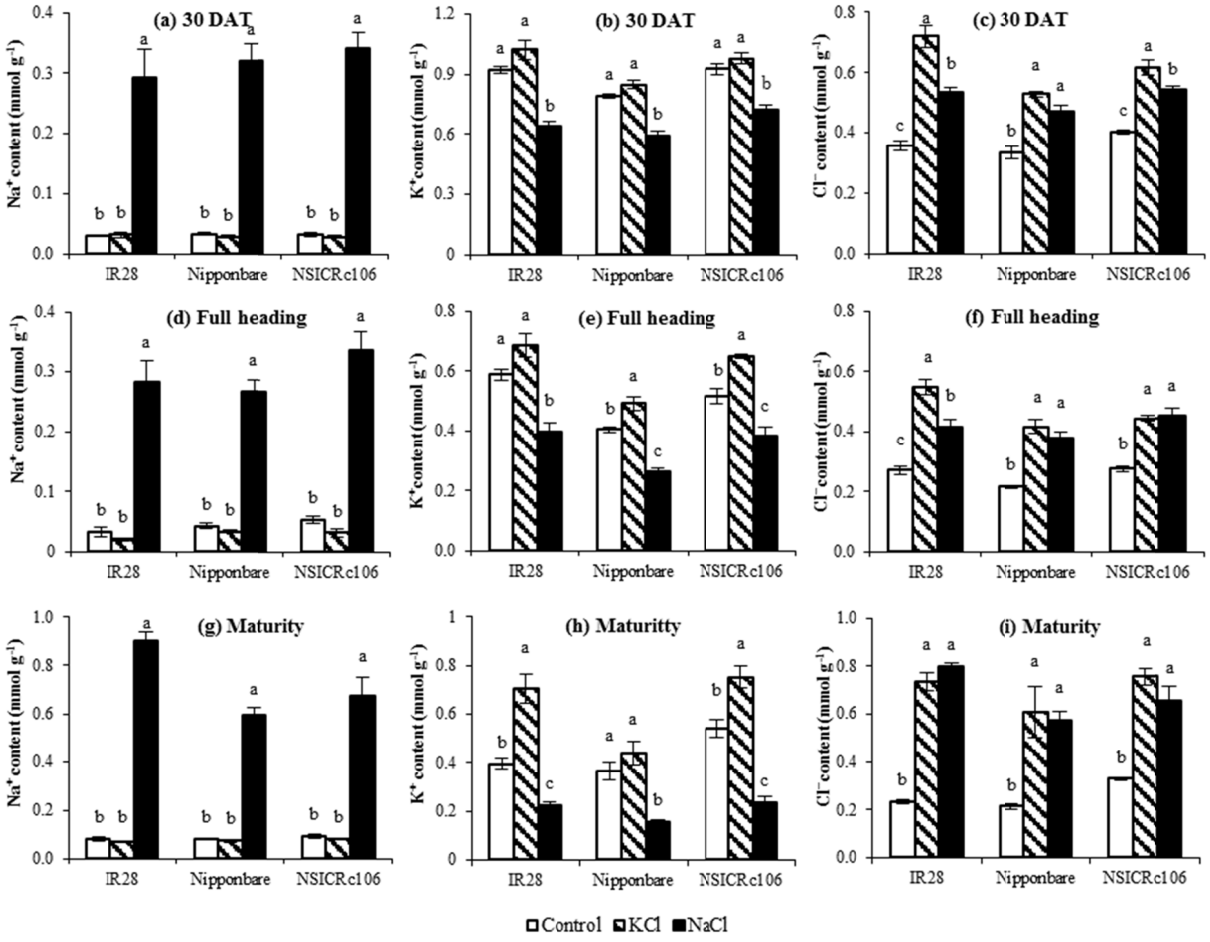

Figure 5. The ion content in shoots at 30 DAT: (a) Na^+, (b) K^+, and (c) Cl^-. The ion content at the full heading stage: (d) Na^+, (e) K^+, and (f) Cl^-. The ion content at the maturity stage: (g) Na^+, (h) K^+, and (i) Cl^-. Bars with the same letters within each variety indicate no significant difference among treatments relating to ion content in shoots based on Tukey's multiple-range test ($p < 0.05$)

3.3 Relationship Between Ion Contents and Plant Dry Weight and Grain Weight

There was no significant correlation between Na^+ content in shoots and relative plant dry weight at all stages (Figures 6a, 6b, and c) as found by Genc, Oldach, Taylor, and Lyons (2016). In addition, there was no significant correlation between Na^+ content in shoots and relative grain weight (Figure 7a). Therefore, Na^+ content in shoots did not relate to the decrease of plant growth and the grain yield of rice under salinity stress. In contrast, a negative correlation was observed between Cl^- content in shoots and relative plant dry weight at all stages. (Figures 6d, 6e, and 6f), especially at the full heading stage. Cl^- content in shoots was strongly correlated with relative dry weight. Moreover, the negative correlation between Cl^- content in shoots and relative grain weight were observed (Figure 7b). This implied that a high Cl^- content in shoots lead to the decrease of plant dry weight and grain weight under salinity stress.

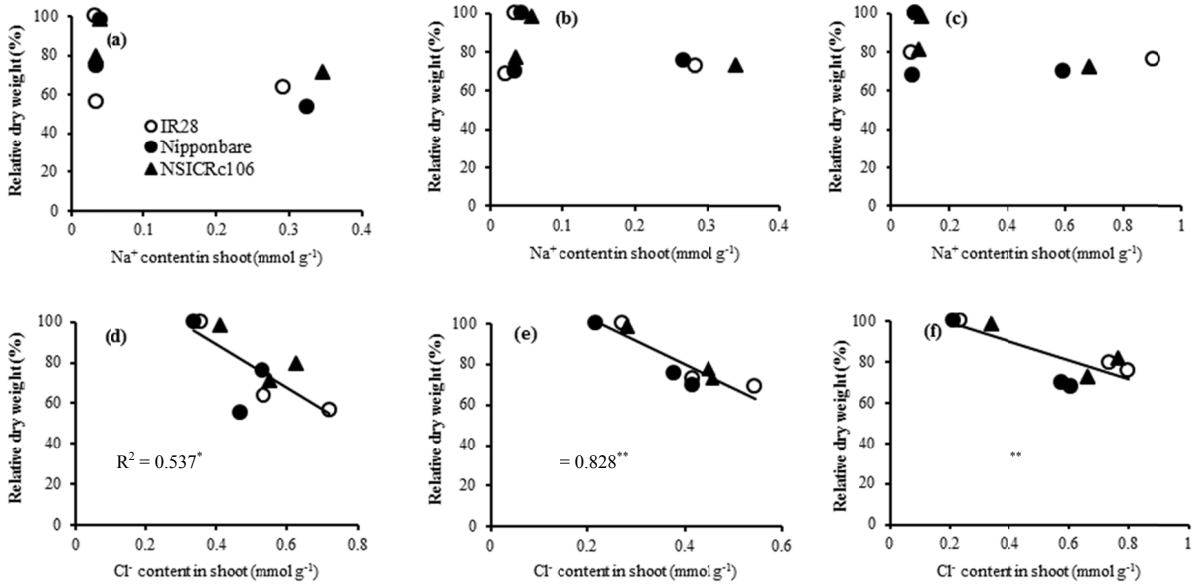

Figure 6. Relationship between Na^+ or Cl^- in shoots and relative plant dry weight at (a,d) 30 DAT, (b,e) the full heading stage, and (c,f) the maturity stage under salinity conditions. Different symbols represent different varieties. * and ** indicate significance at the 5 and 1% level, respectively

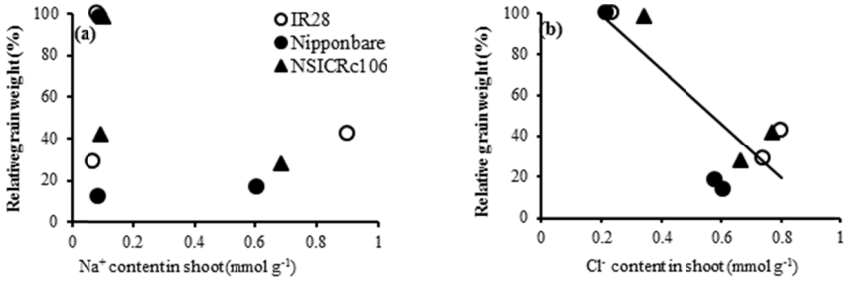

Figure 7. The relationship between relative grain weight and (a) Na^+ or (b) Cl^- content in shoots at the maturity stage under salinity conditions. Different symbols represent different varieties. * and ** indicate significance at the 5 and 1% level, respectively

4. Discussion

The dry weight of whole plant was not different between the NaCl and KCl treatment groups, except for Nipponbare at 30 DAT (Figure 1a). The grain yield and the appearance of deformed spikelets were not different in both treatment groups (Figure 2). These results indicate that NaCl and KCl treatments have a similar effect on rice. There are two possible reasons that the toxicity of Na^+ and K^+ are the same and that Cl^- is the main factor for ion toxicity. First, we discuss whether K^+ toxicity is equivalent to Na^+ toxicity. The plant dry weight of the three varieties after undergoing KCl treatment at 30 DAT was 19-43% that of the control. However, the K^+ content at 30 DAT of plants undergoing KCl treatment was similar to that of the control. As such, it is considered that the K^+ content in the KCl treatment does not relate to the difference in plant dry weight between the control and the KCl treatment at 30 DAT. In addition, the K^+ content at the full heading stage and the maturity stage were lower than that at 30 DAT (Figure 5). Therefore, the influence of K^+ at both stages was thought to be smaller than that at 30 DAT. Furthermore, it is reported that K^+ toxicity in a plant is lower than Na^+ toxicity (Lynch et al., 1987; Martin and Koebner, 1995). Thus, it is concluded that Na^+ and K^+ toxicity are not same in this study. On the other hand, in most cases (except that of IR28 and NSICRc106 at 30 DAT and that of IR28 at the full heading stage), the Cl^- content in plants was similar in both ion treatment groups. Furthermore, the Cl^- content of plants was negatively correlated with the relative value of dry weight and grain yield compared to the control (Figure 7). Thus, it was suggested that plant dry weight and grain yield under long-term salinity conditions was reduced by Cl^- toxicity rather than Na^+ toxicity.

Ion toxicity in rice, barley, and wheat has been thought to be due to Na^+ rather than Cl^-. However, in recent years, excess Cl^- was implicated in the reduction of chlorophyll content (Tavakkoli et al., 2011). Cl^- toxicity cannot be ignored in these crops (Tavakkoli et al., 2011; Khare et al., 2015; Kumar & Khare, 2015). Furthermore, Na^+ and Cl^- have an additive effect to suppress the yield of rice (Kumar & Khare, 2016). However, in our study, the degree of suppression of the grain yield and dry matter in KCl and NaCl treatment were similar, thus, the additive effect of Na^+ and Cl^- was not observed. One possible reason for this discrepancy is the existence of counter ions. It is impossible to make ions other than Na^+ and Cl^- equal. Several studies were done using Na^+ dominant and Cl^- dominant treatments, which are designed to give equimolar concentrations of Na^+ and Cl^- (generated from various salts of Na^+ and Cl^-) to avoid increasing particular counter-anions or counter-cations (Kingsbury & Epstein, 1986; Luo et al., 2005; Tavakkoli et al., 2011; Khare et al., 2015; Kumar & Khare, 2016). However, the ameliorative and/or deteriorative effects of counter-anions or counter-cations may not be completely removed in such experiments. For example, Ca^{2+} availability can change the salinity tolerance in plants (Muhammed, Akbar, & Neue, 1987; Anil et al., 2005). However, K^+ is the only counter ion in this study and, as mentioned above, it is unlikely that K^+ has the toxicity in this study. The other possible reason is the length of the salt treatment. The results in the short-term salt treatment at the early growth stage indicate that Na^+ toxicity is the main factor (Lin & Kao, 2001; Tsai et al., 2004; Luo et al., 2005). On the other hand, the additive effect of Na^+ and Cl^- was observed in the salt treatments from early-reproductive to maturity stages (Kumar & Khare, 2016). This indicates the possibility that Cl^- toxicity appears more clearly under long-term salt treatment. The reason why the additive effect of Na^+ and Cl^- was not observed in this study is that long-term salt treatments from the seedling stage to the maturity stage are carried out, Cl^- toxicity was more severe and Na^+ toxicity was not detected.

In this experiment, three varieties differing in salinity tolerance at the seedling stage were used, and it did not coincide with the salinity tolerance at 30 DAT, the full heading stage, and the maturity stage. The relative whole plant dry weight at 30 DAT under NaCl decreased by 44% for Nipponbare, 36% for IR28, and 27% for NSICRc106 (Figure 1a). However, there was no difference among the varieties relating to the reduction of whole plant dry weight under NaCl treatment, with the range from 25 to 27% and 24 to 30% at the full heading stage and the maturity stage, respectively (Figures 1b and 1c). The salinity tolerance in rice is known to differ during the growing stage (Heenan, Lewin, & Maccaffery, 1988; Makihara, Tsuda, Morita, Hirai, & Kuroda, 1999), and their tolerance at different stages seems to be controlled by independent genes (Singh & Flowers, 2010). The different mechanism of salinity tolerance at different growth stages may relate to the result that the Cl^- toxicity is critical more than Na^+ toxicity under long-term salinity conditions. Individual research on Cl^- toxicity at different growth stages would help in understanding the mechanism of salinity tolerance in rice.

Salinity tolerance can be classified into three main mechanisms: ion exclusion, osmotic tolerance, and tissue tolerance (Munns & Tester, 2008), and our results suggest the importance of Cl^- exclusion in salinity-stressed rice. Recently, it was shown that osmotic tolerance and tissue tolerance to Na^+ and/or Cl^- should be the main foci for further improvement of salinity tolerance in barley, wheat and durum wheat (Genc et al., 2016). However, in rice, it is not clear which mechanism is more critical in salinity tolerance. Further study on this is necessary to understand salinity tolerance in rice.

5. Conclusion

The results of long-term NaCl and KCl treatments using three rice varieties with different salinity tolerances suggested that plant growth and grain productivity of rice under long-term salinity conditions is reduced by Cl^- toxicity rather than Na^+ toxicity. The understanding of the mechanism to reduce Cl^- accumulation in plants is necessary to improve salinity tolerance in rice.

Acknowledgements

We would like to thank Professor Makoto Tsuda for the helpful advice and stimulating discussion, Ms. Ayako Morioka for technical support, and Professor Tohru Kobata for valuable comments on the draft of this paper. This work was supported by JSPS KAKENHI Grant Number 16K07573.

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