Salinity influences plant–pest–predator tritrophic interactions

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# The author deceased during the preparation of the manuscript and has an equal contribution to the lead author. We like to dedicate this article to the memory of the late MS Rahman.

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Abstract

Climate change-induced salinity intrusion into agricultural soils is known to negatively impact crop production and food security. However, the influences of salinity increase on plant-herbivore-natural enemy systems and repercussions for pest suppression services are largely unknown. Here we examine the resultant effects of increased salinity on communities of rice (*Oryza sativa*), brown planthopper (BPH), *Nilaparvata lugens*, and green mirid bug (GMB), *Cyrtorhinus lividipennis* under greenhouse conditions. We found that elevated salinity significantly suppressed the growth of two rice cultivars, leading to reductions in plant quality, yield components, and final grain yield. Meanwhile, BPH population size also generally decreased due to poor host plant quality induced by elevated salinity. The highest BPH density occurred at 2.0 dS/m salinity and declined thereafter with increasing salinity, irrespective of rice cultivar. The highest population density of GMB occurred under control conditions and decreased significantly with increasing salinity. Higher salinity directly affected the rice crop by reducing plant quality measured with reference to biomass production and plant height, in turn, influencing population developmental asynchrony between BPH and GMB, and uncoupling prey-predator dynamics. Our results suggest that increased salinity have harmful effects on plants, insects, as well as plant-pest-predator interactions. The effects measured here, suggest that the top-down effects of predatory insects, rice pests will likely decline in rice produced in coastal areas where salinity intrusion is common. Our findings indicate that elevated salinity influences tritrophic interactions in rice production landscapes and further research should address resilient rice insect pest management in a changing environment.

Keywords: Salinity, rice, insect pest, predator, tritrophic interactions.

Introduction

Demand for food, feed, and energy from agricultural landscapes is expected to increase globally, while at the same time crop production is limited by changing environmental stresses including cold, heat, drought, salt, or chemical pollutants. The performance of herbivorous insects and their natural enemies can be influenced due to the change of nutritional composition and defensive chemicals in plants resultant of environmental abiotic factors. (Horgan et al. 2019, Han et al. 2016, Horgan 2012, Polack et al. 2011, Cakmak and Demiral 2007, Heong and Schoenly, 1998). Understanding connections between worldwide climatic changes and tritrophic interactions is especially significant in agriculture, where the outbreaks of herbivore are anticipated to increase. (Dyer et al. 2013).

Reports of climate change induced salinity intrusion into soils of crop production lands are increasing in Southeast Asia. Climate change causes remarkable changes of soil salinity by increasing more than 1.1°C with reduced precipitation rate. Thus, salinity in agricultural soils increases continuously in space and time (Bannari and Ali 2020). Climate change not only influence the inundation and coastal surge in Bangladesh (Rahman et al. 2018) but also other factors such as soil salinity intrusion, aquatic habitat loss and land subsidence (Shrivastava and Kumar 2015).

Salinity in water and soil is one of the aged environmental problems (McWilliam, 1986), affecting about 352 million hectares of area in the globe (Rengasamy 2006). Inappropriate irrigation practices, rising sea levels, and natural disasters (e.g., tsunamis) intensified by climate change are continuously increasing soil salinization (Dasgupta et al. 2015). Salinity stress currently affects about 20% and 33% of global cultivated and irrigated land, respectively. (Machado and Serralheiro, 2017) and poses a serious threat to the production of rice (*Oryza sativa* L.) worldwide as it is an especially salt-sensitive crop (Zeng and Shannon, 2000a, Shannon *et al*. 1998, Zeng and Shannon, 2000b). Rice is the source of major staple food to half of the global human population and gives around 75 percent of the required calories and 55 percent of the protein uptake in the normal everyday diet in Bangladesh context (Bhuiyan *et al*. 2002, Brolley 2015). The coastal regions of Bangladesh cover 2.85 Mha of land, the majority of which lies in the southwest coastal region (Clarke *et al*. 2015), which produces 16% of the country's rice (Minar *et al*. 2013). These coastal territories are progressively encountering salinity interruptions that hinder the production of rice and other crops there. (Rahman, 2012).

Salinity affects a variety of plant processes including nutrient absorption, ionic balance, plant metabolites (both primary and secondary), tolerance mechanisms, leaf anatomy, antioxidative enzymes and antioxidants, photosynthesis, and water balance all of which influence plant growth (Parida and Das 2005, Chilcutt et al. 2005, Rahneshan et al. 2018, Munns and Tester 2008), and directly and/or indirectly modify plant defense metabolites (Forieri et al. 2016). In rice the metabolism, physiology of nutrient uptake, and production of sugars and amino acids, etc. are affected due to salinity stress condition (Chunthaburee et al. 2016, Horie et al. 2012, Pattanagul and Thitisaksakul 2008, Gupta and Huang 2014). In general, these changes increase antioxidant defenses (Khare et al. 2015) and hormones that help rice plants to survive in saline situations (Chinnusamy et al. 2005, Sawada et al. 2006, Kang et al. 2005).

Salinity-induced changes in host plant quality can significantly impact plant-herbivore interactions. For example, increased salinity has been shown to improve the performance of several herbivores including leaf miners on tomatoes (Han et al. 2016), aphids (*Myzus persicae)* on sweet peppers (*Capsicum annuum* L., Solanaceae) (Polack et al. 2011), and phytophagous mites (e.g. *Tetranychus* sp.) (Cakmak and Demiral 2007, Aucejo-Romero et al.

2004). Increased salinity can also have negative effects on planthoppers (Quais et al. 2019), leaf miners (Schile and Mopper 2006), while having neutral effects on other herbivores (Bowdish and Stiling 1998, Hemminga and van Soelen 1992). Thus, generally speaking, the effect of salinity on herbivores varies with the type of plant, insect species, as well as the degree of salinity stress experienced.

Under natural conditions, herbivores are attacked by natural enemies (predators and parasitoids) which can regulate their abundance (Horgan et al. 2019, Heong and Schoenly, 1998). The overall impacts of salinity stress on tritrophic (plant-pest-predator) interactions are not yet clearly understood but is vital in developing biocontrol programs under stress conditions. Recently, a study by Quais et al. (2019) evaluated the impacts of salinity stress on fitness attributes of the brown planthopper (BPH), *Nilaparvata lugens* Stål (Hemiptera: Delphacidae), a major sucking insect pest of rice (Dyck and Thomas 1979; Ali et al. 2012; Islam and Catling 2012; Ali and Kabir 2020). Higher salinity concentrations reduced BPH fitness traits including fecundity, nymphal development, adult longevity, oviposition, intrinsic rate of growth, reproduction rate, and a concentration-dependent effect was reported (Quais et al. 2019). But this study did not include the next trophic level (i.e. natural enemies) which are common in rice production and can suppress BPH populations and its damage (Heong et al. 1990; Lu et al. 2004). The green mirid bug (GMB) *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae), a major predatory insectof brown planthopper (BPH), is widely distributed in Southeast Asia, Australia, and the pacific (Manjunath et al. 1977, Kamal et al. 1987, Kamal et al. 1998), where it occurs in rice fields and plays an essential role in regulating rice pests (Wang et al. 2018).

We hypothesize that salinity alters the tritrophic interactions among rice, BPH, and GMB possibly by changing the chemical composition of host plants which ultimately leads to developing lower quality foods (eggs, nymphs of BPH) for predatory GMB. Alterations in herbivore performance facilitated by plant quality can likewise adversely affect the performance of parasitoids (Harvey et al. 2005; Lampert et al. 2011; Smilanich and Dyer, 2012). We, therefore, examined the impact of salinity stress on tritrophic interactions using rice, BPH, and GMB. The life cycle of BPH consists of eggs, 5 nymphal stages, and the adult. The total life cycle is 22 - 28 days (Hu et al. 2010). Within their lifetime, one female can lay 299 eggs and can complete 8–11 generations per year in Bangladesh (Ali et al. 2014). The GMB is an omnivore, capable of feeding on plants but prefers planthopper eggs and juvenile nymphs (Shepard et al.1987) and is an effective biocontrol agent which can reduce BPH populations under field conditions (Chaiya et al. 2019, Katti et al. 2007, Preetha et al. 2010). The study reported here is aimed at improving understanding of a biologically significant food web by understanding how changes in salinity interact to affect relationships among host plant quality, planthopper, and their predator.

Materials and Methods

The responses of rice plant, brown planthopper (BPH) and green mirid bug (GMB) to different salinity (0, 2, 4, 6, and 8 dSm^{-1}) levels were assessed under greenhouse conditions at Bangladesh Rice Research Institute (BRRI), Gazipur, Bangladesh (23°59′23′′ N, 90°24′27′′ E). The environmental conditions of the greenhouse were 28 - 32ºC, 65 - 75% RH with a photoperiod of 12:12 (L:D).

Rice cultivars

Two rice cultivars, BRRI dhan47 and BRRI dhan67 were used in this study. These two cultivars were developed and released by BRRI as salinity tolerant varieties (up to 8 dSm^{-1} under field conditions) and are currently recommended for cultivation in the coastal belts of

Bangladesh, where salinity increases are common (Anonymous, 2016, Salam et al. 2007). While these varieties are commonly cultivated in coastal land areas of Bangladesh, they are also common in other non-saline areas. Plant traits including plant height, growth duration, and yield of BRRI dhan47 are 105 cm, 145 days, and 6.0 t/ha respectively. Similarly, plant height, growth duration, and yield of BRRI dhan67 are 100 cm, 145 days, and 6.0 t/ha respectively.

Stock culture of brown planthoppers and green mirid bugs

The BPH and GMB populations used in this study were from BRRI stock cultures maintained on the susceptible rice variety BR3 in a net house conditions throughout the study period. The process for the rearing of stock cultures of BPH is as follows with slight modification as per previous report (Ali et al., 2012). Twenty rice seedlings of 25 d old were transplanted into earthen pots. Three hills were transplanted in each pot and each hill had 2 – 3 seedlings. The pot was filled with 2-3 kg of N, P, K, Zn fertilized soil and two top dressings of N fertilizers were applied before using the potted plants. At 40 - 45 days, potted plants were cleaned by removing the outer sheath of each rice plant. This assured that test plants were free of insects. Two to three cleaned pots were placed in an iron-framed mass rearing cage (45 cm X 45 cm X 60 cm) covered fine mesh net on a galvanized iron plate loaded up with water to one-third of its height, to keep the soil wet. Thirty to 40 gravid BPHs were discharged in each rearing cage having rice plants for oviposition and removed after 48 h with an aspirator. After hatching, rice plants were substituted with fresh potted plants to supply fresh food materials for the development of BPH populations and repeated as necessary. This culture provided same-aged gravid adults of BPH for our experiments. In the case of GMB stock culture, 40–50 GMB were collected from a rice field and released into potted rice plants with BPH eggs and adults. The adults BPH laid fresh eggs daily, which provided food for the GMB. After one week, plants were replaced with newly potted plants (with BPH eggs). These new plants provided sufficient food for proper growth and development of GMB.

Preparation of saline water

Saline water was used to assess the impact of salinity on rice growth and pest development. Four salinity levels, 2, 4, 6, and 8 dSm^{-1} were prepared and used in this study. Commercial salt (NaCl) was used to prepare the different salinity levels. First, 13g NaCl was measured using electric balance and released into 13 L water kept in a plastic bowl and the electrical conductivity (EC) was determined using an EC meter (H199301, Hana). Thereafter, salt was added to reach the target maximum salinity level of 8 dSm^{1} and serially diluted to obtain the other levels. Tap water was used to prepare all saline water and tap water without salt added was used as control.

Experimental design

To grow plants for experiments soil was collected from an existing rice field at BRRI and pulverized so that inert materials, plant roots, visible insects, and plant propagules could be removed. The soil was subsequently sun-dried and thoroughly mixed. Individual plastic pots (size: 13.97 cm diameter and 12.7 cm height) were filled with 2.5 kg dry soil and consequently added water one-day before sowing seeds. The soil was fertilized according to a standard regime (BRRI, 2017). Three pots were placed in a 15 L plastic bowl (46 cm diameter and18 cm height). Five – six pre-germinated seeds (soaked in water for 24 h, drained and incubated for another 48 h), were sown in each pot when the radicle reached 2-3 mm in length. Water was splashed on the germinating seeds and the seeds are pressed down slightly by hand. Seed pots were saturated with water for the first 5 d and then the water level was gradually increased up to 5 centimeters as the seedlings grew. Seedlings were thinned to leave 3 per pot after two weeks. At 25 d, the bowls were filled with saline or control treated water and placed in a galvanized iron tray (**Fig. 1**). The plastic pot was perforated with 60 small holes to allow water entry. All the galvanized iron trays were placed on a 60 cm high iron frame in the greenhouse and protected by clear polythene sheets to prevent rainwater from entering the bowls.

We used five treatments: no salt added as the control with an electrical conductivity (EC) value near 0, and fixed EC values of 2, 4, 6, and 8 dSm^{-1}. Each bowl was considered as one replication for each treatment and was repeated nine times in a completely randomized design (CRD). The electrical conductivity (EC) of each bowl was measured daily and necessary adjustments were made by adding tap water/or salt. When rice seedlings reached 35 d old, 6 gravid female BPH were released into each bowl. After 24 h, 6 GMB adults were released into each bowl. The bowl was individually covered by a nylon net supported with an iron frame to keep the insects inside and protect them from other predators/parasitoids. Both BPH and GMB were removed from rice plants using an aspirator one-week after their release. The plants were observed daily for the emergence of nymphs and their development into adulthood. When nymphs molted into adults, they were counted and withdrawn from the plant and the number of adults in each treatment was quantified. The fecundity and nymphal survivability of BPH in each treatment were assayed using the method described previously (Rashid et al. 2017) using cultivar BRRI dhan67.

When rice reached maturity, plant traits including number of tillers/hill, plant height, shoot and root dry weight, length of panicle, grains/panicle, and 1000-grain weight were determined using the procedures described by Khanam et al. (2018). Under high salinity stress, plant N uptake from the soil is reduced; impacting plant biomass and N-related chemical compositions such as sugars, free amino acids, and soluble proteins (Ashraf et al. 2017; Hakim et al. 2014; Ullrich 2002). Insect pest, BPH sucks these chemicals from rice plants. In this study, we did not directly measure sugars, free amino acids, and soluble proteins content directly but rather used a previously developed regression model to estimate plant quality at different salinity levels (Hakim et al. 2014) and related that to our previous work evaluating BPH development and plant quality (Rashid et al. 2017).

In a separate experiment, we also assayed the damage of rice plants by BPH with or without GMB under non-saline conditions. We also tested the salinity preference zone of BPH. Four rice ecosystems with a rice variety BRRI dhan67 were created in a climate chamber (30ºC, 65-70% RH, and a photoperiod of 12D:12L). Five 15 days old seedlings of BRRI dhan67 were transplanted into earthen plastic pots (size: 13.97 cm diameter and 12.7 cm height) filled with fertilized soils. Three rice plastic pots were placed into one plastic bowl filled with different saline water (0, 2, 4, and 8 dSm^{-1}). Four bowls were placed in a manner that allowed the center of these bowls to be placed in only one pot with rice plant. One rice pot with more than 400 BPH 3^{rd} instar nymphs was put in the middle of four bowls and allowed to establish for 96 h. This pot was placed in the center of four bowls so that insects could move easily to each of the four bowls and held for 7 d (**Fig. S1A**). This setup was covered with a nylon mesh net supported by an iron rod frame. After 96 h, the number of BPH settled down in each treatment was counted. The experiment was repeated four times.

During the experimental period, we also recorded both BPH and GMB abundance on the nearby BRRI research farms using light traps (details in Ali et al. 2014) and analyzed the relationship between BPH and GMB abundance daily.

Statistical analysis

A one-way analysis of variance (ANOVA) was done for the data obtained followed by Tukey's multiple range test ($p = 0.05$) for significant differences in treatments using SPSS version 16 software. The percentage data were transformed by arcsine square root method for normality, and homogeneity of variance of all data was also tested before conducting ANOVA test using the same statistical software. For ANOVA analysis, data were log-transformed before conducting the analysis. The assumption of normality was tested using Q-Q Plots and homogeneity of variances was assayed by Bartlett's test. Regression analysis was conducted between panicle length and salinity using linear regression, and correlation analysis was conducted using Pearson's coefficient ($p < 0.05$). To test the effects of plant traits on the abundance of BPH and GMB, we conducted a multiple regression on species abundance by means of a generalized linear model (GLM) with a Poisson error structure. The plant traits were used as the predictor variables and the abundance of BPH and GMB were used as the response variables. In GLM, the relationship between response and predictor variables is,

$$y_i = \alpha + \beta_1 x1_i + \beta_2 x_{2i} + \beta_3 x_{3i} + ,....+ \beta_p x_{pi} + e_i \qquad i = 1, 2,3....n.$$

It is a general linear response of variable y_i modeled by plant traits and some error terms. The general mathematical equation of the Poisson Regression model is: $log(y)=\alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_{3i} + ...+ \beta_p x_p$, where 'y' is the response variable, α and β are numeric coefficients with α being the intercept, x being the predictor/explanatory variable. The generalized linear model (GLM) was analyzed in R (R Development Core Team 2012).

In addition, we also investigated the direct and indirect impacts of salinity on rice biomass and plant quality with path analysis using the lavaan 5.13 (Rosseel 2012) package in R software (R Development Core Team 2012). We proposed 4 general models that explained direct vs. indirect effects of salinity stress on rice plant biomass, plant quality, BPH, and GMB population.

i) GMB ~ Plant quality + Plant biomass + Salinity stress + BPH
ii) BPH ~ Plant quality + Plant biomass + Salinity stress + GMB
iii) Plant quality ~ Salinity stress
iv) Plant biomass ~ Salinity stress

A least squares estimator was applied which allows for dependent and independent factors (Muthen 1984). Furthermore, a full-information maximum likelihood (FIML) method was used to reduce bias introduced by missing information estimation (Schafer and Graham 2002, Allison 2003). Model fit was evaluated both by the comparative fit index (CFI), and the Root Mean Square Error of Approximation (RMSEA) (Hu et al. 1999).

Results

Impact of salinity on growth and yield parameters of rice cultivars

Rice plant height decreased significantly with increased salinity (**Fig. 2**) ($F_{1, 56}$=39.8, p<0.0001). Salinity also significantly influenced the production of tillers per plant (**Fig. 2**). Both varieties showed decreased tillers with increasing salinity. The results also showed that salinity caused a significant impact on the total above-ground biomass of both rice varieties. Both varieties showed a declining trend of above-ground biomass production at elevated salinity levels. The highest above-ground biomass was observed at control (0 dS/m) and lowest at 8 dS/m (**Table S1**). Similarly, the below-ground biomass (root dry weight) was significantly influenced by salinity (p< 0.05; **Table S1**). The highest dry root weight was observed at 2.0 dS/m salinity in BRRI dhan67 while the highest shoot and root weight was observed at 0 dS/m for BRRI dhan47. The highest root dry weight (19.54g) was observed in BRRI dhan47 whereas the lowest was in BRRI dhan67 (5.83g). BRRI dhan47 gave the highest relative shoot dry weight and the cultivar BRRI dhan67 produced lowest SDW (19.82g). In the case of total dry matter, BRRI dhan47 performed the best (26.10g) while BRRI dhan67 produced the least.

Yield-related parameters including panicle length of both varieties were reduced with increased salinity (**Fig. 3 & Fig. S2**). Panicle length showed a negative linear relationship with salinity with each one-unit elevated salinity (dS/m) decreasing panicle length by 0.48-0.5 cm. This impact was observed in both cultivars (**Fig. 3**). Both the numbers of grains/panicle and the 1000-grain weight (g) were also reduced by increased salinity in both varieties (**Table S1**).

Impact of salinity on pest and natural enemy

Salinity exhibited a significant effect on the development of both BPH and GMB ($p = 0.05$). BPH populations were larger on BRRI dhan47 than BRRI dhan67 (**Fig. 4**). For both cultivars, the highest number of BPH was found at 2.0 dSm^{-1} and thereafter declined gradually with increasing salinity level (**Fig. 4**). Similarly, GMB abundance was highest on BRRI dhan47 and decreased with increasing salinity for both cultivars (**Fig. 4**). Salinity also significantly influenced the fecundity of BPH ($F = 23.12$, $p = 0.023$) with the highest fecundity observed at 2.0 dSm^{-1} salinity and declined thereafter (**Fig. S3**). Moreover, BPH prefers modest saline/or non-saline zone to the saline zone. The highest population of BPH (114.6 ± 12.3) observed in 2.0 dSm^{-1} salinity level followed by 0, 4, and 8 dSm^{-1} (**Fig. S1B**). This result indicates that when given a choice, BPH will move from plants grown under higher salinity to ones growing under lower salinity conditions.

Impact of salinity induced plant traits on pest and natural enemy

In addition to the variance of plant traits between different cultivars, we conducted the ANOVA analysis on the variance between plants under different salinity treatment levels. Salinity had a significant impact on all plant traits, including height, tiller per hill, panicle length, grains, and unfilled grain per panicle, except the 1000 grain weight (**Table 1**). Meanwhile, we observed that treatment and cultivar significantly influenced the density of BPH (**Table 2**). However, only salinity treatment impacted the density of GMB but not cultivar. Likewise, the variations of all plant traits (plant height, tiller per hill, panicle length, grains and unfilled grain per panicle, and 1000gw) caused by treatment and cultivar, largely impacted the density of BPH (**Table 1**). Nevertheless, only the salinity induced plant height had an impact on GMB density (**Table 2**).

Path analysis of direct and indirect salinity impact on plant, pest, and predator

The direct and indirect effects of salinity on the host plant quality, the pest population, i.e. BPH, and its predator, i.e., GMB were validated and refined by the results ofpath analyses (**Fig. 5**). The path analysis illustrates the potential underlying mechanisms for the strong and direct adverse negative impacts of salinity on rice biomass (-0.77) and plant quality (-0.93) (corresponds to the proposed models no. 3 and 4 in materials and methods). Salinity also had a strong direct negative impact on BPH (-0.56) and GMB (-0.97). It also had an indirect negative impact of BPH (-0.30) and GMB (-0.11) via plant biomass and quality (**Fig. 5**) (corresponds to the proposed model no. 1 and 2 in materials and methods). The direct and indirect adverse and negative effects of salinity on the accumulation of plant biomass and host plant quality were also weakened by the decrease in the BPH population at higher salinity and also the indirect effects of predation (via GMB development) (corresponds to the proposed model no. 2 in materials and methods). Elevated salinity (after 2.0 dS/m) reduced rice biomass, reducing plant quality, which induced lower development of BPH populations. These BPH produced lower quality prey (eggs, young nymphs) for GMB. Thus, salinity stress indirectly affected GMB development (**Fig. 5**). The GMB also had a negative impact on BPH populations which increased rice biomass. However, in the absence of salinity stress, GMB possessed a negative impact on BPH population development which resulted in higher biomass of rice (**Fig. S4**). Growth of rice plants was reduced where BPH released without GMB and all plants eventually senesced (**Fig. S4**). These observations supported our proposed models as mentioned in materials and methods for understanding the tritrophic interactions.

Compared to control conditions, at 2.0 dSm^{-1} salinity, BPH populations increased by 7.89 – 14.62% but GMB populations decreased by 13.75 - 14.50% (**Fig. 6**). Thus, salinity stress caused a delinking of prey-predator population dynamics in a tritrophic system**.** From normal conditions to modestly saline conditions (2 dSm^{-1}), BPH showed increasing trends in both cultivars (**Fig. 6**, upper panel) while GMB showed declining trends in both cultivars (**Fig. 6**, lower panel). This result indicates that elevated salinity can disrupt synchrony between BPH and GMB population dynamics.

Discussion

Remarkable changes of salinity in both in agriculture and coastal landscape occurred due to global climate change (Bannari et al. 2020). This study examines the impact of increasing salinity on tri- trophic interactions between rice, its major pest BPH and its key natural enemy

GMB. Our studies confirm that increasing salinity has strong negative effects on rice plant productivity especially on growth and yield as previously reported (Gupta and Huang 2014, Pattanagul and Thitisaksakul 2008, Chunthaburee et al. 2016, Horie et al. 2012). Plant height of two rice cultivars (BRRI dhan47 and BRRI dhan6) significantly decreased with increasing salinity with cultivar's effect (BRRI, 2020) induced by salinity (**Table 1, 2**). Reduction of plant height can be explained by changing the rate of photosynthesis, carbohydrate content, enzyme activity, and growth hormones under salt stress (Mazher et al. 2007; Hakim et al. 2014). Salinity also affected tiller production per plant of rice (**Fig. 2**) which is in agreement of previous reports (Khanam et al., 2018, Zeng et al., 2003; Eugene et al., 1994; Nicolas et al., 1994; Pradheeban et al., 2017). Our study shows that the panicle length - a critical factor in rice grain yield, is significantly reduced by salinity after 4 dS/m salinity levels to both cultivars and showing a significant negative linear relationship with salinity (**Fig. 3**) as previously observed (Hussain et al. 2017; Pradheeban et al. 2017; Marassi et al.1989, Abdullah et al. 2001, Radanielson et al. 2018, Castillo et al. 2007). Other yield contributing factors such as no. of grains per panicle and 1000-grain weight were also reduced due to salinity stress. These caused an increase in sterile florets/unfilled grain as seen in our study (**Table S1**). Thus, the reproductive phase of rice is more vulnerable to salinity stress than other growth and development phases as supported by previous reports (Khatun et al. 1995, Heenan et al. 1988, Zeng and Shannon 2000b, 2000c, Krishnamurthy et al. 1989, Zaman et al. 1997, Cui et al. 1995, Alam et al. 2004, Asch et al.1999, Hussain et al. 2017, Rao et al. 2008, Mohammadi et al. 2014, Chunthaburee et al. 2015). Salinity not only affects the above ground plant biomass but also exerts effects to roots. The shoot and root dry weights of both cultivars were decreased with increasing salinity which corroborates prior studies (Cristo et al. 2001: Kavosi 1995; Yeo and Flowerse 1986; Zeng and Shannon 2000b; Pradheeban et al. 2017, Lin and Kao, 2001, Pushpam and Rangasamy, 2002, Bohra and Doerffling 1993).

The main purpose of this study was to understand and assess the indirect impact of salinity on pests and predators mediated via host plants. Therefore, we used two tolerant rice cultivars to assess the impact of salinity stress on the plants and indirectly on BPH and GMB tritrophic interactions under controlled conditions. Both cultivars can survive up to 8 dS/m salinity and thus provided living hosts for both the BHP and GMB, but host plant quality likely declined due to salinity stress as the content of free amino acids, soluble proteins, and soluble sugars have been shown to decline with increased salinity (Hakim et al. 2014). We also observed that the effects of salinity were consistent with forecasts of overall decreases in the quality of plants with increased salinity level. Previously, we reported that rice plant uptake of N from soil increases the amino acid and free sugar in plants (Rashid et al. 2017). As a result, plants accumulated higher amounts of nitrogen resulting higher soluble protein content in their tissues ultimately play a vital role on BPH growth and development (Rashid et al. 2017). However, salt stress inhibits nutrient uptake, especially N and gas exchange capacity in rice (Hussain et al. 2017, Rashid et al. 2017, Lutts et al. 1996) leading to poor host plant quality for BPH, which also leads to poor quality of eggs and nymphs. Ultimately, GMB feeds on these poor-quality eggs or nymphs, retarding their development indirectly. However, the negative effects of salinity on rice biomass/ or host quality were attenuated with increasing salinity and at the same time, BPHs became poor-quality food for GMB.

The direct effect of salinity on rice plants indirectly impacted BPH and GMB food quality as confirmed the by path analysis (**Fig. 5**). Increases in salinity indirectly decreased BPH development by decreasing quality of plant, both of them were connected with lower levels of GMB development. The salinity stress effect on trophic interactions, i.e. the prey-predator incompatibility, could potentially contribute to the phenological asynchrony which may cause delinking the host-parasitoid relationships as reported previously (Stireman et al. 2005).

Our study reveals that elevated salinity causes a mismatch in the population dynamics of predator and prey. For example, at a salinity of 2 dS/m, BPH populations increased while the GMB populations decreased. This level of salinity is already common in some coastal areas of Bangladesh (Haque, 2006; SRDI; 2010; Islam and Hossain, 2020; Islam et al. 2020) although in topsoil it may vary from 0.3 to 70.0 dS/m (SRDI, 2010) which could be a potential factor leading to possible BPH outbreaks due to spatial mismatching between predator and prey abundance. This could also lead to a phenological mismatch if GMB needs to move for their foods/habitats and thus arrives too late to suppress BPH, leading to a reduction of ecosystem service. The GMB is an important ecosystem service provider for controlling BPH in the Asian rice ecosystem (Katti et al. 2007; Sigsgaard 2007). However, it is also capable of moving by switching to alternative prey (Schaefer and Panizz 2000). Moreover, warming and extreme salinity conditions may further indirectly worsen the negative effects of invasive species by reducing the biological resistance offered by indigenous predatory species (Cheng and Grosholz, 2016).

Recently, Furlong and Zalucki (2017) reported that natural enemies are more susceptible and sensitive to changing conditions compared to their respective hosts. This indicates an asymmetrical host-natural enemy interaction and decreased effectiveness of bio-control program with a changing environment in agroecosystems. Under non-saline conditions, the population dynamics of BPH and GMB are tightly linked. Based on our light trap counts, GMB increases with the increase of the BPH population and shows a strong link between them (**Fig. S4**). The incidence of predatory GMB is positively correlated with populations of

BPH and GLH and their incidence declines with reduced populations of BPH and GLH (IRRI, 1986). Based on light trap counts and previous results (IRRI 1986) it is confirmed that a positive correlation exists between BPH and GMB population under non-saline conditions. However, the present study conducted under saline conditions shows a negative correlation between BPH and GMB under moderately elevated salinity levels (2.0 dSm^{-1}) (**Fig. 6**). As the salinity stress is subjected, it caused a reduction in plant quality, hence BPH became less or non-suitable as a host for GMB and so a negative correlation between BPH and GMB emerged as our studies revealed.

Salinity changes may thus differentially influence each trophic level in the ecosystem, leading to a system decoupling. In predator-prey relationships, decoupling may include switching of predators presumably from one ecosystem to another ecosystem and/or food sources (Rodewald et al. 2011) and stress conditions that decouple species interactions may alter trophic cascades (Cheng and Grosholz 2016). Moreover, the effect of salinity on the predator-prey relationship is likely more significant for higher level than lower trophic levels since the predators depends on the prey to adapt under stressed conditions (Chidawanyika et al. 2029, van der Putten et al. 2009). As such in the rice agroecosystem, predatory GMB are possibly more vulnerable to changes due to salinity stress. Two hypothetical scenarios may occur in rice agroecosystems if the salinity level increases significantly. First, predator populations may decrease due to migration to suitable habitats/resources (Cohen et al. 1993; Brose et al. 2006) resulting in increased BPH pressure in some crop fields. Moreover, organisms at higher trophic levels (predator) may be more firmly united with ecological factors due to higher “sensitivity” (sensu Voigt et al. 2003, 2007). Thus, increasing salinity may displace the GMB population which could cause system decoupling. The second scenario would be changed in distribution patterns of pests and predators in the rice agroecosystem. This scenario might increase pest suppression if for example generalist predators, e.g. ladybird beetles, spiders, carabid beetles commonly found in rice field (Rahman et al. 2017, Afrin et al. 2019) are less sensitive to salinity effects on host plants and herbivores. Our results show that BPH tend to migrate from higher saline zones to modest saline or non-saline zones (**Fig. S1**). Therefore, migration of pests from stressed (e.g. salinity) agroecosystems may contribute to an increase of yield due to reduced pest pressure. Thus, the outcomes of climate-induced stress conditions on predator-prey relations are multilateral and may differentially impact on the crop productivity, plants growth and development and conserving biodiversity.

While the greenhouse studies described here are by necessity artificial, they represent established plant, pest, natural enemy communities and salinity levels frequently observed in coastal areas of Bangladesh (Haque 2006; SRDI 2010; Islam and Hossain, 2020; Islam et al. 2020). As such, we feel they provide relevant insights into trophic asynchrony that may be occurring in the coastal areas. Based on our experimental results, we suggest that efforts in conserving natural enemies or enhancement of natural biocontrol may be negatively affected by the various complex and multileveled interactions between abiotic stresses, especially salinity and biotic communities. Further experimentation involving multiple factors is required for a comprehensive understanding of the multitrophic levels.

Acknowledgments

The authors would like to extend their gratitude to the staff and scientists of the Entomology Division for helping in the greenhouse work and the Bangladesh Rice Research Institute (BRRI) for providing other necessary supports and services. Full funding was provided by USAID-sponsored Partnerships for Enhanced Engagement in Research (PEER) Program’s

Cycle 6 project, entitled “Ecosystem services in a changing climate; assessing critical services in Bangladesh rice production landscapes.” PEER is implemented by the U.S. National Academy of Sciences (NAS) via USAID and NAS Prime Agreement No. AID-OAA-A-11 -00012. TheUS partner on the PEER grant, DA Landis, acknowledges support from the NSF Long-term Ecological Research Program (DEB 1832042) at the Kellogg Biological Station, Michigan State University South Asia Partnership and MSU AgBioResearch. Xinghu thanks the support from China Scholarship Council and University of St Andrews Scholarship.

Author Contributions

M.P.A., M.S.R., and S.S.H. designed and planned the experiments. S.S.H., M.T.H.H., M.M.A., M.M.U. and M.P.A. executed and implemented the project activities. M.P.A. and M.S.R. designed the methodology. M.S.R., M.P.A., and F.N. generated the data. M.S.R., M.P.A., and F.N. compiled data. M.P.A. and X.Q. analyzed the data. M.S.R., M.P.A., and M.T.H.H. wrote the original and revised manuscript. D.A.L. and X.Q. revised and edited the manuscript for clarity.

All of the authors read and approved the final version of the manuscript.

Data Accessibility Statement

All data related to publication available within the manuscript.

Competing Interests Statement

The authors declare no competing interests.

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Table 1. Analysis of variance (ANOVA) of plant traits induced by salinity. For ANOVA analysis, data were log-transformed before conducting the analysis. The assumption of normality was tested using Q-Q Plots and homogeneity of variances was assayed by Bartlett's test. Nine hills per treatment were used to analyze the effect of salinity on them.

	Df	**Sum of square**	**Mean square**	**F-value**	**Pr(>F)**	**Signif. codes**
Plant height	1	111.55	111.55	191.3	1.24E-12	***
Tiller per hill	1	2.73	2.73	4.681	0.0411	*
Panicle length	1	55.14	55.14	94.56	1.29E-09	***
Grains	1	13.66	13.66	23.424	6.94E-05	***
Unfilled grain per panicle	1	43.38	43.38	74.398	1.15E-08	***
1000gw	1	0.12	0.12	0.208	0.6523	
Residuals	23	13.41	0.58			

Significance codes: *** 0.001 ** 0.01 * 0.05

Table 2. Effects of plant traits induced by salinity on BPH and GMB (tested with a generalized linear model (GLM) with a Poisson error structure). Two rice cultivars, BRRI dhan47 and BRRI dhan67 were used. N = 9. The general mathematical equation of the Poisson Regression model is: $log(y)=\alpha + \beta_1x_1 + \beta_2x_2 + \beta_3x_{3i} + \ldots + \beta_px_p$, where 'y' is the response variable, α and β are numeric coefficients with α being the intercept, x being the predictor/explanatory variable.

BPH						**GMB**				
	Estimate	*Std. Error*	*z value*	*Pr(>|z|)*	*Signif. codes*	*Estimate*	*Std. Error*	*z value*	*Pr(>|z|)*	*Signif. codes*
Intercept	9.50	0.79	11.99	< 2e-16	***	-0.320	1.738	-0.18	0.854	
Treatment	-0.15	0.02	-7.29	3.04E-13	***	-0.097	0.044	-2.23	0.026	*
Cultivar	-1.31	0.17	-7.78	7.38E-15	***	-0.762	0.391	-1.95	0.051	.
Plant height	-0.01	0.01	-2.42	0.016	*	0.041	0.014	2.92	0.003	**
Tiller per hill	0.01	0.01	0.85	0.396		-0.047	0.032	-1.47	0.143	
Panicle length	0.05	0.01	3.73	0.000	***	0.016	0.035	0.45	0.651	
Grains	0.00	0.00	1.32	0.186		0.001	0.004	0.18	0.860	
Unfilled grain per panicle	0.01	0.01	2.52	0.012	*	0.011	0.012	0.96	0.337	
1000gw	-0.15	0.02	-7.34	2.18E-13	***	0.026	0.048	0.54	0.587	

Significance codes: *** 0.001 ** 0.01 * 0.05

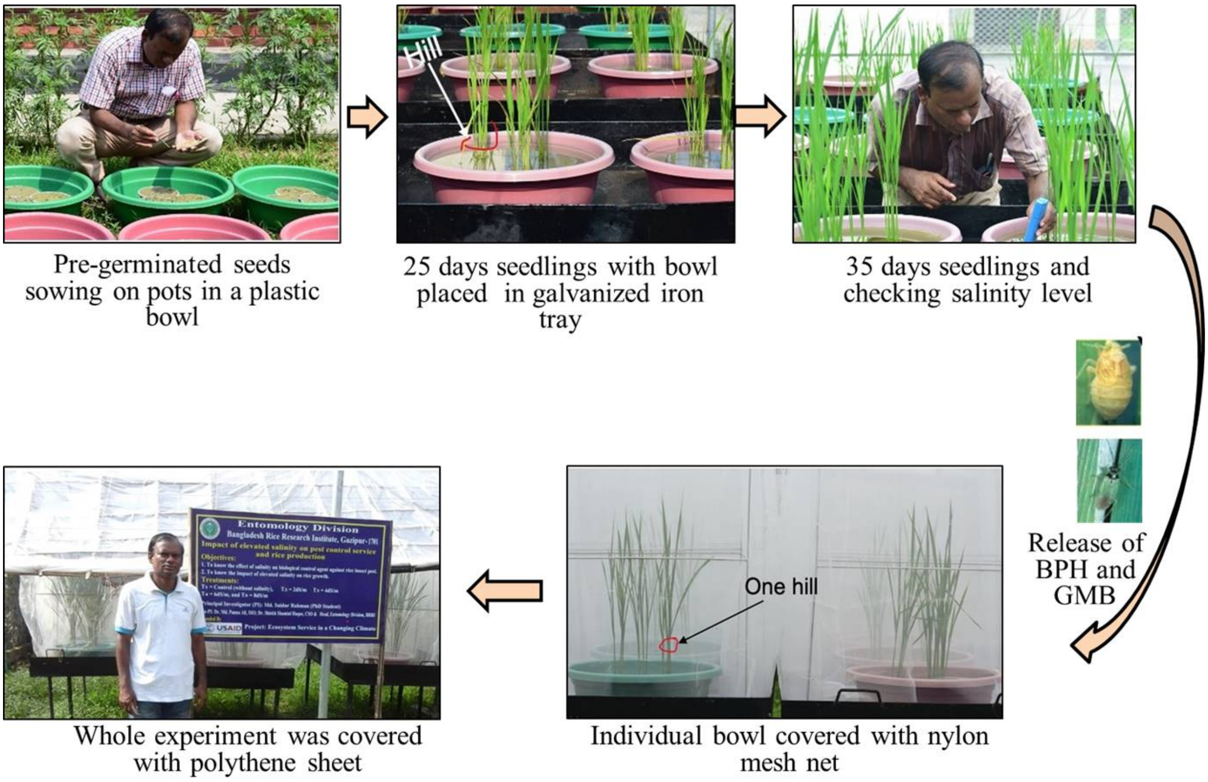

Figure 1. Schematic diagram of greenhouse experimental procedure used in this study.

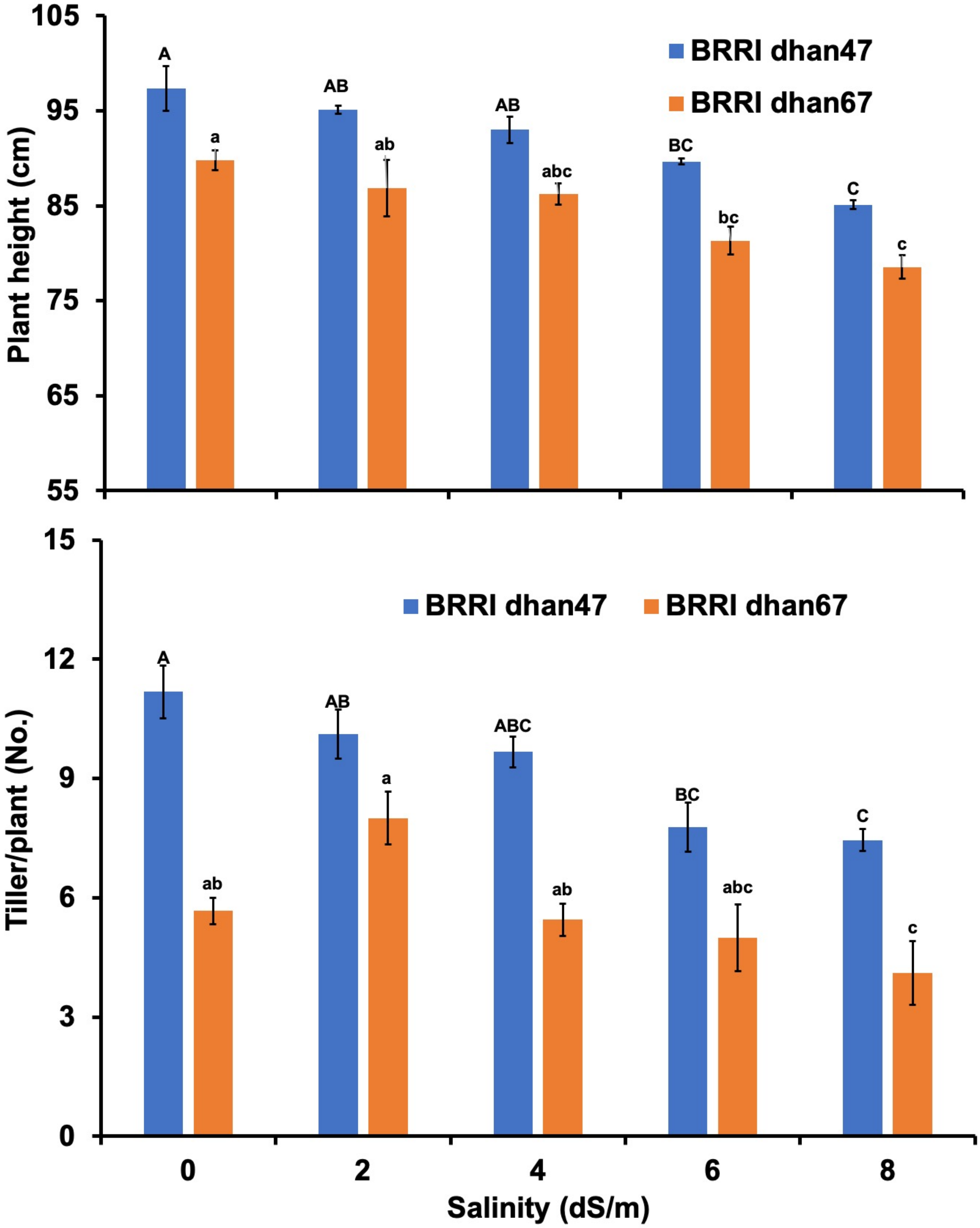

Figure 2. Effect of salinity on the plant height and tiller production per plant. Bar bearing the same letter did not differ significantly at 5% level of significance. Capital letter used for distinguishing cultivars only. Error bar represents standard error. Tukey's honest significance (Tukey's HSD) test was used for means comparison from each other.

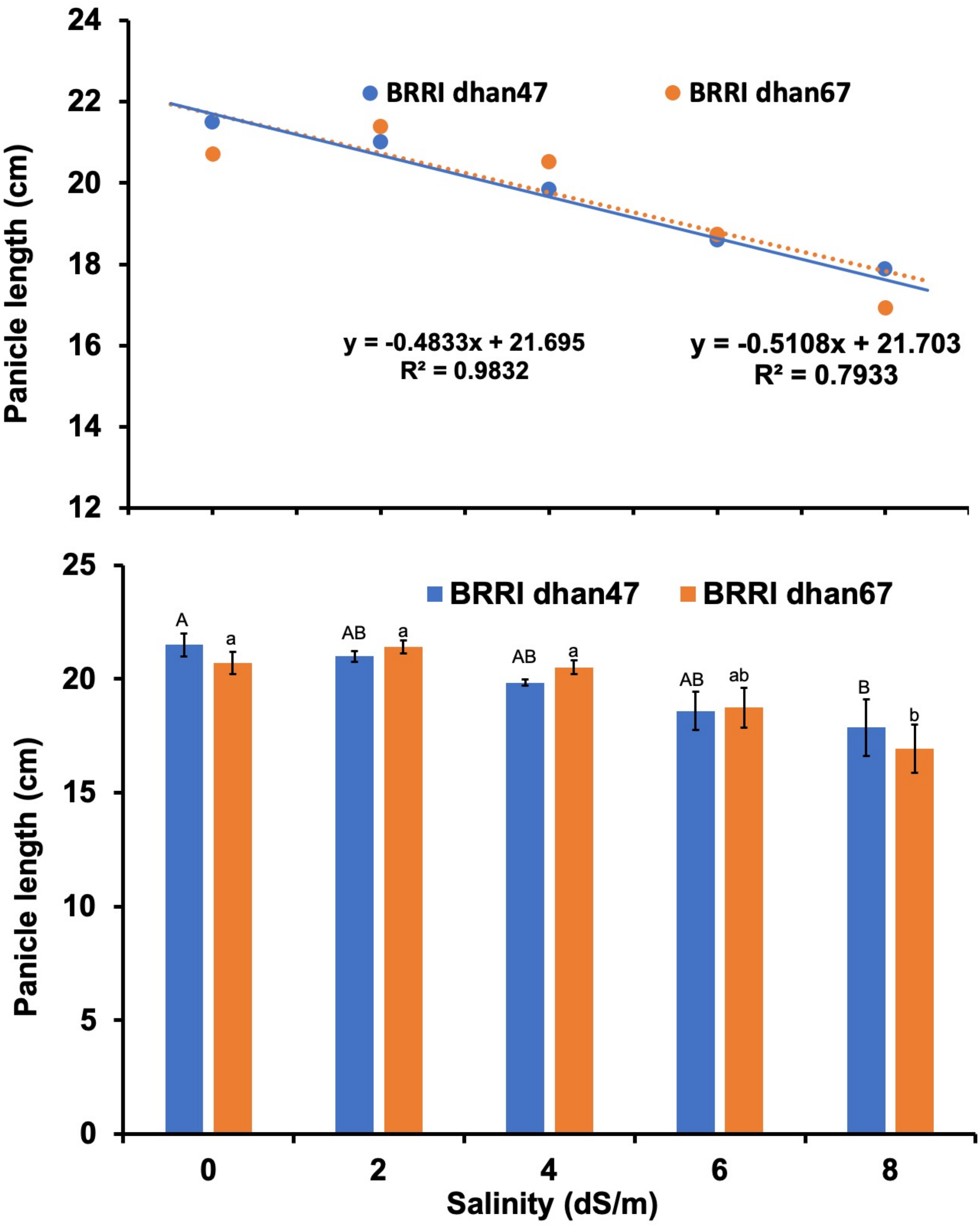

Figure 3. Effect of salinity on panicle length of rice. Bar bearing the same letter did not differ significantly at 5% level of significance. Error bar represents standard error. Tukey's honest significance (Tukey's HSD) test was used for means comparison from each other. Capital letter used for distinguishing cultivars only.

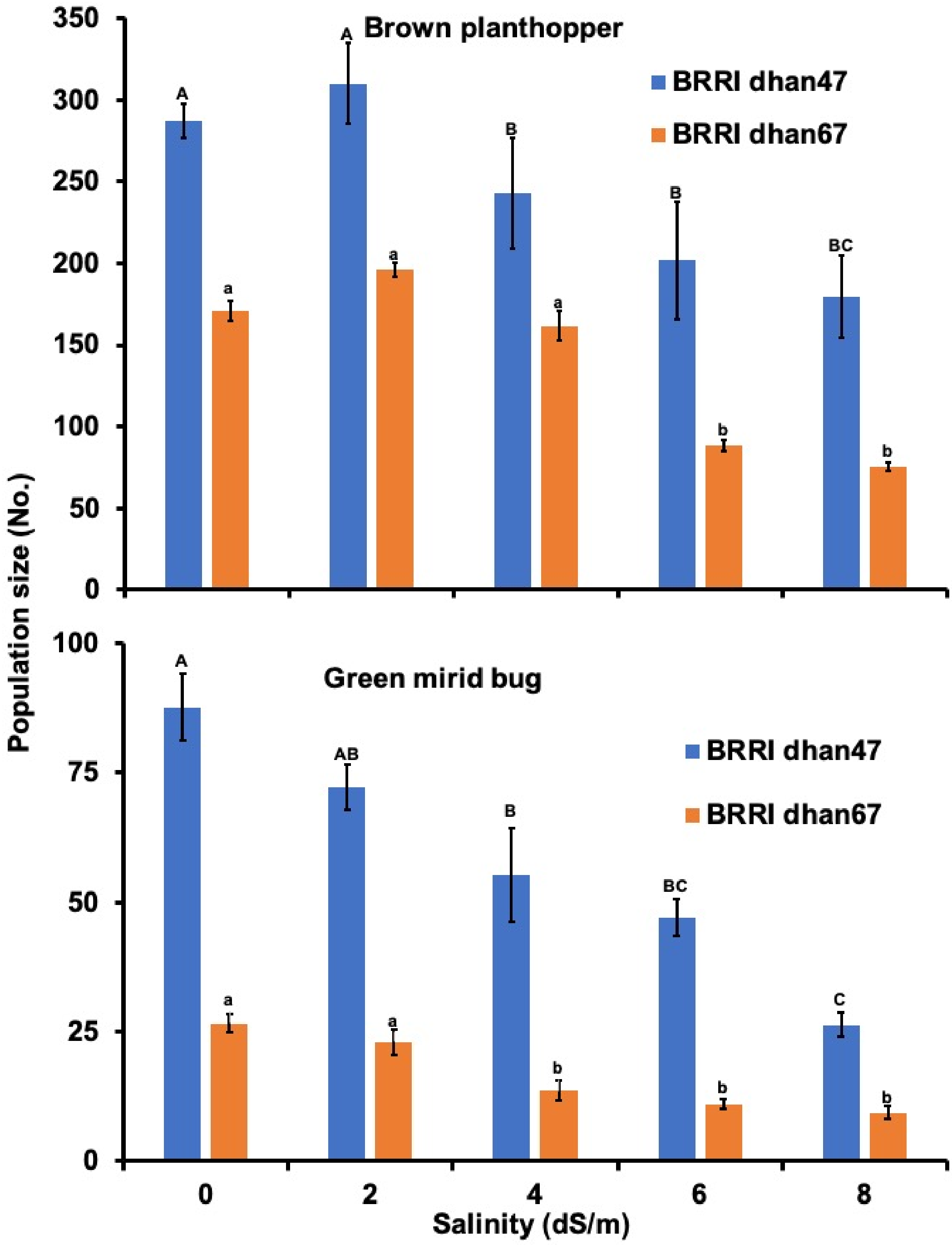

Figure 4. Effect of salinity on the population development of brown planthopper (BPH) and green mirid bug. Bar bearing the same letter does not differ significantly at 5% level of significance. Error bar represents standard errors. Tukey's honest significance (Tukey's HSD) test was used for means comparison from each other. Capital letter used for distinguishing cultivars only.

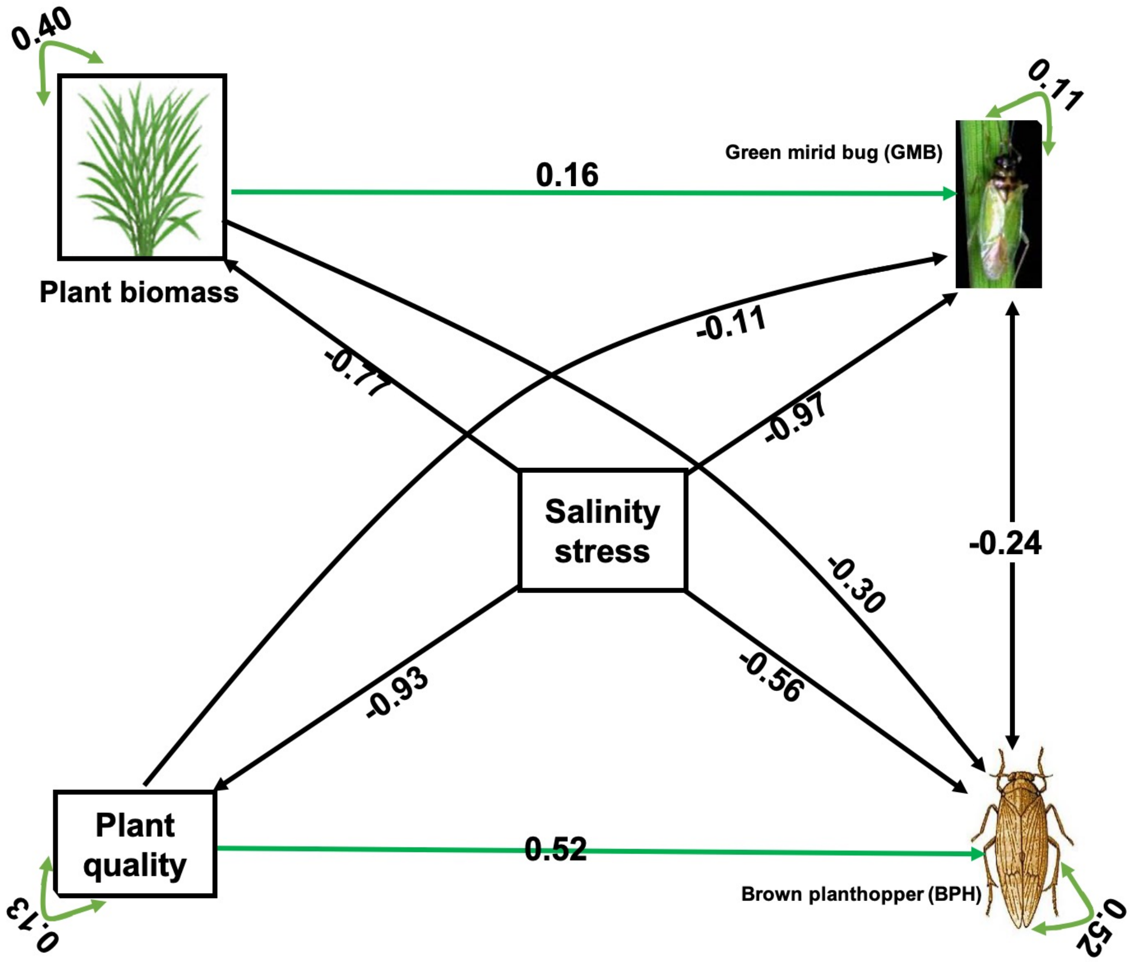

Figure 5. Path diagrams outlined the models of direct and indirect effects of salinity on rice, pest and predator. Direct effects between the variables are indicated by black arrow lines and indirect effects are indicated by green arrow lines, respectively. Standardized path coefficients are from the path model that explained total soluble protein, amino acid and free sugar as plant quality variables and BPH egg, young nymph as prey quality variables. The path model highlights the positive effects of GMB as natural enemies on the plant biomass interceded by decreased BPH population development without salinity stress. Later it is confirmed by another experiment (supplementary figure S5).