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EFFECT OF SALICYLIC ACID ON THE DRY MATTER AND NITROGEN ACCUMULATION, PARTITIONING AND TRANSLOCATION IN TWO CONTRASTING RICE GENOTYPES UNDER SALT STRESS

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Abstract

Salt stress is one of the important abiotic stresses that affect agricultural production. Salicylic acid (SA) plays an important role in plant growth and development as well as against stress. The purpose of this work was to analyze the short-term and long-term effect of SA on the dry matter (DM) and nitrogen (N) accumulation, partitioning, and translocation in two contrasting rice genotypes (salt-tolerant LD5, salt-susceptible MDJ30) under salt stress. Forty two-day-old rice plants were exposed to salinity stress (0, 4.6 dS m^{-1}) for two weeks and then the salt group was sprayed with 60 ml SA (0, 0.5 mmol L^{-1}) per pot for two days. The short-term and long-term effects of SA were analyzed by sampling at 6 and 12 days after the SA treatment, and at heading and maturity stage, respectively. The results showed that salt stress significantly reduced the DM and N accumulation of each above-ground organ, changed allocation pattern and reduced their translocation to panicles. Genotypes showed differences in DM and N distribution and translocation under salt stress. Compared with MDJ30, LD5 accumulated more DM under salt stress, had a higher proportion of stem-sheath DM and maintained the DM translocation to panicle. The response of N accumulation to salt stress in LD5 was higher than that in MDJ30 at tillering stage but was less than that at heading and maturity stage, reflecting that salt tolerant variety gradually adapted to the restriction of N acquisition due to salinization. Exogenous SA promoted the accumulation of DM and N in stem + sheath at short-term and in above-ground organs of rice under salt stress at long-term. SA increased the partitioning ratio of DM and N in panicles of MDJ30 under salt stress but decreased that in LD5. This was mainly due to the fact that SA increased the translocation of assimilates from vegetative organs to panicles of MDJ30, but decreased that of LD5 as its short-term promotion effect resulted in an excessive accumulation in stem + sheath. These results suggested that SA promoted assimilates accumulation in the above-ground organs of rice under salt stress, changed the distribution pattern of nutrients, and its effect on the translocation of assimilates was related to the salt tolerance of genotypes.

Key words: Salt stress, Salicylic acid, Dry matter allocation, Nitrogen translocation, Time effect.

Introduction

The essence of crop yield formation is the process of accumulation, translocation, and allocation of the dry matter (Ye *et al*., 2013). Plant dry matter accumulation determines the biological yield of rice, and the translocation of the photosynthesis production into the panicle determines the economic yield. Nitrogen is one of the most important nutrients for plant growth which affects the dry matter accumulation and partitioning (Demotes-Mainard & Jeuffroy, 2004; Dordas, 2009; Nagata *et al*., 2001 and Poshtmasari *et al*., 2007). N can influence the leaf area development and maintenance as well as photosynthetic efficiency and dry matter partitioning to reproductive organs (Dordas, 2009 and Ye *et al*., 2014). The accumulation, transformation, and utilization of dry matter and nitrogen in vegetative organs and reproductive organs of plants play a decisive role in the growth, yield, and quality of plants. When nitrogen uptake and assimilation cannot meet the high demand for grain, nitrogen transport is especially important during the grain filling (Zhang *et al*., 2017). However, abiotic stresses often limit crop growth and N uptake by a direct or indirect effect. Thus, it is important to understand the dry matter and nitrogen accumulation, partitioning and translocation of crops under stress conditions.

Soil salinity is one of the major abiotic stresses limiting crop growth and productivity worldwide (Farooq *et al*., 2015 and Koca *et al*., 2007). In general, salt stress affect the transport and distribution of nutrients, thereby inhibiting plant nitrogen metabolism processes, such as ion absorption, nitrogen assimilation, amino acid and protein synthesis (Sha *et al*., 2017a). Earlier literature found that salt stress inhibited dry matter and nitrogen accumulation in ryegrass (Li *et al*., 2011), reduced the allocation of nitrogen and carbon assimilates at pre- and post-anthesis to the wheat grains (Zheng *et al*., 2009). The low concentrations and poor translocation of assimilates from the source induced by salt stress reduced grain dry matter of rice (Sultana *et al*., 1999). Pérez-López *et al*., (2014) found that salinity decreased the uptake and translocation rates of N in barley seedlings. However, there have been few reports on nitrogen accumulation, transport, and distribution of rice under long-term salt stress.

SA plays an important role in the defense response to salt stresses in crop species, and its physiological mechanism includes the enhancing antioxidant defense system, improving photosynthesis and respiration, regulating ion

uptake and distribution, regulating material metabolism, and cross-talking with other hormones or signaling molecule (Sha *et al*., 2017a). SA with optional concentrations has been shown to increase biomass, reproductive yield in a variety of species (Martel & Qaderi, 2016) and promote the nitrogen assimilation (Nazar *et al*., 2011 and Ma *et al*., 2006) under salt stress conditions. However, there is little information about the effect of SA on the DM and N allocation and translocation of rice under salt stress. As crop growth is a continuous process, it is not yet clear whether the effect of pre-application of salicylic acid on plant growth under adverse conditions will continue into the late crop growth. Thus, the objectives of the present investigations were to examine (i) the effect of salt stress on the DM and N accumulation, allocation and translocation of two contrasting genotypes, (ii) the temporary effect of SA on DM and N accumulation under salt stress, and (iii) the long-term effect of SA on DM and N allocation and translocation under salt stress during the heading and maturity stage.

Materials and Methods

Experimental materials and treatment: The trial was conducted in the pot farm of Northeast Agricultural University (NEAU, China) from April to October 2016. Rice grains (*Oryza sativa* L. ssp. *japonica*) of salt-tolerant genotype Long dao5 (LD5) and salt-sensitive genotype Mudanjiang 30 (MDJ30) were obtained from the Rice Research Institute of NEAU. Thirty-five-day-old seedlings (4-leaf stage) of uniform size were transferred to a plastic pot (Upper diameter, 24.2 cm; Lower diameter, 20.0 cm; Height, 21.5 cm) containing 10 kg clay loam soil. The soil type was isohumosols (mollisols; FAO phaeozems) and the basic physical and chemical characteristics of this soil are shown in Table 1. The application rate of basal fertilizer per pot was 0.75 g of urea (46% N), 0.60 g of ammonium phosphate (18% N and 46% P_2O_5) and 0.56 g of potassium sulfate (52% K_2O). Experiments used a completely randomized design with three replications. Three treatments were implemented as follows: CK (control), Salt (4.6 dS m^{-1}), SS (4.6 dS m^{-1} with 0.5mmol L^{-1}SA). Each group had 20 pots and each pot had 4 evenly spaced holes and 3 seedlings per hole. To prevent the salt shock of seedlings, each pot of salt group was watered 1 L 50 mmol L^{-1}NaCl solutions every 2 days after all plants recovered from the disturbance (within 7 days after transplanting). In the control treatment tap water of equal quantity was given (EC=0.011dS·m^{-1}). Ten days later, the final salt concentration was reached (EC 4.6±0.1 dS m^{-1}) and salt solutions were no longer added to soils. Water lost by evapotranspiration was compensated for every two days by supplement of tap water to the scale line marked on red chopsticks. After 2 weeks, each pot of salt treatment was divided into two groups. Seedlings of each group were given a foliar spray of 0 or 0.5 mmol L^{-1} SA solutions once per day for two days. The volume of SA spray was 60 ml per pot, and the concentration of SA was selected based on our previous experiment (Sha *et al*., 2017b).

Plant sampling and calculation: Three representative rice plants in each treatment were sampled at 6 and 12 days after the SA treatment (DAT), heading and maturity stage. These samples were separated into two components at tillering (stem + sheath and leaf) and in three components (stem + sheath, leaf, and panicle) at heading and maturity stage. Samples were dried in a hot-air oven at 105°C for 0.5 h, and then at 80°C for 3-4 days until the dry weight was stabilized. After drying, all divided samples were ground to pass a 1 mm screen with a Tissue Lyser II mill. The nitrogen content was determined according to the Kjeldahl method. At maturity, grain yield was determined by harvesting the plants from 3 pots.

Dry matter accumulation (DMA, g $hill^{-1}$) = DMA per hill at a certain stage

DM translocation (DMT, g $hill^{-1}$) = (DMA at heading—DMA at maturity) of vegetative organs.

DMT efficiency (DMTE, %) = (DMT/DMA at heading) ×100.

DMT conversion rate of vegetative organs (DMCRV, %) = (DMT/ DMA increased in panicle from heading to maturity) × 100.

N accumulation (NA, g $hill^{-1}$) =NA per hill at a certain stage

Nitrogen translocation (NT, mg $hill^{-1}$) = (NA at heading—NA at maturity) of vegetative organs.

NT efficiency (NTE, %) = (NT/NA at heading) ×100.

NT conversion rate of vegetative organs (NTCRV, %) = (NT/ NA increased in panicle from heading to maturity) × 100.

Statistical analysis

Three treatments of each rice genotype were subjected to a one-way analysis of variance (ANOVA) using SPSS 18.0. The ANOVA results were subjected to a Duncan test for the significance comparison (p<0.05).

Results

Dry matter accumulation at tillering stage: In order to assess the influence of SA on alleviating salt-induced reduction in dry matter accumulation during the short term, we analyzed the dry matter accumulation at 6 DAT and 12 DAT. Above-ground dry matter accumulation of both rice genotypes with salt significantly declined in comparison to control (Fig. 1). The dry matter reduction of stem + sheath (37.6%, 45.8%), leaf (38.2%, 40.7%) and total (37.9%, 43.7%) in MDJ30 under salinity stress at 6 DAT and 12 DAT were higher than these in LD5. These results show that the seedling of MDJ30 was more seriously affected than LD5 during the tillering stage.

Compared with salt stress alone, exogenous SA with salt stress improved the dry weight of stem + sheath (23.9% and 37.8% for MDJ30, 19.4% and 30.2% for LD5) and total dry matter (20.7% and 31.7% for MDJ30; 17.1% and 26.8% for LD5) at 6 and 12 DAT, but only increased the leaf dry weight at 12 DAT (23.9% for MDJ30 and 22.1% for LD5). The results that SA initially increased the dry matter accumulation in stem + sheath and then in leaf, indicated that SA promoted the accumulation of assimilation and mobilized these nutrients to the temporary storage organ. In addition, the promotion effect of SA on dry matter accumulation in MDJ30 at tillering stage was larger than that in LD5.

Dry matter accumulation and partitioning at heading and maturity stage: Dry matter accumulation (DMA) and its partitioning into different plant parts varied according to the genotypes and growth stage (Table 2). A significant decrease in the DMA of above-ground organs from heading to maturity for both rice genotypes under salinity stress was observed in Table 2. The reduction of stem + sheath, leaf, panicle and total DMA in MDJ30 under salinity stress were separately 30.9%, 35.4%, 40.1% and 33.2% at heading stage, and 28.6%, 27.6%, 32.5% and 30.7% at maturity stage, while these reduction in LD5 were 8.1%, 17.7%, 34.1% and 13.8% at heading stage, and 6.5%, 15.2%, 21.4% and 16.2% at maturity stage. These results showed that the heading stage was more susceptible to salt stress than maturity stage and that the panicle was more susceptible to salt stress than stem + sheath or leaf. The DM partitioning ratio (DMPR) in panicles of LD5 under salt stress significantly declined at heading and maturity stage, and that of MDJ30 only significantly decreased at heading stage. The DMPR of other organs in MDJ30 didn't show significant change during heading and maturity stage, while that of stem + sheath in LD5 significantly increased, which indicated that the more accumulation and distribution of dry matter into stem + sheath (especially before heading) may be beneficial to plant resistance to salt stress.

Compared with salt stress alone, exogenous SA with salt stress significantly improved the DMA of stem + sheath (17.4% and 14.0% for MDJ30, 18.9% and 23.7% for LD5), leaf (15.2%for MDJ30 at heading, 14.5% and 14.8% for LD5), panicle (38.0% and 19.8% for MDJ30, 14.3% and 11.2% for LD5) and total (18.9% and 15.8% for MDJ30; 17.4% and 15.9% for LD5) at heading or /and maturity stage. These results indicated that the effect of SA on the DMA of panicle in MDJ30 was higher than that in LD5, but the promotion effect on stem + sheath and leaf in MDJ30 was less than that in LD5. Exogenous SA significantly improved the DMPR of panicle in MDJ30 from heading to maturity stage and significantly decreased the DMPR of leaves at maturity stage. By contrast, SA significantly decreased the DMPR of panicle in LD5 at maturity stage, and significantly improved the DMPR of stem + sheath. The results showed that the effect of SA on the dry matter allocation varied according to the rice genotypes.

Dry matter translocation at heading and maturity stage: Compared with control, salt stress significantly decreased dry matter translocation (DMT), and the increment of panicle DM in both rice genotypes, and significantly reduced DMT efficiency (DMTE) and DMT conversion rate of vegetative organs (DMTCRV) in MDJ30 (Table 3). DMT of stem + sheath (44.8%) and leaf (51.9%) of MDJ30 under salt stress decreased more than that of LD5 (16.9% for stem + sheath and 22.4% for leaf).In addition, the increment of panicle DM (31.4%) of MDJ30 under salt stress decreased more than that of LD5 (19.5%) from heading to maturity stage. The results suggested that salt stress inhibited the dry matter translocation to the panicle from heading to maturity, especially for the salt-susceptible genotype MDJ30.

Exogenous SA significantly increased DMT (46.4% and 54.1%) and DMTE (24.7% and 33.8%) of stem + sheath and leaf, the increment of DM in panicle (17.4%), and DMTCRV (37.8%) of MDJ30. In contrast, SA significantly decreased DMT (11.9%) and DMTE (25.9%) of stem + sheath and DMTCRV (10.2%) of LD5, and improved the increment of DM in panicle (10.8%) of LD5, but had no obvious effect on the DMT and DMTE of leaves. These results showed that the promotion effects of SA on DMT, DMTE, and DMTCRV of salt-sensitive MDJ30 were larger than that of LD5. The panicle DM improvement of MDJ30 under salinity stress by exogenous SA may be mainly due to its promotion effect on the dry matter translocation from vegetative organ to panicle. However, the panicle DM improvement of LD5 by exogenous SA may be mainly due to its promotion effect on the photoassimilates accumulation after heading stage.

Nitrogen concentration: The N concentration responded to salinity stress varied according to genotypes, organ and development stage (Table 4). At tillering stage, both genotypes differed for aerial plant part N concentration (NC) under salt stress. Salt stress decreased NC in stem+ sheath and leaf of both genotypes at 6 DAT. However, salt stress decreased NC by 10.6% in stem+ sheath and increased by 10.1% in leaf of MDJ30 at 12 DAT, increased by 26.7% in the stem + sheath of LD5 at 12 DAT. At heading and maturity stage, salt stress decreased NC in vegetative organs of both genotypes. At heading stage, the decreases were 14.5% and 14.5% in the leaves, and 18.6% and 30.9% in the stem + sheath of MDJ30 and LD5 under salt stress. At maturity stage, the decreases were 18.5% and 22.2% in the leaves, and 11.3% and 24.1% in the stem + sheath of MDJ30 and LD5 under salt stress. In addition, salt stress increased NC in the panicles of MDJ30 (3.8%) at heading stage, and that of LD5 (7.4%) at maturity stage.

Compared with salt stress, exogenous SA increased NC in the stem + sheath (86.2% and 88.6%) and leaves (39.5% and 50.1%) of MDJ30 and LD5 at 6 DAT, but decreased that (32.2% and 36.8% in stem + sheath, 37.4% and 17.7% in leaves) at 12 DAT. This indicated that there may be a time effect of SA on the NC of rice under salt stress. At heading stage, SA increased NC in the leaves (16.3%) and stem + sheath (15.9%) of MDJ30 and that in leaves (15.1%) of LD5, but decreased NC in the panicles (11.6% and 7.1%) of MDJ30 and LD5. However, only the NC in the stem + sheath was changed by SA under salt stress at maturity stage, and the increases were 9.2% and 29.4% in MDJ30 and LD5.

Nitrogen accumulation at tillering stage: Above-ground nitrogen accumulation (NA) of both rice genotypes under salt stress significantly declined in comparison to control (Fig. 2). The reduction of stem + sheath, leaf, and total NA in MDJ30 under salinity stress were 48.8%, 43.0%, and 45.0% at 6 DAT, and 51.7%, 35.7% and 42.0% at 12 DAT, respectively. These reduction in LD5 under salt stress were 50.6%, 47.1%, and 48.3% at 6 DAT, and 28.0%, 39.6% and 35.8% at 12 DAT, respectively. The results indicated that the sensitivity of nitrogen uptake and accumulation of LD5 to salt stress were higher than that of MDJ30 at the early tillering stage, but was lower than that of MDJ30 with the prolongation of stress.

Table 1. Characteristics of the soil used in the studies.

Soil type	pH	Organic content	N	P	K	Available K	Available P	EC
		(%)	(g kg^{-1})			(mg kg^{-1})	(mg kg^{-1})	(dSm^{-1})
Isohumosols	5.8	3.125	1.73	0.72	0.90	158.5	46.8	0.35

EC – electrical conductivity of a saturated soil

Table 2. Dry matter accumulation (DMA) and its ratio of each aboveground organ per hill of rice during heading and maturity stage.

Variety	Treatment	Stem + sheath		Leaf		Panicle		Total DMA
		DMA (g·hill^{-1})	Ratio (%)	DMA (g·hill^{-1})	Ratio (%)	DMA (g·hill^{-1})	Ratio (%)	
Heading stage								
MDJ30	CK	19.602±0.594a	61.9±1.4a	8.463±0.450a	26.7±1.6a	3.617±0.177a	11.4±0.4a	31.680±0.395a
	Salt	13.538±0.105c	64.0±0.4a	5.466±0.171c	25.8±0.6a	2.165±0.065c	10.2±0.3b	21.169±0.258c
	SS	15.890±0.828b	63.1±1.2a	6.294±0.193b	25.0±1.2a	2.988±0.072b	11.9±0.2a	25.172±0.871b
LD5	CK	16.475±0.493b	63.2±0.5b	6.150±0.201a	23.6±0.3a	3.458±0.128a	13.3±0.2a	26.083±0.788a
	Salt	15.141±0.301c	67.3±1.0a	5.063±0.219b	22.5±0.8ab	2.278±0.052c	10.1±0.3b	22.482±0.337b
	SS	17.999±0.036a	68.2±1.3a	5.799±0.326a	22.0±0.9b	2.603±0.175b	9.9±0.5b	26.401±0.458a
Maturity stage								
MDJ30	CK	16.990±0.168a	33.5±0.7a	5.732±0.258a	11.3±0.6ab	27.957±0.947a	55.2±1.2ab	50.679±0.614a
	Salt	12.127±0.315c	34.5±0.8a	4.152±0.092b	11.8±0.3a	18.864±0.293c	53.7±0.6b	35.142±0.317c
	SS	13.824±0.157b	34.0±0.8a	4.269±0.110b	10.5±0.2b	22.589±0.631b	55.5±0.7a	40.682±0.632b
LD5	CK	13.990±0.271b	31.2±0.7c	4.054±0.304a	9.1±0.5a	26.745±0.788a	59.7±0.7a	44.790±1.172a
	Salt	13.077±0.349c	34.8±0.8b	3.436±0.145b	9.2±0.2a	21.025±0.623c	56.0±0.8b	37.538±0.890b
	SS	16.181±0.192a	37.2±0.8a	3.945±0.151a	9.1±0.2a	23.380±0.782b	53.7±0.6c	43.506±0.991a

Data represent the mean ± SD of three replicates. Within a column for each genotype at each stage, data followed by the different small letter are significantly different at 5% level by Duncan's test

Table 3. Dry matter translocation (DMT), DMT efficiency (DMTE) and DMT conversion rate of vegetative organ (DMTCRV) from heading to maturity stage.

Variety	Treatment	Stem + sheath		Leaf		DMA increased in panicle (g·hill^{-1})	DMTCRV (%)
		DMT (g·hill^{-1})	DMTE (%)	DMT (g·hill^{-1})	DMTE (%)		
MDJ30	CK	2.554±0.298 a	13.0±1.8a	2.730±0.354 a	32.2±3.0a	24.340±0.850 a	21.7±3.3a
	Salt	1.411±0.270c	10.4±2.0b	1.314±0.262c	24.1±4.1b	16.699±0.139c	16.3±0.5b
	SS	2.066±0.261 b	13.0±1.8a	2.025±0.270 b	32.2±3.3a	19.601±0.567b	20.9±1.0a
LD5	CK	2.485±0.112a	15.1±0.3a	2.095±0.166 a	34.1±3.2a	23.287±0.754 a	19.7±0.8a
	Salt	2.064±0.127b	13.6±0.9a	1.627±0.084 b	32.1±0.7a	18.747±0.611 c	19.7±0.6a
	SS	1.818±0.047c	10.1±0.2b	1.854±0.179 b	32.0±1.3a	20.777±0.695 b	17.7±0.6b

Data represent the mean ± SD of three replicates. Within a column for each genotype at each stage, data followed by the different small letter are significantly different at 5% level by Duncan's test

Table 4. Effect of SA on the nitrogen concentration (mg·g^{-1}) at vegetative and reproductive organ of rice under salt stress.

Development stage	Organ	MDJ30			LD5		
		CK	S	SS	CK	S	SS
Tillering stage							
6DAT	Stem + sheath	18.70±1.25a	15.36±1.19b	19.49±0.78a	19.21±1.08a	15.12±0.96b	17.97±1.12a
	Leaf	41.49±1.50a	38.26±1.48b	38.67±1.22ab	41.64±1.44a	34.12±1.04b	39.65±1.78a
12DAT	Stem + sheath	13.66±0.64a	12.22±1.08b	12.12±1.03b	10.53±0.31b	13.15±0.50a	13.15±0.50a
	Leaf	29.93±1.74b	32.95±1.25a	28.09±1.30b	32.49±1.75a	32.16±1.79a	34.10±0.88a
Heading stage	Stem + sheath	5.39±0.25a	4.39±0.22b	5.09±0.15a	5.57±0.30a	3.85±0.07b	4.11±0.18b
	Leaf	21.36±0.42a	18.26±0.24b	21.23±0.25a	21.52±0.05a	18.41±0.21b	21.19±0.12a
	Panicle	12.36±0.06b	12.83±0.23a	11.39±0.14c	11.76±0.18a	11.56±0.37a	10.74±0.22b
Maturity stage	Stem + sheath	4.15±0.24a	3.68±0.37b	4.02±0.20a	3.23±0.27a	2.45±0.13b	3.17±0.27a
	Leaf	6.49±0.59a	5.29±0.26b	5.14±0.21b	7.30±0.18a	5.68±0.39b	5.35±0.20b
	Panicle	10.13±0.42a	10.40±0.42a	9.79±0.45a	8.83±0.39b	9.48±0.42a	8.97±0.32ab

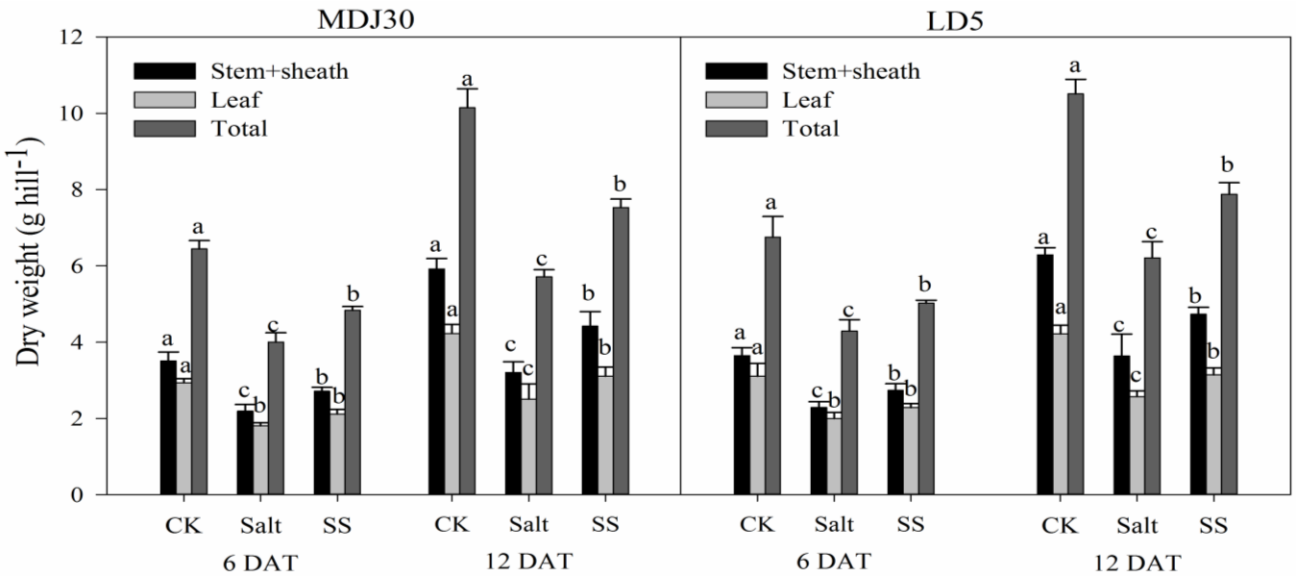

Fig. 1. Effect of exogenous SA on the above-ground dry matter accumulation of MDJ30 and LD5 under salinity stress at 6 DAT and 12 DAT. Forty two-day-old rice plants exposed to salinity stress (4.6 dS m^{-1}) for two weeks and then sprayed with 60 ml exogenous SA per pot for two days. CK, control; Salt, 4.6 dS m^{-1}salt stress; SS, 4.6 dS m^{-1}salt stress with 0.5 mmol L^{-1} SA, DAT, days after salicylic acid treatment. Vertical bars represent the ± standard deviation of means with three replicates.

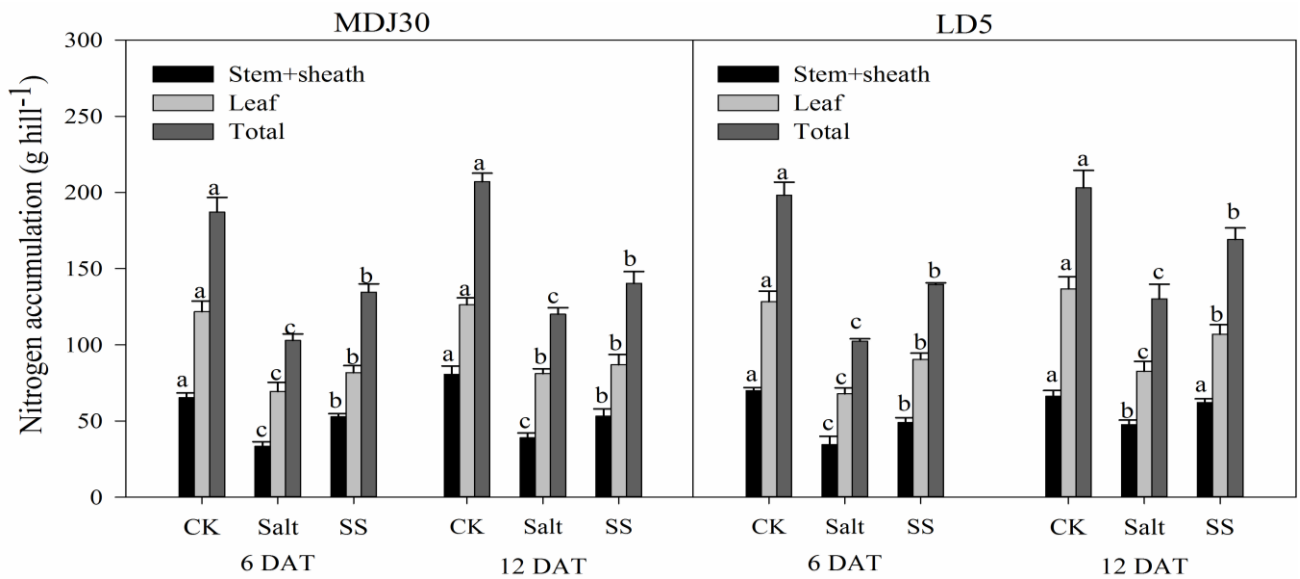

Fig. 2. Effect of SA on the nitrogen accumulation in stem + sheath and leaves of rice at tillering stage under salt stress. Forty two-day-old rice plants exposed to salinity stress (4.6 dS m^{-1}) for two weeks and then sprayed with 60 ml exogenous SA per pot for two days. CK, control; Salt, 4.6 dS m^{-1}salt stress; SS, 4.6 dS m^{-1}salt stress with 0.5 mmol L^{-1} SA, DAT, days after salicylic acid treatment. Vertical bars represent the ± standard deviation of means with three replicates.

Compared with salt stress, exogenous SA significantly improved the NA of stem + sheath (57.6% and 36.8% for MDJ30, 42.0% and 30.5% for LD5), leaf (17.9% for MDJ30 at 6DAT, 33.3% and 29.5% for LD5) and total (30.8% and 16.8% for MDJ30, 36.2% and 29.9% for LD5) at 6 DAT or/and 12 DAT. The results showed that the promotion effect of SA on the nitrogen uptake and accumulation in stem + sheath was larger than that in leaf, and the effect on total nitrogen accumulation in MDJ30 was less than that in LD5.

Nitrogen accumulation and partitioning at heading and maturity stage: The amount of Nitrogen accumulation (NA) in stem + sheath and leaf at heading was larger than that at maturity (Table 5). Salt stress significantly decreased the NA of above-ground organs from heading to maturity for both rice genotypes. The NA reduction of stem + sheath, leaf, panicle and total in MDJ30 under salinity stress were 43.8%, 44.8%, 37.9% and 43.5% at heading stage, and 36.8%, 40.9%, 30.7% and 32.8% at maturity stage, while these reduction in LD5 were 36.0%, 29.5%, 35.2% and 32.7% at heading stage, and 29.0%, 34.2%, 15.6% and 19.3% at maturity stage. The results were consistent with that of NA at tillering stage, where the NA sensitivity to salt stress of LD5 was less than that

of MDJ30 with prolongation of stress. The NA of stem + sheath and leaf was more susceptible to salt stress than that of panicles. There was no significant change in the N partitioning ratio (NPR) of each above-ground organ under salt stress in comparison with control at heading stage, but the NPR in panicles of two rice genotypes under salt stress increased significantly at maturity stage. The NPR of other organs in MDJ30 showed no significant change at maturity stage, while that of leaf in LD5 significantly decreased, which indicated that the nitrogen accumulation in leaves of salt-tolerant genotype LD5 was more easily transported to panicle than that of MDJ30.

Compared with salt stress alone, exogenous SA with salt stress significantly improved the NA of stem + sheath (36.4% and 24.9% for MDJ30, 26.0% and 59.7% for LD5), leaf (33.8% and 31.8% for MDJ30 and LD5 at heading), panicle (22.6% and 12.7% for MDJ30) and total (33.0% and 24.9% for MDJ30; 26.1% and 12.4% for LD5) at heading or/and maturity stage. These results indicated that the effect of SA on the NA of the total above-ground organ in MDJ30 was higher than that in LD5, and the promotion effect on NA of panicle was less than that in stem + sheath. During maturity stage, exogenous SA significantly improved the NPR of stem + sheath in both genotypes, decreased the NPR of leaf in MDJ30 and the NPR of panicle in LD5. The results indicated that SA may be caused the nitrogen retention in stem + sheath at maturity stage under salt stress.

Nitrogen translocation at heading and maturity stage: Compared with control, salt stress significantly decreased nitrogen translocation (NT), NT conversion rate of vegetative organs (NTCRV), NT efficiency (NTE) of stem + sheath, and the increment of nitrogen in panicles of both rice genotypes (Table 6). NT of stem + sheath (57.8%) and leaf (45.8%) of MDJ30 under salt stress decreased more than that of LD5 (42.9% for stem + sheath, and 28.2% for leaf).In addition, the increment of nitrogen in panicle (29.4%) of MDJ30 under salt stress decreased more than that of LD5 (11.5%) from heading to maturity stage. The results suggested that salt stress inhibited the nitrogen translocation to the panicle from heading to maturity, especially for the salt-susceptible genotype MDJ30.

Exogenous SA significantly increased NT (70.8% and 43.4%) and NTE (25.7% and 7.2%) of stem + sheath and leaf, the increment of nitrogen in panicle (11.1%), and NTCRV (33.0%) of MDJ30 under salt stress. By contrast, SA significantly decreased NTE (32.0%) of stem + sheath of LD5, improved NT (38.1%) and NTE (4.1%) of leaf, and NTCRV (18.2%) of LD5, but had no obvious effect on the increment of nitrogen in panicles. These results showed that the promotion effects of SA on NT, NTE, and NTCRV of salt-sensitive MDJ30 were larger than that of LD5.In addition, exogenous SA alleviated the inhibition effect of salt stress on nitrogen translocation from vegetative organ to panicle, especially from leaves.

Discussion

Dry matter accumulation, partitioning, and translocation: DMA is the basis of rice yield formation and is positively correlated with the survival rate of seedlings under salt stress (Maiale *et al*., 2004 and Zhang *et al*., 2012). In the present study, salinity stress caused a reduction in rice biomass production during tillering and maturity stage (Fig. 1 and Table 2), which was in conformity with earlier observations of rice (Demiral & Türkan, 2006 and Nounjan & Theerakulpisut, 2012). In addition, the reproductive organ was much more sensitive to salt stress than the vegetative organs, as the decrease of panicle dry matter was larger than that of leaf and stem + sheath. This was consistent with the result of Khatun *et al*., (1995). Zhang *et al*., (2012) found that seedling survival rate after 15 days of salt stress was positively correlated with leaf and stem dry weight at transplanting. Though salt stress did not cause plant death in this experiment, two rice genotypes differ in salt tolerance showed obvious differences in DMA. It appears that the salt-tolerant genotype LD5 was more likely to accumulate more dry matter than salt-suspective genotype under stress conditions, which was contrary to the normal condition. Early reports indicated that saline inhibition of plant growth may be due to the decrease in water availability and/or ionic effects (Pérez-López *et al*., 2014; Parida & Das, 2005 and Parihar *et al*., 2015). Exogenous SA contracted the stress caused by salinity and significantly increased the DMA of above-ground organs in both rice genotypes under salt stress (Fig. 1 and Table 2). The physiological mechanism of SA regulating plant biomass under salt stress could be caused by improved water relations and enhancing photosynthesis (Farheen *et al*., 2018; Hayat *et al*., 2010; Khodary, 2004; Li *et al*., 2014 and Liu *et al*., 2013). Interestingly, SA initially increased the DMA in stem + sheath at 6 DAT, and then in leaf at 12 DAT (Fig. 1), which indicated that SA promoted the production of assimilates and gave priority to the transfer of these nutrients to the temporary storage organ. It has been evoked that carbohydrate accumulated in leaves would feedback to inhibit photosynthesis, thereby matching the demand reduction due to growth inhibition (Hanin *et al*., 2016 and Paul & Foyer, 2001). The effect of SA on the transport of assimilates to stem and sheath may alleviate the feedback inhibition of photosynthesis to a certain extent. Moreover, the promotion effect of SA on the DMA of stem + sheath was larger than that of leaves, which was accord with Wang *et al*., (2017).

Dry matter allocation affects plant growth rate, growth pattern, nutrition acquisition capacity, and architecture, which is one of the important strategies for plant adaptation stress (Bidel *et al*., 2000; Liu *et al*., 2006 and Wang *et al*., 2013). Wang *et al*., (2013) reported that both alfalfa and barley adapted to salinization by distributing more DM in root and leaves but not in the stem. However, the DMPR of leaves in salt-sensitive MDJ30 was larger than that in salt-tolerant LD5 both under normal and salinization conditions; compared with control, salt stress increased the DMPR of stem + sheath in LD5 and decreased the DMPR of panicle in LD5 and MDJ30 during heading or/and maturity stage (Table 2).

This indicated that increasing the DMPR of stem + sheath may be beneficial to improve plant salt tolerance, which was inconsistent with Wang *et al*., (2013). However, the efficient distribution of cereal dry matter to the plant parts of economic importance is critical to yield stability in particular under stress condition (Kumar *et al*., 2006). In this study, the effect of SA on the DMPR was related to the genotypic difference in salt tolerance. Under salt stress, exogenous SA increased the DMPR of stem and sheath and decreased that of panicles in LD5 at maturity stage, but increased the DMPR of panicles and decreased that of leaves in MDJ30 (Table 2). This may be due to the difference in the senescence degree of the two contrasting genotypes with SA application. Delayed senescence during grain filling under water-deficient stress can result in straw leaving more nonstructural carbohydrates, and accelerated leaf senescence can promote grain filling by more remobilization of pre-flowering carbon reserves (Kumar *et al*., 2006).

Rice grain yield was derived from the remobilization of assimilates temporary storage in the vegetative organs and from the current assimilation of direct transfer to the grain (Masoni *et al*., 2007). The contribution of pre-anthesis assimilates to grains may be critical to maintaining grains yield when unfavorable climatic conditions reduce photosynthesis, moisture and mineral uptake (Dordas, 2009). Masoni *et al*., (2007) found that the suppression of photosynthesis and reduction of carbohydrates promoted dry matter translocation of vegetative organs under stress conditions. As shown in the study of Sultana *et al*., (1999), the reduction in grain dry matter caused by salt stress was due to the low current assimilation and low translocation of the assimilates from the source. Our results showed that salt stress significantly reduced the DMT of vegetative organs in both rice genotypes and decreased the DMTE and DMTCRV in MDJ30 (Table 3), which was inconsistent with previous foundings that adversity conditions could promote the remobilization of assimilates to panicles or grains (Kumar *et al*., 2006; Masoni *et al*., 2007 and Tian *et al*., 2016). According to the presume of Plaut *et al*., (2004), there may be competition between two potential sinks under water stress or salinity, namely, the developing kernels and a stress adjusting process in the leaves requiring assimilates. They suggested that dry matter stored in vegetative organs of water-stressed plants are a much more limited source, as it was retained probably to sustain osmotic adjustment. This may explicate the DMTE of salt-sensitive MDJ30 decreased under salt stress. Moreover, the DMT and DMTE of vegetative organs in LD5 were higher than that in MDJ30, indicating that salt-tolerant genotypes can maintain stably higher dry matter assimilation and translocation under salt stress, which was consistent with Tian *et al*., (2016). Exogenous SA improved the increase of DM in the panicles of both genotypes, increased the DMT, DMTE, and DMTCRV in MDJ30 but decreased that in LD5 under salt stress (Table 3). This indicated that the role of SA in increasing the DM of panicle depends on the genotypes, as it improved the pre-heading assimilates translocated from vegetative organs to panicles of salt-sensitive genotype and improved the post-heading photosynthesis of salt-tolerant genotype.

Nitrogen accumulation, partitioning, and translocation: In this study, the effect of salinity on NC varied according to genotypes, organ and development stage (Table 4), which was agreed with the report of Maighany & Ebrahimzadeh (2004). At tillering stage, the NC in stem + sheath and leaves of LD5 was more sensitive to salinity than MDJ30 (Table 4). Interestingly, the NC in stem + sheath of two genotypes under salt stress showed opposite performance at 12 DAT. The increase of NC in stem + sheath of LD5 may be due to the lower demand of leaves, as the green leaves per plant were lower than MDJ30 (Data were not shown). Salt stress decreased NC in vegetative organs of both genotypes at heading and maturity, increased NC in the panicles of MDJ30 at heading stage, and that of LD5 at maturity stage (Table 4). The decrease of N concentration caused by salinity may be explained by the limitation of N uptake, lower demand of sink and translocation to the panicle. It seems that stem + sheath and leaves are more like the propagation between the root and the panicle (Ye *et al*., 2013). Exogenous SA increased NC in vegetative organs under salinity at 6 DAT, heading and maturity stage, decreased NC in vegetative organs at 12 DAT and in the panicles at heading stage. This time effect could be explained by the promotion of N uptake and growth dilution. Early reports found that SA promoted N concentration and induced the activity of NR and NiR in mungbean cultivars (Akhtar *et al*., 2013 and Nazar *et al*., 2011). This was accord with our finding at 6 DAT, heading and maturity stage. When the increase in biomass accumulation induced by SA is larger than the increase in N acquisition, this results in a decline of N concentration, and this effect usually named growth dilution.

N accumulation is determined by the N concentration and biomass, and the pre-anthesis contribution of biomass to N accumulation was more important than N concentration(Dordas, 2009). Salinity reduced the N content per plant of barley seedling (Pérez-López *et al*., 2014). Our work showed that salt stress reduced nitrogen accumulation in aerial parts of plants (Fig. 2 or/and Table 5) due to the biomass reduction, regardless of the change in NC with genotype, organ and development stage. The reduction of N uptake under saline conditions was due to the competition or antagonism between Na^+ and NH_4^+ and/or Cl^- and NO_3^-(Parihar *et al*., 2015). The response of N accumulation to salt stress in LD5 was higher than that in MDJ30 at tillering stage but was less than that at heading and maturity stage, which reflect that salt tolerant variety was gradually adapted to the restriction of N acquisition due to salinization. The decrease of N accumulation in panicle under salt stress was less than that in leaf and stem + sheath, which was contrary to the dry matter, indicating that N accumulation was less sensitive to salt stress than that of dry matter in the panicle. Exogenous SA increased the N accumulation in the above-ground organs of two genotypes under salt stress (Fig. 2 and Table 5), because of its promoting effect on N uptake (Akhtar *et al*., 2013 and Nazar *et al*., 2011) and dry matter assimilation (Hayat *et al*., 2010; Khodary, 2004; Li *et al*., 2014 and Liu *et al*., 2013).

Table 5. Nitrogen accumulation (NA) and its ratio of each aboveground organ per hill of rice during heading to maturity stage.

Variety	Treatment	Stem + Sheath		Leaf		Panicle		Total NA (mg hill^{-1})
		NA (mg hill^{-1})	Ratio (%)	NA (mg hill^{-1})	Ratio (%)	NA (mg hill^{-1})	Ratio (%)	
Heading stage								
MDJ30	CK	105.7±7.7 a	31.9±2.3 a	180.8±11.8a	54.6±2.8a	44.7±2.4 a	13.5±0.6a	331.2±11.0 a
	Salt	59.4±3.8 c	31.7±0.7a	99.8± 4.3c	53.4±0.6a	27.8±0.6c	14.9±0.6a	187.0±8.1c
	SS	81.0±6.5 b	32.6±1.8a	133.6±2.7b	53.8±1.6a	34.0±0.5b	13.7±0.2ab	248.6±7.3 b
LD5	CK	91.8±4.5 a	34.7±0.9a	132.3±4.1 a	50.0±0.6a	40.7±1.3 a	15.4±0.3a	264.7±8.7 a
	Salt	58.7±2.2c	32.9±1.3a	93.2±4.3c	52.3±1.0a	26.3±1.4b	14.8±0.8a	178.2±5.0c
	SS	73.9±2.9 b	32.9±1.6a	122.9±7.5 b	54.7±1.7a	27.9±1.3 b	12.4±0.2b	224.7±8.6 b
Maturity stage								
MDJ30	CK	70.4±2.5 a	18.0±0.5ab	37.2±3.1 a	9.5±1.0a	283.1±8.8 a	72.5±0.8b	390.7±8.1 a
	Salt	44.5±3.1 c	16.9±0.7b	22.0±0.6b	8.4±0.5a	196.1±8.0c	74.7±0.8a	262.6±9.9c
	SS	55.6±2.2 b	18.6±1.0a	21.9±1.2b	7.4±0.5b	221.0±9.5b	74.0±1.5ab	298.5±7.4b
LD5	CK	45.2±4.6 b	14.6±1.7b	29.6±2.9 a	9.5±0.6a	236.2±16.4a	75.9±2.1b	311.0±17.2a
	Salt	32.1±2.4c	12.8±1.1b	19.5±1.2b	7.8±0.7b	199.3±10.3b	79.4±1.7a	250.9±8.5c
	SS	51.2±4.1a	18.2±1.3a	21.1±0.9b	7.5±0.3b	209.6±6.1b	74.4±1.7b	281.9±5.7b

Data represent the mean ± SD of three replicates. Within a column for each genotype at each stage, data followed by the different small letter are significantly different at 5% level by Duncan's test. HS, heading stage; MS, maturity stage

Table 6. Nitrogen translocation (NT), NT efficiency (NTE) and NT conversion rate of vegetative organ (NTCRV) from heading to maturity stage.

Variety	Treatment	Stem + sheath		Leaf		N increased in panicle (mg·hill^{-1})	NTCRV (%)
		NT (mg·hill^{-1})	NTE (%)	NT (mg·hill^{-1})	NTE (%)		
MDJ30	CK	35.3±2.9 a	33.4±1.2a	143.6±8.8 a	79.5±0.6 b	238.5±10.5 a	75.2±6.3 a
	Salt	14.9±2.8 c	25.0±3.1b	77.9±3.7c	78.0±0.5 b	168.4±8.2c	55.3±6.5b
	SS	25.4±3.0 b	31.4±1.4a	111.7±2.5 b	83.6±0.9 a	187.0±9.8b	73.6±5.4 a
LD5	CK	46.6±4.8 a	50.8±2.2 a	102.7±2.7 a	77.6±1.7b	195.5±7.1a	76.4±1.6 a
	Salt	26.6±4.2b	45.2±1.8 b	73.7±4.7b	79.0±1.8 b	173.0±6.8b	58.0±1.1 b
	SS	22.7±2.8b	30.8±2.0c	101.8±6.9 a	82.8±0.8 a	181.7±6.9ab	68.6±3.1 a

Data represent the mean ± SD of three replicates. Within a column for each genotype, data followed by the different small letter are significantly different at 5% level by Duncan's test

Understanding element distribution among plant organs is essential to explain the evolution of plant functional diversity (Ye *et al*., 2014). The average N partition ratio in stem + sheath, leaf and panicle increased substantially from 32.8%, 53.1% and 14.1% at heading to 17.9%, 8.4% and 73.7% at maturity. The rapid increase in panicle N ratio indicated that the panicle was the major and most active sink for N assimilation. According to Pérez-López *et al*., (2014), salinity changed the N partitioning among organs in barley seedlings. In this study, genotypes show differences in N partitioning into different organs under salt stress at maturity stage when compared with control (Table 5). The N proportions in panicles under salt stress significantly increased, but that in the leaves of LD5 significantly decreased, demonstrating that panicles rather than leaves under salt stress need more N than normal condition. This was consistent with the above mentioned that panicle was the most active sink. SA significantly improved the N proportions in stem + sheath of both genotypes, decreased that in leaves of MDJ30 and that in the panicles of LD5 at maturity. The results indicated that SA may be caused the nitrogen retention in stem + sheath at maturity stage under salt stress.

In the present study, the N accumulation of vegetative parts at maturity was considerably less than at heading, reflecting higher N remobilization. The contribution rate of translocated N to panicle was ranged 55.3%-76.2% (Table 6), indicating that a large part of panicle N was translocated from vegetative organs. This was in line with early reports (Masoni *et al*., 2007 and Ntanos & Koutroubas, 2002). The ratio of translocated N to panicle was 75.2%-76.4% under control, and 55.3%-58.0% under salt stress. Thus, the most panicle N of the normal plant came from pre-heading, while under salt stress condition, half of the panicle N was synthesized during grain filling. Salinity decreased the uptake and translocation rates of N in barley seedlings (Pérez-López *et al*., 2014). This phenomenon is also observed in our study, salt stress significantly decreased nitrogen translocation and its contribution rate to panicle (Table 6). So far, there is little information about the effect of SA on the N translocation of rice under salt stress. Exogenous SA significantly increased contribution rate of translocated N from vegetative organs (especially leaves) to panicle of two genotypes under salt stress. However, two genotypes with SA and salt stress showed different performance on the translocation N from stem + sheath. SA increased N

translocation from stem + sheath of MDJ30 but decreased that of LD5. This may be due to SA increasing nitrogen uptake by plants under salt stress, whereas excess nitrogen accumulation in salt-tolerant varieties led to their retention in stems and sheaths.

Conclusion

Taken together, this study suggests that salt-tolerant genotype LD5 was effective in mobilizing stored carbohydrates from the vegetative organs to the panicles, thereby allowing reserved carbohydrates to be allocated to storage organs as a mechanism to cope with salt stress. These pattern of dry matter and N accumulation, translocation and partitioning enabled LD5 to withstand salt stress. SA promoted assimilates accumulation in the above-ground organs of rice under salt stress, changed the distribution pattern of nutrients, and its effect on the translocation of assimilates was related to the salt tolerance of genotypes.

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