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Describing the physiological responses of different rice genotypes to salt stress using sigmoid and piecewise linear functions

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ABSTRACT

Rice is the staple food for almost half of the world population. In South and South East Asia, about 40% of rice production is from deltaic regions that are vulnerable to salt stress. A quantitative approach was developed for characterizing genotypic variability in biomass production, leaf transpiration rate and leaf net photosynthesis responses to salinity during the vegetative stage, with the aim of developing efficient screening protocols to accelerate breeding varieties adapted to salt-affected areas. Three varieties were evaluated in pots under greenhouse conditions and in the field, with average soil salinity ranging from 2 to 12 dS m^{-1}. Plant biomass, net photosynthesis rate, leaf transpiration rate and leaf conductance were measured at regular intervals. Crop responses were fitted using a logistic function with three parameters: 1) maximum rate under control conditions (Y_{max}), 2) salinity level for 50% of reduction (b), and 3) rate of reduction (*a*). Variation in the three parameters correlated significantly with variation in plant biomass production under increasing salinity. Salt stress levels that caused 50% reduction in net leaf photosynthesis and transpiration rates were higher in the tolerant genotype BRRI Dhan47 (16.5 dS m^{-1} and 14.3 dS m^{-1}, respectively) than the sensitive genotype IR29 (11.1 dS m^{-1} and 6.8 dS m^{-1}). In BRRI Dhan47, the threshold beyond which growth was significantly reduced was above 5 dS m^{-1} and the rate of growth reduction beyond this threshold was as low as 4% per unit increase in salinity. This quantitative approach to screening for salinity tolerance in rice offers a means to better understand rice growth under salt stress and, using simulation modelling, can provide an improved tool for varietal characterization.

1. Introduction

Salinity is one of the main limiting environmental factors for crop production worldwide. Its occurrence and severity are expected to increase by around 25% by 2050 in vulnerable regions, particularly in deltaic costal zones (Dasgupta et al., 2014) where rice growing areas account for more than 65% of global production, making salinity one of the major threats to food security. Rice has been classified as salt-sensitive (Maas and Hoffman, 1977). Salinity has different effects on yield and growth, depending on crop stage, stress severity and duration, as well as the tolerance of the variety (Lutts et al., 1995; Zeng and Shannon, 2000). Rice yield has been estimated to decrease by 50% at a salinity level of 6.9 dS m^{-1} (Grattan et al., 2002). Addressing salt stress by developing improved salt-tolerant rice cultivars could mitigate the effects of salinity on rice production and contribute to improving food security at a global scale.

Salinity tolerance in rice results from complex interactions between environmental and genetic factors. Numerous studies have been conducted to understand salt stress tolerance mechanisms such as minimizing sodium (Na^+) uptake and excluding Na^+ from the shoot (Munns and Tester, 2008; Platten et al., 2013; Ismail and Horie, 2017). Candidate genes have been identified that confer salinity tolerance through regulating ion transport, osmoprotection and growth acceleration (Munns and Tester, 2008; Horie et al., 2012; Ismail and Horie, 2017). This understanding has contributed significantly to the successful breeding of salt-tolerant varieties and for identifying suitable donors for breeding programs (Garg et al., 2002; Islam et al., 2008). However, quantifying the contribution of these mechanisms at the cellular and molecular level in relation to their functions at the whole plant scale and under field conditions still remains unresolved.

Maas and Hoffman (1977) described plant responses to salinity using a simple quadratic equation, which defines the rate of yield

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Table 1
Summary of the four experiments conducted in this study, including genotypes used, salinity treatments, dates of sowing and start and termination of salt stress treatments. DAS: Days after sowing; Control: non-stressed conditions; T1, T2, T3 Treatments with approximately 20, 55 and 90 mM of NaCl applied to maintain solution electrical conductivities equivalent to 4, 8 and 12 dS m^{-1}, respectively.

Experiments	Sowing date	Start of stress DAS	End of stress DAS	Genotypes	Location (Philippines)	Salinity treatments
Expt. 1	June 13, 2012	21	42	IR29, IR64, BRRI Dhan47	IRRI Experiment station, Los Baños	Control, T1, T2, T3
Expt. 2	February 11, 2013	20	47	IR29, IR64, BRRI Dhan47	IRRI Experiment station, Los Baños	Control, T1, T2, T3
Expt. 3	May 20, 2013	18	41	IR29, BRRI Dhan47	IRRI Experiment station Los Baños	Control, T2
Expt. 4	January 26, 2013	19	113	IR29, IR64, BRRI Dhan47	On farm experiment Infanta, Quezon city	Control, T2

decrease per unit of salinity increase, and the critical level of salinity at which a significant decrease in yield was observed. Thus far, these parameters have not been correlated with physiological processes occurring in the plant. Considering that yield results from the combination of numerous complex processes, the use of this equation may not be suitable for screening for salinity tolerance traits. Understanding salinity response processes at different scales within the plant could play an important role in accelerating progress for developing salt-tolerant high yielding rice varieties (Horie et al., 2012). Ion and nutrient imbalances, adjustment of water status, stomatal conductance, and reduction in photosynthetic activity are among the physiological responses occurring at the plant level (Horie et al., 2012). These responses have been reported to follow a two-step process with an initial water deficit effect over a short term and an ion toxicity effect over a longer term (Munns et al., 1995). Specific responses to salt stress involve mechanisms limiting salt entry and excluding salt at the whole plant and/or cellular level, especially from active tissues such as young leaves and reproductive parts. This mechanism preserves the photosynthetic apparatus and other physiological processes necessary for plant survival and growth. Salinity also has a direct effect on cell expansion and division, as typically reflected by a reduction in leaf area (Matthews et al., 1984; Netondo et al., 2004). Genotypic variability in the concentration of Na^+ accumulating in plant tissue under salt stress was reported to be associated with variation in photosynthesis (Moradi and Ismail, 2007). This can even be observed at salinity levels lower than 2 dS m^{-1}, at which symptoms of the effects of salinity are not yet visible (Yeo, 1998).

In addition to variations in salt exclusion and salt partitioning to roots and old tissues, variability in responses of photosynthetic traits to salinity is also important − largely the result of variability in tissue tolerance of accumulated salts. Tolerance to salinity during the vegetative and reproductive stages of rice involves numerous different mechanisms that contribute to the whole plant growth and productivity (Moradi et al., 2003; Singh and Flowers, 2010). Exposure of rice to salinity around the time of panicle initiation and flowering affects the growth and development of panicles and spikelets causing spikelet sterility, thus limiting sink size and grain formation. Senescence of expanded leaves is also accelerated by salinity, partially reducing assimilation due to the reduction of the photosynthetically active leaf area and further reducing assimilates allocated to grains. These processes result in changing source-sink relationships within the crop, leading to a reduction in grain yield.

Quantifying the variability of these physiological mechanisms using mathematical equations provides a means to describe and disaggregate the contribution of different limiting factors, particularly the genotypic component of the variability in crop responses. This approach could be used to develop trait-based modelling − a framework to test hypotheses about crop performance and to integrate the complex unpredictable variability of soil salinity in the field, as one of the main limitations in developing adapted varieties and technologies to overcome the effects of salinity (Skaggs et al., 2006; Crescimanno and Garofalo, 2006; Soltani and Sinclair, 2012).

In this study, a mathematical equation was developed to quantify effects of salinity on rice crops during the vegetative stage. Three genotypes with contrasting salinity tolerance were evaluated in both greenhouse and field experiments. Plant growth and leaf gas exchange, in response to four different levels of salinity treatment during the vegetative stage, were assessed. The patterns of these responses were used to develop an equation incorporating traits and varietal differences related to salt stress.

2. Materials and methods

2.1. Plant materials and growth conditions

Rice response to salinity treatment during vegetative stage was characterized over a series of four experiments (Table 1). Genotypic variability in growth responses to salinity was evaluated in three greenhouse experiments (Experiment 1, 2 and 3). A field experiment was used to evaluate responses at the plant population (crop) level and to validate genotypic variability and salinity effects observed in the greenhouse experiments. The greenhouse experiments were conducted at the International Rice Research Institute (IRRI) Los Baños, Philippines (14.17 N, 121.26 E), using three rice genotypes (Table 1); IR29, IR64 and BRRI Dhan47, characterized as sensitive, intermediate and tolerant of salt stress, respectively (Moradi et al., 2003; Islam et al., 2008). The genotypes were grown under four salinity levels, with electrical conductivities (EC) of 2 dS m^{-1}, 4 dS m^{-1}, 8 dS m^{-1} and 12 dS m^{-1}, which were achieved by adding 0, 20, 55 and 90 mM of NaCl, respectively, to the nutrient solution (Supplementary Table 1).

Seeds were sown in polyvinyl chloride (PVC) pots filled with about 2.5 kg of gravel (20 cm depth and 20 cm of diameter) in Experiments 1, 2 and 3. The three experiments were arranged in randomized block design with salinity treatment as main factor and genotypes as the subplot factor. The pots were submerged in tanks filled with a nutrient solution. Each tank contained 96 pots arranged to maintain 20 cm spacing between plants. Four tanks corresponding to the four salinity treatments were used in Experiments 1 and 2. Two tanks were used (control and Treatment 2) in Experiment 3. Each genotype was represented by 32 pots in each tank with one plant per pot, with pots rotated weekly when the nutrient solution was renewed. The pH of the nutrient solution in each tank was adjusted daily to 5.5, and salinity was recorded hourly using a 5TE sensor connected to an EM50 datalogger (Decagon Devices, Inc. USA, Supplementary Fig. 1) at 10 cm depth. Plants were grown in a nutrient solution from sowing until the start of the salinity treatment, then exposed to their respective salinity treatments from 21 to 50 d after sowing (DAS) in Treatments 1 and 2. For Treatment 3 (12 dS m^{-1}), the treatment was terminated at 35 DAS (when most of the fully expanded leaves of the sensitive genotype, IR29, senesced) to permit recovery before flowering, after which plants were maintained using the control treatment solution. The climatic conditions inside the greenhouse were monitored daily by an