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FIELD-6795; No. of Pages 12
ARTICLE IN PRESS
Field Crops Research xxx (2016) xxx–xxx
Contents lists available at ScienceDirect
Field Crops Research
journal homepage: www.elsevier.com/locate/fcr

Agronomic manipulations can enhance the productivity of anaerobic tolerant rice sown in flooded soils in rainfed areas

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ARTICLE INFO

Article history:
Received 28 January 2016
Received in revised form 21 August 2016
Accepted 23 August 2016
Available online xxx

Keywords:
Anaerobic germination
Seedling emergence
Soluble sugar
Starch
Yield

ABSTRACT

Poor seedling emergence and establishment are a major restraint for adopting direct seeding in rice. This is especially critical in rainfed lowlands where floods can occur immediately after sowing, creating anaerobic conditions during germination and early seedling growth. Developing rice cultivars that can germinate in flooded soils will ensure good crop establishment. Several major quantitative trait loci (QTLs) for tolerance of anaerobic conditions during germination (anaerobic germination; AG) were identified from different landraces; and near isogenic lines (NILs) containing one of these QTLs (*qAG-9-2*, *AG1*) in the background of IR64 were developed. This study is an attempt to determine the effectiveness of *AG1* QTL in improving germination of two IR64-AG NILs; IR 93312-30-101-20-3-66-6 (IR64–AG131) and IR93312-30-101-20-13-64-21 (IR64-AG132) sown under flooded conditions. The study also evaluated selected agronomic practices anticipated to further enhance crop establishment in flooded soils. IR64-AG NILs showed 81% and 217% higher plant populations over IR64-Sub1 and IR64, respectively, and this was also reflected as significantly higher grain yields. IR64-AG NILs mobilized relatively more starch into soluble sugars while submerged and maintained higher soluble sugar supply to the developing embryo resulting in faster and higher germination rates than the non-AG genotypes. Agronomic manipulations like higher seed rate (60 kg ha^{-1}), better seeding methods and nutrient application improved seedling growth after germination and emergence, increasing plant height, leaf area, number of tillers and biomass accumulation. These improvements were reflected as higher grain yield even in the intolerant cultivar IR64. Application of 20% more phosphorus with the recommended N-P-K resulted in 21%, 16% and 19% higher grain yield in IR64-AG, IR64-Sub1 and IR64, respectively, over the control. The results established that combining proper crop establishment practices with tolerant genotype could enhance crop establishment in flooded soils using direct seeding methods, with consequent reduction in production costs and water use and subsequent increase in farmers' income.

1. Introduction

Rice is cultivated in a wide range of environments, from tropical to temperate and from aerobic soils in uplands to wet lowlands with uncontrolled flooding. Irrigated lowland rice systems comprise about 55% of the total rice area worldwide and provide 70% of global rice production, while rainfed lowlands and flood-prone areas constitute about 35% of the total rice area, but providing only 25% of global rice production because of uncontrolled hydrology and various abiotic and biotic factors associated with rainfed ecosystems (Ismail et al., 2012). Significant rainfed lowland areas in Asia and Africa are affected by flash floods every year (Khush, 1984; Mackill et al., 2012), causing complete submergence from a few days to two weeks. These types of floods devastate over 20 million ha of rice fields in Asia each year (Jackson and Ram, 2003; Jackson and Ismail, 2015).

In rainfed areas where direct seeded rice (DSR) is practiced, farmers encounter flooding and/or waterlogging when it rains immediately after seeding, which leads to severe reduction in, or complete failure of crop establishment because of the high sen-

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http://dx.doi.org/10.1016/j.fcr.2016.08.026
0378-4290/

Please cite this article in press as: Lal, B., et al., Agronomic manipulations can enhance the productivity of anaerobic tolerant rice sown in flooded soils in rainfed areas. Field Crops Res. (2016), http://dx.doi.org/10.1016/j.fcr.2016.08.026

sitivity of rice to low oxygen stress caused by flooding during germination (Yamauchi et al., 1993; Ismail et al., 2009; Angaji et al., 2010; Joshi et al., 2013; Miro and Ismail, 2013). This problem of poor crop emergence and establishment in flooded soils is further compounded by subsequent invasion of weeds, especially weedy and red rice. Varieties that can germinate in flooded soils could be beneficial for direct-seeded systems and even for intensively irrigated systems, where early flooding can suppress weeds apart from improving crop establishment (Ismail et al., 2012, 2013). These varieties will minimize production cost by facilitating adoption of DSR and provide means for weed management.

Rice is unique in being capable of growing well in waterlogged and submerged soils because of its well-developed aerenchyma system that facilitates aeration of the roots and the rhizosphere, thus alleviating most of the stresses experienced under low oxygen (Setter et al., 1997; Jackson and Ram, 2003). But it is extremely intolerant to anaerobic conditions during germination and early growth of the embryo (Yamauchi et al., 1993; Ismail et al., 2009; Angaji et al., 2010). Rice seeds can germinate and, to some degree extend their coleoptiles under hypoxic and even anoxic conditions, but fail to develop roots and leaves (Taylor, 1942; Ella and Setter, 1999), because of its limited ability to mobilize and use energy reserves when oxygen is limiting (Ismail et al., 2009). Cell division is active during the first 48 h of submergence, and that is the period when oxygen is mostly required (Atwell et al., 1982). Since cellular expansion consumes less energy than cell division, the latter is the main process governing elongation of the coleoptiles under anoxia.

Genotypes that are more tolerant of flooding during germination seem to have better capabilities for breaking starch into simple sugars, as demonstrated by faster depletion of starch in their germinating seeds compared with intolerant genotypes (Ismail et al., 2009). When flooding occurs just after direct seeding, tolerant genotypes germinate faster and their coleoptiles grow at a relatively faster rate to emerge from flooded soils. These genotypes are also capable of forming roots and leaves in shallow water depths (Ismail et al., 2009; Angaji et al., 2010).

Several major quantitative trait loci (QTLs) for tolerance of AG were identified from different landraces (Angaji et al., 2010; Collard et al., 2013; Septiningsih et al., 2013a,b; Miro and Ismail, 2013; Baltazar et al., 2014), and one of them, *qAG-9-2* (AG1) was derived from Khao Hlan On, a landrace from Myanmar (Angaji et al., 2010). Near isogenic lines (NILs) containing AG1 in the background of IR64 were developed, two of them were IR93312-30-101-20-3-66-6 (IR64-AG131) and IR93312-30-101-20-13-64-21 (IR64-AG132). Subsequent studies confirmed that there was no yield penalty due to the introgression of this QTL in several genetic backgrounds, including IR64 (Toledo et al., 2015). Furthermore, the gene underlying AG1, *OsTPP7*, was identified through map-based cloning. This gene increases the sink strength in proliferating heterotrophic tissues by maintaining signaling for low sugar availability, thus enhancing starch mobilization to drive growth kinetics of the germinating embryo and elongating coleoptile, which consequently enhance AG tolerance (Kretzschmar et al., 2015).

In rainfed areas of eastern India, early flooding due to early rains is hindering the adoption of direct seeding because of poor crop establishment. Rice varieties that can survive transient submergence after establishment have now become available through the incorporation of the *SUB1* QTL, however, these varieties are sensitive to flooding during germination. Sub1 varieties were developed using a marker-assisted backcrossing (MABC) approach, where a small genomic region containing the *SUB1A* gene was introgressed into several modern high-yielding rice varieties at International Rice Research Institute (IRRI), Philippines (Neeraja et al., 2007; Septiningsih et al., 2009; Iftekharuddaula et al., 2011; Ismail et al., 2013). The *SUB1* versions of these varieties can survive 10–18 days of complete submergence during vegetative phase depending on floodwater and weather conditions, with 1 to over 2 t ha^{-1} increase in yield in farmers' fields following submergence (Singh et al., 2009, 2011, 2014; Mackill et al., 2012; Ismail et al., 2013). Despite the considerable impacts of these varieties, they can not be used for direct seeding because of their high sensitivity to anaerobic conditions during germination. Incorporating AG tolerance into these and other new high-yielding varieties will provide insurance for farmers to leverage the benefits of higher yields and lower production costs.

This study was conducted using IR64-AG NILs (IR64-AG131 and IR64-AG132; tolerant to AG but intolerant to submergence), IR64-Sub1 (tolerant to submergence; intolerant to AG), and IR64 (intolerant to submergence and AG) to evaluate the impact of AG tolerance conferred by the *AG1* QTL in the IR64 background, and to compare the responses of these lines to selected agronomic practices desired to further augment expression of tolerance in famers fields. The study compared (i) germination and growth attributes of IR64-AG NILs with IR64 and IR64-Sub1 under controlled submergence; (ii) the use of different establishment methods across both tolerant and sensitive genotypes; and (iii) evaluated the effects of selected agronomic practices on the performance of AG tolerant and sensitive genotypes under flooded field condition.

2. Materials and methods

2.1. Site characterization

The experiments were carried out at the Indian Council of Agricultural Research-National Rice Research Institute (ICAR-NRRI), Cuttack (20° 45′N, 85° 93′E; elevation 24 m above mean sea level). The soil of the experimental site is an Aeric Endoaquept with sandy clay loam texture (31.2% clay, 16.7% silt, 52.1% sand), bulk density of 1.42 Mg m^{-3}, pH (using 1:2.5, soil: water suspension) 6.5, electrical conductivity (EC) 0.073 dS m^{-1}; and with 211, 14.8 and 123 kg available N, P, K ha^{-1}, respectively. Field experiments were conducted in the kharif season (June to December), during which weather conditions remained normal, with maximum temperature of 27.3–32.9 °C (2013), 26.7–35.3 °C (2014) and 27.7–33.8 °C (2015); minimum temperature of 15.1–26.0 °C (2013), 13.7–25.8 °C (2014) and 17.6–26.1 °C (2015). Rainfall was 1524, 1434 and 1175 mm during 2013, 2014 and 2015, respectively.

2.2. Experimental details

The details of the three sets of experiments conducted during this study are presented below. These experiments were conducted to evaluate the performance of IR64, IR64-Sub1, and two AG NILs [IR64-AG131 (IR 93312-30-101-20-3-66-6) and IR64-AG132 (IR93312-30-101-20-13-64-21)] under varying flooding stress; and the impact of crop and nutrient management practices on their yield and yield attributes.

2.2.1. Germination and growth of IR64-AG NILs under control soil flooding conditions (Experiment I)

The experiment was conducted using a factorial randomized block design (FRBD) during the kharif (wet) season of 2013, with the objective to evaluate the germination and growth attributes of IR64-AG NILs, IR64 and IR64-Sub1. A 100 pre-soaked seeds of each cultivar were directly sown in plastic trays (37 × 35 × 25 cm) containing 10 kg of farm soil (Sandy clay loam, pH 6.3, EC-0.071 dS m^{-1}, available N, P and K were 52.5, 4.2 and 61.4 mg kg^{-1} soil, respectively). Fertilizers at 0.49 g urea, 1.14 g single super phosphate (SSP), and 0.31 g muriate of potash were applied to each tray as N, P, and K sources, respectively. The trays were watered immediately after seeding and a water head of 5 cm was maintained above soil sur-