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Mini Review

Importance of anaerobic seed germination and seedling development in direct-seeded rice with special reference to Sri Lanka

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Abstract: Direct-seeded rice (DSR) is becoming more popular among paddy farmers but it results in irregular stand establishment and high weed infestation. Early season flooding is another constraint to rice production in tropics as well as some of the major rice-growing areas in global scale and Sri Lanka is not an exception. Ability of some rice (Oryza sativa L.) genotypes to tolerate flooding during germination and seedling growth or anaerobic germination (AG) tolerance could help in overcoming the major obstacles in DSR. The rice cultivars, their mechanisms and the major QTLs governing AG-tolerance have been identified and two genes namely AG1 and AG2 have been incorporated to popular rice varieties for direct use. However, limited attempts have been made to screen Sri Lankan rice entries for AG tolerance. This review emphasizes the progress of AG-tolerance research, current challenges, future prospects as well as the importance of screening and identifying AG-tolerant rice varieties and validating management options to use this technology in DSR system in Sri Lanka.

Keywords: Anaerobic germination, Direct seeding, Management options, Rice, Tolerant mechanisms

Introduction

Shift from transplanting to direct seeding for rice crop establishment has been evident in Sri Lanka due to non-availability of labor and about 95% of the total area cultivated is direct-seeded (Weerakoon *et al.,* 2011). The main biological constraint in direct seeded rice (DSR) systems is weed infestation (Chauhan and Yadev, 2013). Globally, yield losses due to uncontrolled weeds have been estimated to be about 32 %, (Abdul *et al.*, 2013) and Season-long weed competition in DSR may cause yield reductions up to 80 % (Sunil *et al.*, 2010). In Sri Lanka, yield losses caused by uncontrolled weeds ranges from 20-30% (Amarasinghe and Marambe, 1998) or 30-40% (Herath Banda *et al.*, 1998).

Impact of water management on weed control in rice is well-established and has long been practiced as an effective agronomic practice in lowland transplanted rice (Rao *et al.*, 2007). However, in DSR systems, fields are drained-off before sowing and standing water is introduced 7-10 days after sowing, as new high yielding rice varieties are extremely sensitive to flooding during germination

(Ismail *et al.,* 2012). Hence, farmers usually rely on herbicides to control weeds under DSR systems worldwide (Phuong *et al.,* 2005) but, this could be environmentally-risky when misused, and their recommended dosages are ineffective against herbicide-resistant weeds. A significant increase in the weedy rice infestation in DSR has also been observed during the past two decades (Marambe and Amarasinghe, 2000; Abeysekara *et al.,* 2015). With the increase in air temperature, weed flora could shift towards temperature-tolerant weeds creating additional burden on weed management (Weerakoon *et al.,* 2011).

DSR results in poor germination and uneven stand establishment due to the sown seeds are subjected to desiccation in dry conditions or to water stress in the submerged conditions (Ismail *et al.,* 2012). If the land is not well-leveled or water management is poor, drowning due to heavy rainfall and damage by birds and rodents are common under DSR. Thus, farmers usually use 2-3 times higher seed rates than that of recommended level to overcome these problems and to compensate for losses, but this may result in mutual shading and intra-specific competition for resources, increased insect and disease infestation and rat damage (Bond *et al.,* 2005).

Flooding is another constraint to rice (*Oryza sativa* L.) production resulting in yield losses and yield fluctuations, especially in rain-fed lowlands of the tropics. Heavy rains during germination result in submergence and cause poor crop stand. Out of natural disasters causing rice crop losses in Sri Lanka, 39% is due to damages from unexpected and uncontrolled floods (DCS, 2012). The incidence of flooding was found to be the most prevalent hazard in the recent past where flooding damaged 197,181 ha of rice lands cultivated during the major cultivating season in 2011, while 73,000 ha of rice lands were destroyed and crop output declined by 2.5-2.6 million tons in the year 2013 (FAO, 2013). A significant proportion of rice lands in the Wet Zone (WZ) is abandoned or fallowed long term due to continuous water logging, flash floods and soil problems associated with poor drainage (Bentota *et al.*, 2010; Walisinghe *et al.*, 2013). Further, predictions have shown that the Southern province of Sri Lanka may experience a higher rainfall in the years to come (Punyawardena *et al.*, 2013) alarming that some additional areas, which are currently not vulnerable to flooding and submergence, may become vulnerable due to climate change.

The ability of some rice varieties to germinate, grow and survive under oxygen-limiting conditions is known as anaerobic germination (AG) tolerance (Ella and Setter, 1999). Among the cereal seeds studied to-date, only rice can germinate and elongate coleoptiles under low O_2 (hypoxia) or very low/absence of O_2 (anoxia). AG-tolerant rice varieties with an associated management package could be a good alternative to overcome the problems associated in DSR (Ismail *et al.,* 2012). The technique could be beneficial to suppress weeds economically and in an environmentally friendly manner. It is an inexpensive management strategy for resource-poor farmers in the developing countries like Sri Lanka and is more feasible for adoption on a comparatively larger scale than other management practices, thus enhancing the productivity of DSR systems. The AG- tolerant rice varieties will also be useful to minimize the flooding risk in the Wet Zone.

Screening of rice germplasm for AG tolerance

Yamauchi *et al.* (1993) screened 258 accessions from the gene bank of International Rice Research Institute (IRRI) and 404 from the International Network for the Genetic Evaluation of Rice (INGER) using two days pre-germinated seeds sown at 2.5 cm soil depth and submerged with 2-5 cm of water. Twelve genotypes were found to be tolerant with emergence in the range of 54-78% compared with 7-19% for the sensitive genotypes. Ling *et al.* (2004) evaluated 359 indica and japonica accessions using water depth of 20 cm at 30 °C and reasonable variations in coleoptiles elongation were observed after 5 days.

Following a large scale screening of more than 8000 accessions and breeding lines at IRRI, (Ismail *et al.*, 2012) a small number of rice genotypes (0.23 %) with greater AG tolerance (over 70 % of survival) were identified based on the ability to generate shoots and roots within 3 weeks after dry sowing coupled with flooding at 8-10 cm height (Table 1). These efforts revealed a vast genetic variation in AG-tolerance and provided opportunities to develop rice varieties that can overcome obstacles associated with DSR including early flooding and weed management (Ella *et al.* 2010; Ismail *et al.* 2012).

Table1. Rice accessions tolerant to anaerobic seed germination and seedling development.

Accession	Origin	Survival percentage under anaerobic condition
Khao Hlan On	Myanmar	75
Mazhan Red	China	90
Khaiyan	Bangladesh	90
Kalongchi	Bangladesh	90
Nanhi	India	80
Cody	USA	70
Dholamon 64-3	Bangladesh	80
Liu Tiao-Nuo	China	85
Sossoka	Guinea	85
Kaolack	Guinea	85
IR 42 (Sensitive)	Philippines	5
FR 13A (Sensitive)	India	20

Source: Ismail *et al.* (2012)

Molecular Genetics and Breeding for AG-tolerance

Two mapping populations have been used for genetic studies using two AG-tolerant donors, '*Khao Hlan On*' and '*Mazhan Red*' (Angaji *et al.,* 2010). Rice variety *Khao Hlan On* was crossed with *IR 64* and five QTLs were identified, one each on chromosome 1, 3 and 7 and two on chromosome 9, which explained 18-34% of the phenotypic variability (Ismail *et al,.* 2009). The largest QTL (referred as AG1) derived from *Khao Hlan On* was mapped on the long arm of chromosome 7 and 9 are considered as major QTLs. It was further fine-mapped and cloned to facilitate their use in breeding (Angaji *et al.,* 2010). Another QTL was detected in short arm of chromosome 7 (referred as AG2) from F2 population of IR42/Mazhan Red and was fine mapped (Septiningsih *et al*., 2013). Furthermore, SUB1, a major gene for tolerance of complete submergence for up to 2 weeks, is available for pyramiding with AG tolerance.

Two varieties, IR 64-SUB1 and Ciherang-SUB1 were used as recurrent parents in developing improved lines for anaerobic condition tolerance during germination (Septiningsih *et al*., 2013). They can be directly used for cultivation or could be further incorporated with tolerance of different types of flooding or with key traits necessary to enhance tolerance for other abiotic and biotic stresses based on the needs of the target environment.

Mechanisms Associated with AG-tolerance

Varieties that are tolerant to AG have developed different strategies to cope up with O_2-limited conditions, including anaerobic respiration to sustain energy supply, initiation and maintenance of carbohydrate catabolism in germinating seeds and maintenance of cellular extensibility of the growing embryo (Ismail *et al*., 2009). Some of those mechanisms are described below.

Conversion of aerobic to anaerobic respiration

The main adjustment to limitations of energy supply under anoxia or hypoxia during germination is the shift from aerobic to anaerobic respiration (Perata and Alpi, 1993). Anaerobic respiration uses alcohol, lactate and alanine fermentation pathways to regenerate NAD^+ required for glycolysis. Among them, alcoholic fermentation is considered the most important

(Kato-Noguchi, 1999). It produces only 2 ATPs per glucose molecule compared to 38 ATPs produced through aerobic respiration and therefore, protein synthesis is redirected to produce only those enzymes, which are essential for the metabolism of carbohydrates (Greenway and Setter, 1996). An ATP production rate of about 10 % of the aerated conditions is maintained in the AG-tolerant and moderately-tolerant lines (Edwards *et al*., 2012).

Changes in cytoplasmic pH

The role of lactate in anoxic rice coleoptiles is related to a pH decrease that would then activate alcoholic fermentation (Roberts *et al*., 1984). The ratio of succinate:lactate was also found to be relevant to the final cytoplasmic acidosis and tolerant lines produce more succinate than lactate (Menegus *et al*., 1989). The nitrate assimilated in AG-tolerant rice seeds are converted to ammonium, which would maintain the pH and are capable of controlling cytoplasmic and vacuolar pH, enabling survival in longer periods under anoxia (Kulichikhin *et al*., 2009; Greenway *et al*., 2012).

High α-amylase activity and ability to break down starch to soluble sugars

Two enzymes; sucrose synthase for sucrose breakdown and α-amylases for starch breakdown are important for carbohydrate catabolism in rice seeds germinating under hypoxia/anoxia (Magneschi and Perata, 2009). However, sucrose synthase is functional in rice under submerged conditions at the same rate as in air and there is no apparent difference in the activity of AG tolerant and sensitive genotypes (Ismail *et al*., 2009). Maintenance of higher activity of α-amylases has been widely reported in seeds of AG tolerant genotypes (Perata and Alpi, 1993; Yamaguchi *et al.,* 1994; Hung *et al.,* 1999). Tolerant rice genotypes store relatively more soluble sugars in their endosperm and have greater ability to break down starch into soluble sugars during the germination than sensitive genotypes (Ismail *et al*., 2012).

Low peroxidase activity

Peroxidases are involved in the formation of diferuloyl cross-links to matrix polysaccharides and are responsible for the assembly of lignins and proteins in the cell wall (Fry, 1979). Higher peroxidase activity is negatively correlated with seed germination, seedling survival and coleoptile elongation under submergence and seeds of AG tolerant rice genotypes showed substantially lower peroxidase activity (Ismail *et al.,* 2009).

Enhance ethylene production and ability to elongate coleoptiles

Involvement of ethylene in internode and coleoptile elongation in deep-water rice is well known (Jackson, 2003). Under submergence, ethylene involves in coleoptile elongation when cell expansion is predominant and has an effect in decreasing peroxidase activity (Ismail *et al*., 2009). The ABA interacts with ethylene as a positive regulator but the roles of different hormones under submergence are varied with genetic and environmental variables such as O_2 and CO_2 concentrations, temperature and flood water conditions (Ismail *et al*., 2009). The CO_2 that accumulates in plant tissues in the absence of carbon fixation can also promote coleoptile elongation (Rasikin and Kende, 1984).

Rice can germinate under submerge conditions, but only tolerant genotypes have the ability of rapid coleoptile elongation and root formation. The coleoptile growth is slow and fails to develop further in sensitive genotypes (Ismail *et al.,* 2009). Cell division is more active only during the first 48 hours of submergence (Atwell *et al*., 1982). As cellular expansion consumes less energy than cell division, the latter is the main process governing coleoptiles elongation under anoxia which is regulated by ethylene (Magneschi and Perata, 2009).

Coleoptile elongation is also related to the role of specific expansions under anaerobic conditions for their action in cell wall loosening (Ismail *et al*., 2009; Magneschi and Perata, 2009). These include EXPA2 and EXPA4 (Choi *et al*., 2003), EXPA7 and EXPB12 (Lasanthi-Kudahettige *et al*., 2007) EXPA1, EXPB11, and EXPB17 (Takahashi *et al.* 2011). The action of tubulin a-1 chain (TUBA1) and actin depolymerizing factor 4 (ADF4) were suggested to be involved in fast coleoptile elongation as both genes are regulated during rice germination under anoxia (Sadiq *et al*., 2011).

Factors Affecting AG-tolerance in the Field Condition

Seed longevity and handling

A decrease in germination under submergence was reported when using comparatively older seeds due to increase in lipid peroxidation and decrease in superoxide dismutase and catalase activities (Ella *et al.*2011; Septiningsih *et al.*, 2013). This implies the importance of using fresh seeds even for tolerant genotypes. The seeds stored at lower temperature (5-8 °C) have a higher survival rate than those stored at ambient temperature due to decrease in lipid peroxidase activity (Ella *et al.,* 2010).

Seed pre-conditioning or priming

Any seed pre-treatment (pre-soaking or priming) that can enhance antioxidant activities, improves seed germination, uniformity and early seedling growth, particularly when seeds are sown under suboptimal conditions (Ella *et al.,* 2011). Seed priming involves soaking with water (hydro-priming) or with an organic solvent (osmo-priming) followed by partial dehydration and further drying before radical emergence (Ella *et al.,* 2011). It increases seed vigor, longevity and the activity of α-amylase (Farooq *et al*., 2007; Anwar *et al*., 2012).

Priming also increases superoxide dismutase (SOD), catalase (CAT), scavenge reactive oxygen species and carbohydrate mobilization and decreases lipid peroxidation activity than in non-primed seeds particularly in flooding intolerant entries (Ella *et al.,* 2011). Yoshida (1981) reported that, coating the seeds with calcium peroxide is effective in improving seedling emergence and subsequent growth under anaerobic conditions in lowland DSR anaerobic as molecular O_2 is released as it reacts with water. Use of $CaCl_2$ and KCl also enhances seed germination under anoxia emphasizing the effectiveness of combining genetic tolerance with appropriate seed pre-treatment to improve seedling establishment of rice sown in flooded soils (Ella *et al.,* 2011). High and synchronized emergence of primed seeds can also ensure vigorous crop stand with rapid canopy development giving rice plants a preliminary advantage over weeds (Anwar *et al*., 2012).

Flood water depth and water quality

Under field conditions, seedling survival decreases about 5 % and 18 % when flood water depth increases from 2-4 cm to 5-7 and 8-10 cm, respectively (Ella *et al.,* 2010). As shallow water depth tends to increase weed growth, adjusting water depth to about 5 cm coupled with healthy seeds of tolerant genotypes can probably suppress the growth of most weeds without much reduction in seedling survival and establishment (Ella *et al.,* 2010). Flooding at a depth up to 5 cm at sowing and maintaining it for at least 14 days is effective in controlling the emergence and growth of the weed, *Fimbristylis miliacea* (Begum *et al*., 2006).

In the presence of algae, seedling survival decreases considerably even in tolerant genotypes due to limiting of O_2 and light transmission under water (Ella *et al.,* 2010). Algae can be a problem in water-seeded rice, especially when rice grows slowly and water is warm. Seedling survival is significantly higher in intermediate water temperatures of 24-26 °C but decreases substantially when flood water is warmer (30-32 °C) or cooler (18-20 °C), (Ella *et al.,* 2010). The tolerant genotypes produce shoots at a similar rate both in intermediate and higher temperatures, but the root growth is affected at higher temperatures. Alpha-Amylase activity in germinating seeds is also high at intermediate and higher temperatures but decreases in lower temperatures suggesting that an optimum threshold temperature is needed for seed germination and seedling survival under flooded conditions (Ella *et al.,* 2010).

Seed rate and seedbed management

The optimal seedbed conditions can further improve the performance of AG-tolerant cultivars and a proper leveling is essential to maintain a desired water depth (Ella *et al*., 2011). A study in DSR systems in India showed that seeding rates ranging from 15 to 125 kg ha^{-1} had no effect on the grain yield of rice grown in weed-free conditions (Chauhan and Yadev, 2013). In the presence of weeds, however, maximum grain yield was achieved at seed rate of 95 to 125 kg ha^{-1}.

Traits Used in Screening of AG-tolerance

Seedling survival rate and Coleoptile elongation

The main trait used in screening of AG tolerance is seedling survival rate after 21 days of submergence under 10 cm water head and the surviving seedlings are those that emerge above water surface by fast germination and coleoptile elongation (Ismail *et al*., 2009; Angaji *et al*., 2010).

Enzyme activities

Activities of enzymes such as α-amylases, anaerobic respiration enzymes and others from the tricarboxylic acid cycle in the anaerobic pathways are used in screening (Ismail *et al*., 2009). Colorimetric reactions for many enzymes including dehydrogenases and peroxidases have been developed, making enzyme analysis as a valid screening methodology for anaerobic germination (Berta and Ismail, 2013).

Other morphological traits

Traits such as coleoptile diameter, days to emergence of first leaf, and the first leaf width and length, root characteristics such as root length, diameter, secondary root development and root hairs may be relevant when studying genotypes with intermediate tolerance or when comparing different groups (Berta and Ismail, 2013). Traits associated with seed aging such as the extent of lipid peroxidation, could potentially be used as markers for indirect selection.

Constraints in using AG-tolerance in DSR

The varieties that have been identified as AG-tolerant are landraces, which cannot be directly used in DSR due to their low yielding capacities (Ismail *et al.* 2012). Even though, the major QTLs governing AG tolerance were identified and incorporated into popular varieties for direct use, the contribution of each QTL to AG-tolerance usually ranged from small to medium i.e.18-30 % (Septiningsih *et al*., 2013). This may not be high enough to withstand flooding during germination under field condition, where stress severity is usually varied from field to field and is strongly affected by flood water, seed handling and seedbed conditions (Ella *et al.,* 2010). Therefore, discovering novel major QTLs from diverse tolerance donors will give more opportunities to establish the best combination of multiple QTLs from different target environments.

The effectiveness of flooding for weed management will depend on the responses of various weeds associated with rice to early flooding. Shallow flooding has no effect on weed control once they are established (Ella *et al.* 2010; Ismail *et al.,* 2012). Further, new ecotypes of weed species such as *Cyperus rotundus* have acquired adaptive features to survive water logging and flooding may no longer be effective in controlling these specific weeds (Pena-Fronteras *et al.,* 2009).

Combination of proper seed-handling strategies, seedbed management options, good agronomic practices and genetic tolerance are prerequisites to the successfulness in better crop establishment following DSR in soils prone to early-season floods (Ella *et al*., 2011). The AG-tolerant varieties and the management recommendation should be further validated in research and farmer field conditions to have practical implications (Ella *et al.,* 2010).

Importance of AG-tolerance in DSR in Sri Lanka

Rice is the staple food of Sri Lankans providing livelihoods for more than 879,000 farmer families (20 % of the population) in the country (DCS, 2012). Three major rice growing environments in Sri Lanka are identified viz. i) irrigated or rain-fed favorable lands, ii) rain-fed drought-prone lands and iii) rain-fed submergence-prone lands (Sandanayake *et al.*, 1990). All low-lying rice growing areas of the country are vulnerable to heavy rains and flooding during the monsoon seasons (Ranawake, *et al.,* 2014). The major rice growing areas of the south-west coastal plain are often has experienced seasonal flooding (Fernando and Suranganee, 2009). The Wet Zone (WZ) accounts for nearly 25 % of the paddy extent but a significant proportion of rice lands is abandoned or fallowed long term due to water lodging, flooding and soil problems associated with poor drainage (Bentota *et al.,* 2010). Different varieties such as At

362, Ld 368, Bg 369 and Bg 357 and improved field establishment methods such as seedling broadcasting (parachute method) were tested for boggy paddy lands with submerged water regimes (Weerasinghe *et al*., 2014). However, the productivity of the WZ still remains low as 2.75 tha^{-1}, which is far below than that of Dry (DZ) and Intermediate (IZ) zones (Walisinghe *et al.,* 2013). Use of AG-tolerant rice varieties with an associated technology package thus, would be a good alternative to overcome low productivity of the flood prone areas of the WZ.

The WZ is also vulnerable to climate change, where Galle and Matara districts in the southern province of Sri Lanka and the neighboring areas, are likely to experience more positive anomalies of rainfall and reached about 50% increase by 2080s compared to the period of 1961-1990 (Punyawardena *et al.*, 2013). Muthuwaththa and Liyanage (2013) reported that the mean annual rainfall of Sri Lanka will increase about 7% (155 mm additional rainfall) in year 2050 compared with the period of 1970-2000 and the highest proportional increase is predicted to be in the southern and south-eastern parts of the country. This implies that some additional areas, which are not vulnerable to flooding and submergence at present, may become vulnerable in the future. Cultivation of suitable AG-tolerant rice varieties will be a good option to minimize the risk of flood hazards in the area.

Weed infestation is the most disastrous constraint to the production in DSR across all rice growing agro-ecologies and the problem of poor crop emergence and establishment in DSR get confounded by invasion of weeds and weedy rice species (Marambe, 2009; Gunawardena *et al*., 2013). A significant increase in weedy rice population has been observed in major rice growing districts during the past years (Abeysekara, 2010). Further, weed flora may shift towards temperature-tolerant weeds due to increase in both the maximum and minimum air temperatures in Sri Lanka create an additional burden on weed management. Rapid growth rate of propanil-resistant and propanil-susceptible barnyard grass [*Echinochloa crusgalli* (L) Beauv.] has been reported in Sri Lanka with increasing environment temperature (Marambe and Amarasinghe, 2002). Therefore, an intensive weed management strategy is required to achieve sustainability of DSR in future and AG tolerant is one of the potential tools where early flooding can suppress weeds in economically and environmentally friendly way.

Increasing water and labour scarcities threaten the sustainability of rice cultivation in Sri Lanka and more than 50% of the cost goes to labour (Weerakoon *et al.,* 2011). Further, there is a progressive shortage of labor as young people prefer to migrate and engage in other businesses securing high income due to uncertainty and highly variable profit margin in rice cultivation. Therefore, rice crop is needed to be cultivated with comparatively less labor in the future. Adoption to mechanization in DSR with advance technologies will minimize the labor usage while attracting the younger generation to rice farming. The AG-tolerance could be beneficial even for such intensive farming systems.

Location-specific technologies for different agro-ecological zones should be developed to reduce the cost of production and to increase resource use efficiency to achieve sustainable optimum DSR yields. The AG-tolerance results in enormous savings in the production costs as it reduces the cost of manual or mechanical weeding or the use of hazardous chemicals for weed control. It is an inexpensive management strategy for poor farmers in the developing countries like Sri Lanka and is more feasible for adoption on a larger scale than other management practices. However, limited attempts have been made to screen Sri Lankan rice genotypes for AG- tolerance.

Magneschi *et al.* (2008) screened 23 Sri Lankan rice entries under simulated anaerobic condition and found that Bg 94-1 developed the longest coleoptiles (13.8 ± 4.5 mm) while At 306 and Bg 745 had the shortest (1.3 ± 0.5) after four days of submergence. Herath *et al.* (2010) tested the effect of water seeding on germination, growth and weed control of rice and reported that intermediate bold varieties performed better in water-seeding situation. However, the ability of local rice germplasm to survive under flooded condition during germination and seedling development has not yet been fully exploited. Illangakoon *et al.* (2016) screened 37 rice varieties including newly improved varieties and traditional cultivars with Mazhan Red (tolerant check) and FR 13 A (Susceptible check) for AG- tolerance at10 cm of water depth under screen house condition. They found that approximately 64% of the test varieties had survival score less than the susceptible check while Bg 300 followed by Bg 310 and At 308 showed moderate tolerance (Figure 1).

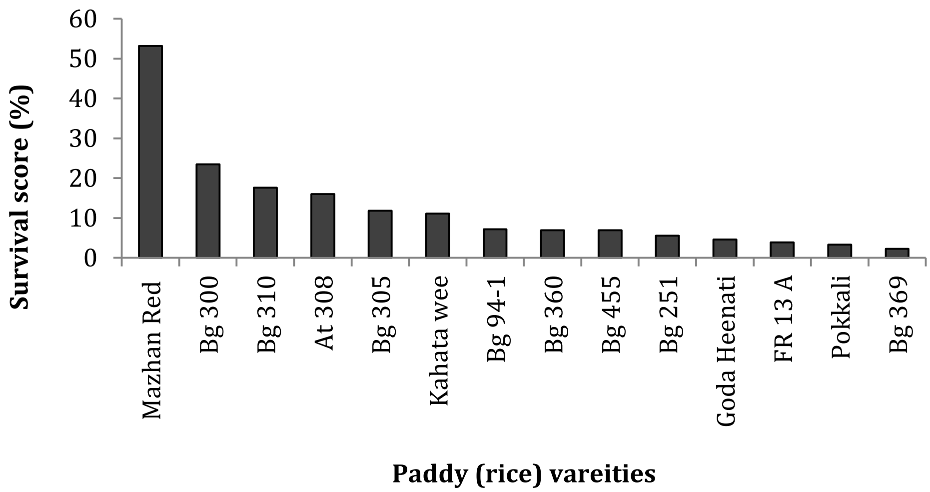

Figure 1. Survival % of rice varieties germinated at 10 cm of water depth under screen house condition (Mazhan Red – tolerant check, FR 13 A - susceptible check)

Conclusion

Screening of existing rice germplasm, identification of better AG tolerant varieties, testing their adaptabilities and validation of management options including seed pre-treatment, flood water depth, duration and seed rate thus should be attempted and understood to make use of this technology in DSR in a rice-growing country like Sri Lanka

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