Management of viviparous germination in rice: a strategy for development of climate resilient rice cultivation

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ABSTRACT

Rice yield has been affected severely by recent incidence of cyclonic storms with heavy rains flooding rice fields in the grain maturation period of October-November in the eastern part of India. The high yielding cultivars, the cultivation of which mostly sustain rice bowl of the farmers and consumers, lack dormancy to escape onslaught of the erratic weather. Pre-harvest grains absorb rain water as the plants lodge on the ground. Viviparous germination spoils food quality of rain soaked seeds down grading market value of the produce. Incidence of such calamities on the rise, stability of rice production can be maintained through introgression of seed dormancy trait of wild into non-dormant high yielding rice. Similar to other angiosperms, dormancy is regulated in rice seed by a balance between ABA and GA, both steroidal hormones, one being counter productive to the other. The role of ethylene in dormancy release has been proposed more recently for several plants. Rice being sensitive to ethylene should be included in the list, but evidences are wanting in favour of the assumption. The review elucidates the pathway for ethylene production in germinating rice seeds and suggests management of viviparous germination for climate resilient cultivation.

Key words: Rice, vivipary, germination, dormancy, ethylene

Rice has been the most important human food crop on earth. The twelve thousand year old antiquity reveals that no other crop of economic importance has provided food calories to man as much as that of rice. In addition to food for sustenance, the long lasting relationship between man and rice has been embellished in social, cultural and ritual exhibitions. The evolutionary history comprises rice cultivation beholden with several changes in domestication, dispersal and diversification (Chang 2003). The versatility of adaptation is un-paralleled in other important cereal crops like wheat, maize or barley. Unlike other cereals, rice is considered a semi-aquatic species best suited for cultivation in anaerobic wetland habitats, but it has germplasm that can grow in dry land situations. The rainfed rice has exhibited traits for adaptation to the broadest range of hydrological conditions, beginning with the parched deserts of Al Hasa Oasis, Saudi Arabia with 100mm rain fall to the wettest area of 5100 mm rains in Arakans, Myanmar. The expression of phenotypic features varies with soil water regime; in particular, depth of water level in the field dictates crop phenology. Although water is the predominant factor for adaptation, rice habitats also occupy an extreme range of ecological niches accompanying drastic variation of photoperiod, temperature and solar radiation. The semi-aquatic origin of rice is perfectly evident in wetland rice growing in ditches with abundance of water. Salient phonotypic features embodied in wetland rice are thin leaves with no distinction of pallisade and spongy parenchyma, presence of thin cuticle with less than 5% wax load of other crops, number of stomata tenfold greater than dry land grasses and reduced stomatal size. These characteristics determine for high water loss pattern of the plant (Lafitte and Bennett 2002). Presence of lysigenous aerenchyma channel extending from the

leaves to the root tips works as a snorkel for free supply of oxygen to roots and other organs submerged under water (Yamauchi *et al.* 2013). The roots are also adapted to the typical nutrient cycling of anaerobic flooded soil. The semi-aquatic ancestry involved in the evolution of rice to dry terrestrial habitat (Vaughan 1994) is best illustrated in aerobic dry land rice. Usually rice requires a large amount of water to grow it, but manages survival under water limited environments better than other crops. The water deficiency related adaptive mechanisms, designed to maintain water balance in the plant, are expressed in morphological (deep rooting habit, reduced leaf area, short growth duration, low plant height, less tillers and leaves, leaf rolling), physiological (low stomatal conductance, minimal photosynthesis, feeble transpiration, high membrane stability, ABA accumulation), biochemical (accumulation of osmo-protectants) and molecular (expression of genes encoding defense related proteins) parameters, resulting in low biomass partitioning and poor grain yield (Pandey and Shukla 2015). Because of these advantages for tolerance of water-related stresses (Bouman *et al.* 2007), rice cultivation has unique and profound implication for environment and livelihood of rice consumers world wide. Hence, overall goal of research undertaken hitherto has been for improving water productivity in rice culture by promoting food production and water saving in moisture stress-prone ecosystems. In contrast, scant attention is given to development of climate resilient crop for flood-prone ecosystems.

Climate resilient crop for flood-prone ecosystems

Water control has a major influence on the success of rice cultivation. Rice originally was domesticated in South-East Asia. The climate throughout this region has the distinction of attracting heavy annual rainfall, most of which is concentrated from late May to early October (Huke and Huke 1990). The rainfall pattern matches favourably with rice growing season. However, in the recent years climate change induced erratic weather patterns have caused famine for millions of people around the globe. In particular, with fewer infrastructures for crop management, the consequences of erratic weather have been dire and critical on food security of developing nations. Weather related

disasters include drought, cyclones and flooding. It is observed that the frequency and intensity of the climate induced stresses have increased with the progress of time. For rice crop management, innovative research so far, has recommended some climate resilient cultivars that hold potential to salvage a part of the maximum yield in the presence of inclement weather. However, stress tolerance has been development stage specific for the crop. Survival is at stake when a natural calamity, like unseasonal rainfall, strikes at grain maturation phase, precluding completion of life cycle. Un-seasonal rainfall accompanied by cyclones has caused considerable damage to rice cultivation in the states of eastern India. Incessant rains during the first two weeks of May, 1995 caused severe damage to grain quality of rice in Odisha and Andhra Pradesh. Such rain falls also occurred in the years 1996, 1997 and 1998. Super cyclone caused extensive damage to rice crop of Odisha in 1999. Cyclonic storm damaged rice crop again in Andhra Pradesh and partly in Odisha in 2011-12. Similar incidences also happened in October, 2013 and 2014, Phailin and Hudhud respectively. In these incidents, mature rice crop soaked with rain water, lodged to the ground and the grains lost colour and taste, resulting in zero market value for the farmers. The high yielding rice cultivars, widely used today, do not have any resistance to rain water induced precocious germination. In contrast, some of the weedy and wild rice cultivars are strongly dormant and germinate only when the seed comes in contact with water in the succeeding year, 8-9 months after harvest. It is surmised that lack of seed dormancy is responsible for the loss of grain quality during precocious germination. As of today, physiological/molecular biology research work has not been undertaken to evaluate inherent mechanism of resistance to precocious germination within the traditional rice genotypes available in the country side and exploit the trait for pyramidisation with high yielding rice.

Viviparous germination in rice

In rice grain size is a stable genetic character. It is determined by the hull space enclosed between lemma and palea. Soon after fertilization, the embryo and endosperm grow in the hull vicinity to occupy the space completely subject to transport of assimilates from the vegetative organs. Assimilate entry into the kernel

occurs in an aqueous medium. By day four after anthesis, the storage of water soluble carbohydrates in starch granules is initiated; the growth of starch granules is completed by day 30, i.e. the time of grain maturity (Hoshikawa 1993). Accumulation of structural dry matter expels water out leading to seed desiccation (Mohapatra *et al*. 1993). It is possible that establishment of seed dormancy is strongly correlated with loss of water during the grain maturation phase. Strong dormancy resists imbibitions of water at the harvesting phase. In contrast, incidence of unseasonal rains on grains nearing maturity induces precocious germination in the moisture soaked non-dormant cultivars. Precocious germination is defined as pre-harvest sprouting of seed while still attached to the mother plant with incomplete closure of development. In angiosperm seeds, structural changes occur in both endosperm and embryo following double fertilization, but development of the latter usually precedes the former. By day 12th after fertilization, increase in size virtually stops in rice kernel, while endosperm growth continues till day 30 (Hoshikawa 1993). Storage of food reserve in endosperm not only provides nutrients at the disposal of embryo, but also acts a mechanical barrier for its growth (Yan *et al*. 2014). In precocious germination, a rejuvenated embryo breaks seed dormancy early due to persistent high humidity and feeds upon the stored reserve of premature endosperm. This phenomenon in non-dormant cultivars significantly damages seed vigour, germination percentage and seedling emergence rate (Shon *et al*. 2014), resulting in poor quality of seeds. The economic losses accrued are heavy because of down gradation of rice quality from food to feed.

Role of hormones in management of seed germination

Post-fertilization, development takes place in rice caryopsis for two important structures, the embryo and endosperm of which the latter plays an important role in supporting growth of the former by providing nutrients and protecting it from external hazards. The starchy endosperm is surrounded by aleurone layers of living cells. The scutellum separates the embryo from the endosperm. Dry seeds upon imbibitions of water initiate gene expression in the embryo for synthesis of gibberellin; the hormone diffuses into aleurone layers,

where amylase and other hydrolyzing enzymes are synthesized for degradation of stored reserve in endosperm. Soluble assimilates generated there from come to the embryo for seedling growth. Although rejuvenation of dormant embryo growth, with signals cued by favourable external factors, has been primarily responsible for germination, the role of endosperm in the signal perception process has been added more recently. It is suggested that germination is a systemic response that involves bi-directional interaction of both embryo and endosperm (Yan *et al*. 2014). Hence, physiological control of seed dormancy can not be assessed on the basis of activity of the embryo only. In pursuance, growth and development of both the structures should be examined in relation to each other right from the double fertilization stage.

Growth related characteristics and physiological status during maturation phase determine the pattern of seed dormancy. The transcriptome profile of kernel alters temporally in the early half of seed maturation period (Huh *et al*. 2013). The second half of grain filling, being a period of storage of seed reserve, seldom exhibits brisk metabolism and congruent genomic expressions. The new pattern of genomic expression contributes to synthesis of two antagonistic hormones ABA and GA and fixing of a balance between them. It ultimately determines the nature of seed dormancy. The dormant cultivars possess high ABA/GA ratio compared to non-dormant cultivars (Liu *et al*. 2014). Nambara *et al*. (2010) reported positive role of ABA in induction and maintenance of seed dormancy. ABA synthesis dictates depth of seed dormancy. During seed development both maternal and embryonic ABA production prevents precocious germination (Karssen *et al*. 1983; Kanno *et al*. 2010). In contrast to ABA, gibberellins promote seed germination (Yamaguchi 2008) and breaking of dormancy. The literature is very rich with reports on the role of gibberellins on dormancy release and germination of seeds (Finkelstein *et al*., 2008; Cutler *et al*. 2010; Nambara *et al*. 2010; Miransari and Smith 2014). However, it is astonishing that the role of gaseous hormone ethylene has been under estimated and un-emphasized. Matilla and Matilla-Vazquez (2008), while working on ET-mutants found evidence for ethylene breaking seed dormancy in some species. The hormone interacts with ABA to rupture seed coat of germinating seeds (Linkies *et al*.

2009). The counter balance of ABA by ethylene in seed germination is further consolidated in a more recent review (Corbineau *et al.* 2014).

While we surmise a positive role of ethylene for dormancy release similar to gibberellins, there have been few attempts to explore the proposition with empirical evidences in rice, where management of viviparous germination has assumed significance greater than any other crop under the present scenario. Rice kernel is a grain caryopsis, where pericarp fuses with endosperm and embryo combine during the later half of seed development. A matured dry seed germinates by uptake of water and the process is completed with the protrusion of radicle through the pericarp (Bewley 1997). Yang *et al.* (2007) has divided seed germination in rice into three distinct phases. In the first phase the seed gains weight by rapid uptake of water and mRNA synthesis in it is stimulated. The second phase accounts for rejuvenation of cell metabolism that is responsible for break down of seed reserve and mobilization of solutes, cell structure repair and cell wall loosening and coleoptiles elongation. In the third phase, more water enters into kernel, aerobic respiration is promoted and cell division process is initiated, which ultimately facilitates protrusion of radicle (Fig. 1). The radicle emerges through a rupture in the pericarp. It is suggested that ethylene is the hormone, which acts low during inception of dormancy, but its action becomes vigorous upon imbibitions of water and initiation of germination (Matilla and Matilla-Vazquez 2008). It is possible that that ethylene may act as a signal to promote cell expansion (Shakeel *et al.* 2013)
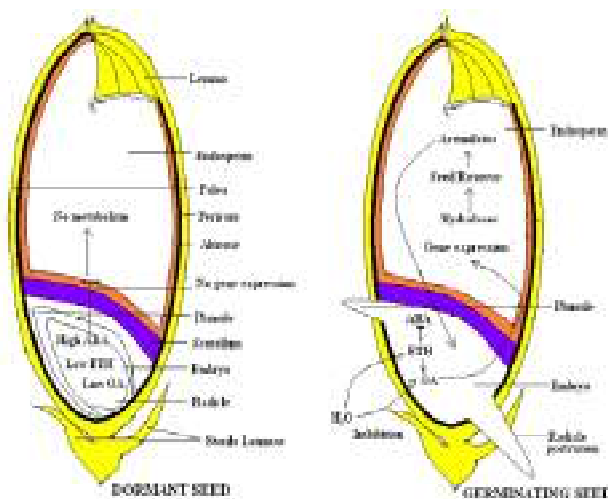

Fig.1. Physiological events of dormancy in rice seeds

with initial uptake of water by the seed. Similar to GA, ethylene is counter productive to ABA action. But there is lack of evidence, in which phase ethylene production is stimulated in a germinating rice seed. In this context, this review proposes several queries for management of viviparous germination in rice, because it is equally ethylene sensitive like the model plant Arabidopsis (Yang *et al.* 2015). Does ethylene evolution coincide with rupture of pericarp by radicle or loosening of cell wall in a germinating seed? Does uptake of water alter cell turgor or osmotic potential to induce ethylene synthesis and signaling? Do the dormant seeds escape viviparous germination by not absorbing rain water? Do the lemma and palea of dormant seeds contribute to special protection against soaking of rain water? Can ethylene action be down regulated by promoting inhibition or synthesis of the chemical and/or biotechnological interventions? Answer to these questions is wanted for urgent solution to the problem of climate change related precocious germination of rice.

REFERENCES

Bewley JD1997.Seed germination and dormancy. Plant Cell 9:1055-1066

Bouman BAM, Humphreys E, TuongTP and Barker R 2007. Rice and water. Adv. Agron. 92: 187-237

Chang TT 2003.Origin, domestication and diversification. Chapter 1.1, Rice: origin, history, technology and production. Editors- CW Smith and RH Dilday, John Wiley & Sons, Inc., New Jersy, USA. Pp.3-25

Corbineau F, Xia Q, Bailly C and El-Maarouf-Bouteau H 2014. Ethylene, a key factor in the regulation of seed dormancy. Front. Plant Sci. 5: 539

Cutler SR, Rodriguez PL, Finkelstein RR and Abrams SR 2010. Abscissic acid: emergence of a core signaling network. Ann. Rev. Plant Biol. 61: 651-679

Finkelstein RR, Reeves W, Ariizumi T and Steber C 2008. Molecular aspects of seed dormancy. Ann. Rev. Plant Biol. 59: 387-415

Hoshikawa K 1993. Anthesis, fertilization and development of caryopsis. Chapter 2. Science of rice plant. Volume I - Morphology. Editors Matsuo T, Hoshikawa K. Food and Agricultural Policy Research Center, Tokyo. pp. 339-376

Huh SM, Hwang Y-S, Shin YS and Yoon IS 2013. Comparative transcriptome profiling of developing caryopses from two rice cultivars with differential dormancy.

Jr. Plant Physiol. 170: 1090-1100

Huke RE and Huke EH 1990. Rice: Then and now. International Rice Research Institute, Philippines

Kanno Y, Jikumaru Y, Hanada A, Nambara E, Abrams SR, Kamiya Y and Seo M 2010. Comprehensive hormone profiling in developing Arabidopsis seeds: examination of the site of ABA biosynthesis, ABA transport and hormone interactions. Plant Cell Physiol. 51: 1988-2001

Karssen CM, Brinkhorst-van der Swan DLC, Breekland AE and Koornneef M 1983. Induction of dormancy during seed development by endogenous abscisic acid: studies on abscisic acid deficient genotypes of Arabidopsis thaliana (L.) Heynh. Planta 157: 158-165

Lafitte H R and Bennett J 2002. Requirements for aerobic rice: Physiological and molecular considerations. In "Water?Wise Rice Production" (B. A. M. Bouman, H. Hengsdijk, B. Hardy, P. S. Bindraban, T. P. Tuong, and J. K. Ladha, Eds.), pp. 259-274. International Rice Research Institute, Los Banos, Philippines

Linkies A, Muller K, Morris K, Tureckova V, Wenk M., Cadman CSC, Corbineau F, Strnad M, Lynn JR, Finch-Savage WE and Leubner-Metzgera G 2009. Ethylene interacts with Abscisic Acid to regulate endosperm rupture during germination: A comparative approach using Lepidium sativum and Arabidopsis thaliana. The Plant Cell 21: 3803-3822

Liu Y, Fang J, Xu F, Chu J, Yan C, Michael R. Schlappi MR, Wang Y and Chu C 2014. Expression patterns of ABA and GA metabolism genes and hormone levels during rice seed development and imbibitions: A comparison of dormant and non-dormant rice cultivars. Jr. Genet. Genom 41: 327-338

Matilla AJ and Matilla-Va´zquez MA 2008. Involvement of ethylene in seed physiology. Plant Sci. 175: 87-97

Miransari M andSmith DL 2014. Plant hormones and seed germination. Env. Exp. Bot. 99: 110-121

Mohapatra PK, Patel R and Sahu SK 1993.Time of flowering affects grain quality and spikelet partitioning within the rice panicle. Australian Jr. Plant Physiol. 20: 231-241

Nambara E, Okamoto M, Tatematsu K, Yano R, Seo M and Kamiya Y 2010. Abscisic acid and the control of seed dormancy and germination. Seed Sci. Res. 20: 55-67

Pandey V and Shukla A 2015. Acclimation and tolerance strategies of rice under drought stress. Rice Sci. 22: 147-161

Shakeel SN, Wang X, Binder BM and Schaller GE 2013. Mechanisms of signal transduction by ethylene: overlapping and non-overlapping signalling roles in a receptor family. AoB PLANTS 5: plt010; doi:10.1093/aobpla/plt010

Shon J, Kim J, Jung H, Kim B-K, Choi K-J and Yang W 2014. Effect of pre-harvest sprouting on seed viability, germination and seedling emergence rate of rice. Korean Jr. Crop Sci. 59: 427-434

Vaughan DA 1994. The wild relatives of rice: A genetic resources handbook. International Rice Research Institute, Philippines

Yamaguchi S 2008. Gibberellin metabolism and its regulation. Ann. Rev. Plant Biol. 59: 225-251

Yamauchi T, Shimamura S, Nakazono M and Mochizuki T 2013. Aerenchyma formation in crop species: A review. Field Crops Res. 152: 8-16

Yan D, Duermeyer L, Leoveanu C andNambara E 2014. The functions of the endosperm during seed germination. Plant Cell Physiol. 55: 1521-1533

Yang C, Lu X, Ma B, Chen S-Y and Zhang J-S 2015. Ethylene signaling in rice and Arabidopsis: conserved and diverged aspects. Mol. Plant 8: 495-505

Yang P, Li X, Wang X, Chen H, Chen F and Shen S 2007. Proteomic analysis of rice (Oryza sativa) seeds during germination. Proteomics 7: 3358-3368