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Cold Stress in Rice at Early Growth Stage – An Overview

Brijesh Kumar Singh*, Monoj Sutradhar, Amit Kumar Singh and Nirmal Mandal

Department of Agricultural Biotechnology, Faculty of Agriculture, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, Nadia-741252

*Corresponding Author E-mail: brijeshsingh714@gmail.com

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ABSTRACT

The changing climate accompanied with cold temperature which unmasks itself as a devastating stress for most of the high yielding rice cultivars in twenty first century. The early growth stage which include germination, seedling formation get severely damaged by cold stress leading into crop failure or major yield loss. However, the genotypes grown in colder climates of high altitude and temperate regions have evolved themselves to avoid or survive cold stress in course of time. In order to achieve cold tolerance in high yielding rice, a thorough understanding of this tolerance mechanism at physiological, metabolic and genomic level is imperative. So, the present review on rice covers the cold damage evaluation, characterization, physiological response to stress and tolerance mechanism in brief.

Key words: *Rice, Early stage, Seedling, Cold, Stress, Tolerance*

INTRODUCTION

Rice (*Oryza sativa* L.) is an annual grass which belongs to the family *Gramineae, subfamily* Poaceae[2]. It is one of the earliest domesticated and principal staple food crop for more than one third of the worlds' population. In Asia, more than 90% of the worlds' rice is grown, where almost 60% of the worlds' population lives[4]. Abiotic stress related with temperature due to changing climatic conditions of twenty first century is the burning concern for plant scientists worldwide[68,82]. Low temperature in particular has alarming consequences on plant growth and development, since these processes have optimum temperature requirements specific for each and every plant species.

Low temperatures pose a major climatic problem for all rice growing countries including Australia, China, Japan, Nepal, Russia and South Korea[17]. The Australian rice industry, which has the highest yield (10 t h^{-1}) in the world experiences cold stress once in about every 4 years and resulted in about 30 - 40 % yield loss accounting $120 million due to cold-induced sterility[55].

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In India, cold rice is grown in about 1 million ha of hill regions in Jammu and Kashmir, Uttaranchal and North eastern hill states accounting 2.3% of total area under rice. The average yield of this cold rice is about 1.1 t h^{-1} as against the average national yield of 9.1 t h^{-1}. Major productivity constraints of these areas include low temperature, blast, drought spell and very short span of cropping season. The cold temperature stress in those areas affect rice mostly at early stage and seldom at the flowering stages too, resulting in sterility and devastating yield reduction. Since, rice is a temperature-sensitive field crop, low temperature induced yield loss is a worldwide problem[63].

Types of Low Temperature Injury

A plant can endure through two types of injuries after low temperature exposure[78]. 1) *Chilling injury* occurs due to lower temperature just above freezing point of water. This phenomenon remains reversible initially but ultimately causes cell death due to prolonged cold spell. Sometimes the progressive colder temperature beyond critical range may result in hardening and/or acclimatization of plants which can lessen and/or abolish stress injury. 2) *Freezing injury* is induced by the low temperature below freezing point. The intracellular freezing becomes fatal for the protoplasmic structure when the ice crystals grow large enough to disrupt the cells. In extra cellular freezing, the protoplasm of the plant becomes dehydrated because a water vapour deficit is created as cellular water is transferred to ice crystals formed in the intercellular spaces. Rice crop is more commonly abused by the first kind of injury, i.e. chilling injury, whereas, freezing injury may also occur once in a while[78].

Tools To Evaluate Cold Stress in Rice

Most of the physiological assessment of rice in terms of cold tolerance or sensibility have been made in two phases of growth: seedling and booting. In both of them cold temperature has harmful effects on crop productivity, as in the first one the number of established plants is affected and in the booting stage pollen sterility is induced by cold, decreasing the final number of grains. A wide range of practices such as altered cold intensities and episodes of exposure are usually applied to assess the cold injury and tolerance in these developmental phases. Only a few of them are non-destructive. Primarily, the visual symptoms as wilting and yellowing of leaves at seedling stage are correlated with cold stress in general[73,77,89]. So, the degree of leaf withering is used as an essential measure for recording chilling damage[54]. Chilling injury and low temperature chlorosis is been used as a scoring measure for cold tolerance/susceptibility during seedling stage.

Moreover, seedling survival is also used as a scoring measure for cold tolerance, since susceptible seedlings struggle in upholding average metabolic rates under cold and eventually die[52]. There are standard screening methodologies (Table 1) described by several scientists to screen rice genotypes effectively for cold response under controlled temperature conditions at germination (seedling) stage are given below.

Table 1: Methods and traits evaluated in germination stage for cold tolerance selection in rice

Methodology of screening	Evaluated trait	Reference
10, 15, 20, and 25°C for 5 to 30 days (on the basis of temperature)	Germination rate (radicle protrusion)	Bertin *et al*[7]
13 °C for 28 days and 28 °C for 7 days	Germination index and scoring for cold tolerance 1-9	Priyanka *et al*[64]
17°C for 7 days	Germination (%) and its speed	Sthapit and Witcombe[76]
13°C to 15°C for 7 days	Percentage of germination	Lee *et al*[44]
15°C for 12-16 days	Low temperature germinability (LTG)	Sheng *et al*[70]
15°C for 10 days	Coleoptile length	Hou *et al*[25]
15°C for 6 days	Germination rate	Chen *et al*[10]
13/20°C day/night and control condition 25/20°C day/night15 days	Leaf discoloration, SPAD value chlorophyll content	Park *et al*[62]
12-h light (15000 LX) 12-h dark. The seedlings were initially exposed to 14°C for 2 h followed by 12°C for 4 h and 10°C for 4 h.	Seedling sensitive	Yang *et al*[90]
10 °C for 10 days, 10 °C for 13 days	Seedling survival percentage	Zhang *et al*[96]
12℃. for 10 days	Seedling vigor	Han *et al*[22]
4°C for 48 h	Cold induced injury	Xiao *et al*[84]
25 °C for 4 days	Dormancy	Xie *et al*[86]
18–19°C cold-water irrigation (field) 17–18°C cold-air (glasshouse)	Cold sensitive	Jena *et al*[33]
4°C for 9 days, 4°C for 11 days and 4°C for14 days	Cold stress tolerance index and withering index	Juan *et al*[35]
14℃ for 7 d, 11 d, 14 d, and 17 d	Low temperature vigor of germination (LVG)	Han *et al*[23]
50°C for 48 h to break dormancy, 32°C for 36 h, 5°C for 10 days, 20°C for 10 days to recover	Seedling survival	Pan *et al*[61]
13°C for 28 days, 28°C for 7 days	Coleoptile and radicle length under	Bosetti *et al*[9]
13°C for 28 days, 28°C for 7 days	Radicle and coleoptile length and germination index	Dashtmian *et al*[15]

Most of the reported studies have mentioned the seedling survival rate of transgenic plants as baseline criteria for tolerance to cold stress[11,26,27,28,31,39,46,47,50,73,77,87,88,89,95]. However, an on/off character like survival proved to be incompetent in the actual field condition since cold tolerance is a variable trait, and it is not even a useful trait for QTL detection. In few of the other studies, quantitative analysis of shoot and root biomass were also used for evaluation of contrasting genotypes[1] and/ or transgenic plants[79] at any developmental stages, since plant growth and development is often negatively subjected to cold stress[66]. However, most of the evaluation methods have the drawback of being destructive, time intense and are not suitable for plant breeding curriculums where huge number of lines in the field need to be assessed.

Low Temperature at Germination Stages

Seed germination is the most important stage in plant life cycle where thrusts the seed to grow into a plant run and produces many seeds. Conditions essential for germination are water, air, temperature and light. In case of rice, quiescent as well as non-dormant seeds just need rehydration after proclamation from primary dormancy. However, the germination of rice seed is affected greatly by temperature. The temperature colder than the favourable range[57] (18°C to 33°C) retard the germination progression starting from imbibition, activation and succeeding manifestation.

Cold temperature slows down the diffusion resulting in disrupted imbibition process and escape of solutes from the seeds. However, Yoshida[93] reported the successive stages of germination (i.e. growth of coleoptile and radical) as the most vulnerable phases to cold spell. It (cold stress) results in retarded cell division and cell elongation in plants because of unbalanced metabolic activities at such low temperature[49]. Rice is a tropical and/or sub-tropical plant which requires a fairly high temperature ranging from 20°C to 40°C[75]. The standard temperature for rice seed germination is considered to be approximately 30°C. The temperature below 20°C results in gradual decrease of germination rate[80] (**Table 5).** Moreover, Yoshida[94] considered 10°C as the minimum critical temperature of rice germination.

Table 5: Temperature and seed germination

Temp.			
	30°C	→ Optimum	→ Very good germination
	20°C	→ Critical	→ Medium Germination
	10°C	→ Limiting	→ Germination Failure

Cold stress in rice delays germination and emergence; soil temperature of below 10°C can result in complete failure of germination[94]. Screening for cold tolerance based on germination and seeding growth have been attempted in rice as well[13] and there was marked genetic variability for the traits[67]. Yoshida[94] studied the effect of cold stress at three phases; germination, imbibition, activation and post germination growth. The effect of cold stress was more pronounced at the phase of imbibing and this was regarded as the most sensitive phase. The exposure of seeds to cold stress during this phase has resulted in increased escape of solutes from the seeds. This has been attributed to the incomplete plasma membrane of the dry seed and the disturbance caused on its reconstruction[12]. Cold stress at this stage has been reported to target the cellular membrane and thus is the primary cause of other metabolic disorders usually observed within the cells[49]. Despite the fact that seed germination under low temperature is a main problem in rice plant, there's still an extended manner to go to elucidate the mechanism of seed germination. Lately, purposeful genomic techniques have been implemented to observe and to elucidate the mechanism of seed germination in rice.

Low Temperature at Seedling Stage

Plants require an optimal temperature range for their growth, development and ultimate survival[45]. Low temperature has a strong impact on growth, survival, reproduction and distribution of plants. The seedlings get severely damaged by cold stress when they are grown in winter environments. As a result, the productivity decreases in temperate areas[50,85]. In the Northern and North-eastern parts of India, cold spell prevails in winter season during December to February and the minimum temperature remains often below 12-15°C. Infact, the minimum temperature occasionally reaches below 20°C during March and April in some parts of the northern states of India.

Even though, rice is being cultivated in a wide range of environments (tropical, sub-tropical, temperate), it is still a tropical C_3 crop[38], which yields best under warm temperatures and high solar radiation[16]. It is been reported[53,65] to be more sensitive to cold stress than any other cereal crops, especially during seedling, tillering, panicle development and flowering stages. The critical temperature for rice growth varies with different developmental phases such as 10°C for germination and 17°C for the reproductive stages. Temperature drops to about 10°C during seedling establishment (October to early November) such low temperature significantly reduces seedling growth and establishment[30]. Nishiyama[59] and Yoshida[92] also reported that the critical low temperature differs according to variety, duration of low temperature and the plant's physiological development. Nakagahra *et al*[56]., Sharifi[69] and Lou *et al*[48]., found that rice is vulnerable to damage by temperatures below 15°C, especially, the early seedling phase which is the foundation for stable seedling formation following strong vegetative growth. Induction of colder temperature during seedling stage results in lower number of seedlings, shrinked tillering[71], higher plant mortality[6,19,51], and also induce non-uniform crop maturity[72].

The seedling growth drop in rice due to low temperature poses a major threat in tropical and sub-tropical zones at high elevation as well as regions where cold mountain water is used for irrigation. In such areas, water temperature below 15° C causes poor germination, delay in seedling emergence, poor seedling establishment, slow growth, yellowing and drying of leaves, reduced tillering which ultimately lead to seedling death[36,51,56]. Cold stress also affects chlorophyll content and thus interferes in photolysis[37,40]. Most of the high yielding varieties cannot be used in direct sowing because of low germination rate at low temperature.

Bardhan and Biswas[5] reported the adversely affects of low temperature on seedling dry matter since low temperature affects the photosynthetic activity. Dai *et al*[14]., reported a positive relationship between root oxidizing activity and dry matter production in rice seedlings under cold stress which also could be used as a criteria for cold tolerant rice variety selection.

Table 1: Response of the rice plant to varying temperature at different stages

Growth stage	Critical temperature		
	Low	Optimum	High
Germination	16-19	18-40	45
Seedling emergence and establishment	12-35	15-30	35
Rooting	16	25-28	35
Leaf elongation	7-12	31	45
Tillering	9-16	25-31	33
Initiation of panicle primordia	15	-	-
Panicle differentiation	15-20	-	30
Anthesis	22	30-33	35-36
Ripening	12-18	20-29	> 30

Physiological Response of Rice to Low Temperature

Low temperature adversely affects a wide range of physiological processes from seed germination to maturity, and ultimately causes a serious yield reduction in rice. Changes in physiological activities precede the development of visual symptoms. At colder temperature, the rate of respiration and ion leakage increase; but the photosynthetic activity and carbohydrate metabolism decrease. Nutrient deficiency at root is one of the consequences of low temperature[20]. Low temperature induces chlorosis in developing young leaves, which remain white, even under permissive temperature conditions, without withering[91]. Chilling temperature even induce starch build-up in chloroplast which hinders photosynthetic activities due to feedback inhibition of photosynthetic enzymes. Photo-inhibition of photosynthetic machinery is enhanced at chilling temperatures due to decreased utilisation of excitation energy[74]. Several factors such as type of plant species, developmental stage, nutrition, irradiance and other climatic conditions before, during and after the chilling exposure influences the degree of dysfunction. Rice genotypes belonging to *indica* subspecies are known to be more sensitive to low temperatures than *japonica* rice[12,24]. Early germination and microspore genesis stages in rice are considered as the most sensitive to low temperature stress[8,12,21]. Low temperature at seedling and / or panicle development stage is greatly exacerbated by increased nitrogen application. Chilling causes greater injury under illuminated conditions, owing to photo oxidation damage determined by the increase of harmful active oxygen species[41,83]. Cloudy conditions or darkness during chilling stress reduced the damage in photosynthetic machinery.

Mechanism of Cold Tolerance in Rice

Low temperature or cold tolerance is the ability of plants to survive and perform under cold stress conditions. The capacity to maintain total plant yield is a tolerance criteria considered by several workers. It allows all possible yield compensatory mechanisms to occur during the vegetative and reproductive period. Rice plants have evolved various survival mechanisms (tolerance) through changes in their morphophysiological and biochemical behaviour.

It has been found that sucrose and other simple sugars accumulate during the acquisition of cold tolerance in most species and is believed to be instrumental in protecting membranes during freezing, but this alone is not sufficient to confer full tolerance. This fact is presage by the bewildering complexity of changes in gene expression that accompanies the acquisition of cold and freezing tolerance in species capable of cold acclimation[78]. Although the actual function of most of these cold-induced genes in the development of cold tolerance is unknown. It is known that many cold-regulated genes contain a drought responsive DNA element (ORE) that interacts with the transcriptional activator CBF1 (C-Repeat Binding Factors)[78]. Constitutive expression of CBF1 confers considerable cold/freezing tolerance to unacclimatized plants confirming its central role in the acclimatization process[32,34] although it is also not alone sufficient for full development of cold acclimatization. Thus, while native temperate plants respond to repeated exposures to cool temperature by progressively acquiring greater tolerance through intricate if only partially understood acclimation process, warm climate species respond by accumulating damage and progressively becoming physiologically unfit.

The modest level of genetic variation for chilling tolerance that does exist in these warm climate species appears to reside in their recovery ability rather than in their acclamatory capacity.

The morphological adaptations with decreasing temperature are often linked to decrease in leaf area ratio (LAR), specific leaf area (SLA) and relative growth rate (RGR). Increase in leaf thickness is an adaptation mechanism to protect the photosynthetic machinery against the cold[81]. Rice genotypes having high respiratory homeostasis (H), *i.e.* an ability of the plants to maintain similar respiration rates at growth temperatures, showed greater tolerance and maintained both shoot and root growth under cold conditions.

Plants have also developed antioxidant systems which shield cellular organelles and membranes from abating effects of cold induced reactive oxygen species[18,42]. Antioxidant enzymes, such as SOD, CAT and POX, can react with, and neutralize the activity of AOS[60]. In conjunction with these enzymes antioxidant compounds such as ascorbate, glutathione, etc. also help in removal of noxious oxygen compounds[83]. Cold tolerant rice cultivars have been reported to maintain higher activities of defence enzymes and higher content of antioxidants with little effect on electrolyte leakage[29,42].

There are certain organic compounds called osmoprotectants which accumulate in plants during acclimatization in continuously altering environment. These include amino acid (proline), betaine (), sugar (trehalose) and polyamines such as spermine, spermidine and putrescine. In addition to the direct protective effects, osmoprotectants are also involved in the up regulation of several genes (new proteins are synthesized) such as *Weor* 410 and *Weor* 413[3]. Except glycine betaine, all other osmoprotectants occur in rice tissues at low levels. Cold tolerant cultivars, which accumulate higher spermine, produce more viable pollen grains leading to low spikelet sterility[58]. Higher gibberellic acid (GA) content in the seedlings resulted in greater seedling cold tolerance (biomass production) in rice cultivars. However, GA content in the leaves at reproductive stage could not be significantly correlated with spikelet sterility[55]. Recent studies on production and accumulation of organic compounds (osmoprotectants) in rice cultivars under cold temperatures lead[55] to present the following mechanism for low temperature tolerance in rice.

Higher GA production leads to greater α-amylase activity thus liberating simple sugars for the growth of the germinating seeds. On the other hand, osmoprotectants such as spermine could protect activity of enzymes such as α -amylase, various physiological processes including photosynthesis, and could enhance the development of engorged prolin A. A similar association has been shown between high proline content in pollen and high pollen fertility[43] have recently demonstrated the importance of spermine in drought tolerance in rice. Rice plants engineered to produce higher spermine were able to tolerate drought through anti-senescence compared to the wild type plants with lower capacity to accumulate spermine.

Future Directions

So far, the scientists have only approached to identify individual types of responses in rice due to cold stress. Different types of alterations in those responses by using breeding and genome modification techniques have already provided with expected level of tolerance. However, those approaches have also resulted in unwanted collateral translates or missing translational products along with the expected one. In the bigger picture of cold tolerance and susceptibility, a sustainable outcome is possible only if the researchers consider all the regulatory mechanisms and pathway in a single event of approach, when only the targeted phases are being affected without influencing the rest of the off target phases. The revolution in modern molecular biological techniques such as the genome editing with CRISPR/cas system, mega-nucleases sound promising in such endeavours of twenty first century.

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