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Ecophysiology of anaerobiosis stress due to flood and waterlogging in rice

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ABSTRACT

Purpose: Significant research on yield improvement of wetland rice provided a greater understanding of stress physiology, but less on ecophysiology of anaerobiosis stress. This paper explores soil conditions that exist because of waterlogging and submergence, reviews the current research of the effect of the ecophysiology of abiotic stress, and the plant's adaptability through its various biochemical pathways and physiological processes. **Findings**: Rice has morphologically avoided anoxia due to flooding and submergence ecosystems through its aerenchyma tissues that facilitate oxygen diffusion from shoot to root-tips. The plant hormone system plays a central role in the initiation and regulation of most of these adaptive responses. The biochemical responses of submerged rice are mainly mechanisms of avoiding internal anoxia as the oxygen deficit shift the energy metabolism to anaerobic, with greater activity of glycolytic pathway, fermentation enzymes, and involvement of antioxidant defense mechanisms to cope with the post hypoxia/anoxia oxidative stress. Physiological processes including aerobic respiration, photosynthesis, and phytochrome photo-equilibrium of the submerged rice shoots have evolved to adapt to waterlogging stress. Most of the post-anoxic injury is due to the generation of reactive oxygen and toxic oxidative products as acetaldehyde, hydrogen peroxide and hydroxyl radical. **Limitations**: This was minimal due to accessibility to the literature. **Directions for future research:** Future research should be directed towards rice tolerance to waterlogging as well as low water availability and salinity.

INTRODUCTION

The rice crop (*Oryza sativa* L.) is commercially cultivated under controlled semi-flooded conditions as transplanted seedlings or direct-seeded under submerged anaerobic conditions and subsequently germinated (Bridgemohan & Bridgemohan, 2014a). The photosynthetic plant tissues are capable of ethylene-mediated elongation that can quickly bring the leaves and stems above the water into an aerobic state (Visser et al., 2003). This characteristic of rice compared to other cereals gives the plant comparative stress adaptability to both paddy-field which are usually with excess water as either submerged or waterlogged (Nishiuchi, 2012). Rice is adaptable to varying agro-ecological zones including steep hillsides, seasonal rain-fed conditions, controlled irrigation or perennial waterlogged soils (Bridgemohan & Bridgemohan, 2014b). The zones are characterized by marked differences in depth of submergence and duration of soil waterlogging or flooding (Colmer, 2002) or the extreme of soil moisture deficit (Bridgemohan, 1995).

The plant has ecophysiologically adapted to the complex micro-ecosystem processes at the cellular level to the individual plants. Flooding and extended submergence create major biotic and abiotic stresses on the rice crop which may not be indifferent to water deficits, salinity and extreme temperatures (Bridgemohan & Mohammed, 2019). The rice plants adapt to their ever-changing environment from prevailing inundated wetlands with water-saturated soils which exclude oxygen, and deprivation arises from an imbalance between reduced diffusion of gases in water compared with air and the lower rate of oxygen consumption by micro-organisms and plant roots.

Flooded rice soil becomes rapidly devoid of oxygen at depths below a few millimeters resulting in tissue oxygen deficiency. The rice roots are essentially aerobic organs, and when aerobic respiration ceases, levels of energy-rich adenylates declines, causing a drop-in ion uptake and transport. The plants respond by certain morphological, physiological and biochemical changes induced by the flooding. These are manifested in anatomical structures that are conducive to support internal transport of oxygen by diffusion or mass flow.

This paper explores special soil conditions that exist because of waterlogging and submergence, reviews the current research of the effect of the ecophysiology of these abiotic stress on rice, and the plant's adaptability through its various biochemical pathways and physiological processes.

Ecology of waterlogging

Waterlogged soils are usually anaerobic and chemically reduced (Colmer, 2002) as water fills in the soil pores and the oxygen concentration decreases (Akhtar & Nazir, 2013), whereby physical properties and nutrient availability deteriorates (Patrick & Mahapatra, 1968). Increased duration of flooding exacerbates and limits the quantity of dissolved oxygen in the soil-pore available for microbial respiration in the rhizosphere (Reddy & Patrick, 1986; Jackson & Ram, 2003).

However, the supply of soil oxygen to the flooded soil is improved through two avenues:

- diffusion through the overlying floodwater, and
- transport through the stems of rice to the roots and subsequent diffusion into the rhizosphere.

This results in the development of two distinct soil layers in the soil:

- oxidized or aerobic soil layer with high microbial activity,

- and reduced or anaerobic soil layer.

Soil oxygen

Surplus soil water disturbs rice root growth and function, as it prevents adequate gas exchange at the root surface, direct entry of oxygen by gas diffusion and disposal of physiologically active gases and volatiles (Jackson & Ram, 2003). The depletion of O_2 creates an anaerobic condition for crop growth. Soil oxygen stimulates the growth of certain bacteria that rapidly diminish nitrate (NO_3) availability to roots and, produce highly soluble and toxic $Mn^{2+}$and Fe^{2+} which is eventually converted to SO_4^{2+} which are respiratory poison H_2S (Jackson & Ram, 2003). The long term saturated soils exhibit increased incidence of soil-borne fungal and bacterial diseases, and the increase of oxygen shortage promotes internal anoxia.

pH

The pH of the floodwater in rice fields is the chemical equilibria that exist between the CO_2 balance achieved by the aquatic biota and the various solutes, solids, and gases in the water (Mikkelsen et al., 1978). The values undergo diurnal changes, increasing by midday (pH 9.5-10) and decreasing (4 to 5) in the night. The pH of shallow floodwater is greatly affected by the total respiration activity of all the heterotrophic organisms and the gross photosynthesis of the species present. Ammonium fertilizers into high pH water are highly susceptible to direct NH_3 volatilization losses, but losses will vary depending upon water pH, nitrogen source, rate and time, and method of application.

Nitrogen

Nitrogen is the most limiting nutrient element affecting growth in most rice-growing soils. Rice grown under flooded soils differ from dry arable soils as it is affected by N_2 transformations and fertilizer use due to a low supply of oxygen (Keeney & Sahrawat, 1986). The anaerobic metabolism in flooded soils is dominated by bacteria, with marked end products from the arable soils. This is manifested in the presence of oxidized and reduced soil layers where both aerobic and anaerobic N_2 metabolisms can occur in close proximity. Oxidation-reduction systems in the soil become unstable when the oxygen supply is restricted (Patrick & Mahapatra, 1968). The nitrate, manganate compounds, ferric compounds, and sulfate are stable in well-aerated soils but become unstable when devoid of soil oxygen.

Denitrification losses

The available nitrate is lost through denitrification by the facultative anaerobes to substitute nitrate for oxygen. Nitrogen transformations in a flooded rice soil are similar to N trans-formations in drained soil systems, although the special soil/environmental conditions prevailing in flooded rice soils alter the rate at which these processes occur (Reddy & Patrick, 1986).

The key N_2 transformations in a flooded soil system include:

- mineralization of organic N_2,
- nitrification of NH_3,
- NH_3 volatilization,
- denitrification and
- N_2 fixation.

The agronomic and ecological significance of these processes in the gain or loss of N_2 from a flooded soil and sediment system is influenced by the water level and quality. Deliberate flooding or poor drainage is detrimental to crop growth and degrades soil quality. Nitrogen mineralization and nitrogen availability have potential to increase lowland rice yields (Ceesay et al., 2006), and proper agronomic and ecological management can increase the gain of N_2 in flooded soils through proper water management.

Phosphorus sorptivity

Under prolonged waterlogging, rice soils show large increases in acetate and oxalate extractable iron and phosphorus sorptivity (Willett & Higgins, 1978). The growth of rice plants exhibits no significant effects on phosphorus sorptivity or extractable iron. During oxidation of previously flooded soils, levels of phosphorus sorptivity and oxalate iron decreased rapidly but did not return to levels occurring before reduction. There is a domination of phosphorus sorption processes by ferrous hydrous oxides during the flooded (reduced) phase and by poorly crystalline ferric hydrous oxides during the post-flooding re-oxidation phase.

Non-exchangeable K

The extensive, shallow root system of flood-irrigated rice plus the increased K availability after flooding makes rice an effective scavenger of soil K (Bridgemohan, 1995; Slaton et al., 2009; Slaton et al., 2005). Chakravorti and Patnaik (1990) examined the release and fixation of non-exchangeable K in flooded rice soils and observed that its contribution towards the total K uptake increased in the latter stages of cropping. The release of non-exchangeable K was great in the alluvial soil types and that a fixed form increased with the increasing amount of added K and reached almost a plateau, followed again by an increase. The K concentration of rice plants usually reaches its maximum concentration during active tillering which coincides to 2 to 4 weeks after the flooding. Usually, the K concentration of rice increases briefly after the permanent flood is applied at the 5-leaf stage and reflects the enhanced K availability in flooded soil. K uptake pattern of flood-irrigated rice indicates it is sufficient during vegetative growth, and that the K uptake in the soil and fertilizer K are absorbed rapidly and efficiently shortly after flooding (Bridgemohan & Bridgemohan, 2014b; Slaton et al., 2005).

Sulphate

Under waterlogging conditions, sulfate is reduced to sulphide by anaerobic bacteria. Both nitrate and ammonium ions can be assimilated by the rice plant (Hosner et al., 1973). Lin et al. (2010), investigated the mechanism of sulphur transformation in paddy soil and how it affected Cu biogeochemical processes. The findings implied that Cu existed mainly in two forms. The Cu (II) was in the rice rhizosphere and the other part of Cu was transformed to Cu (I) in anoxic bulk soil. With higher Eh in the rice rhizosphere, the transformation of sulphur and organic compounds together contributed to more soluble and exchangeable Cu. The combined action of organisms-maintained Cu homeostasis through active cation binding to bioactive molecules. The study indicated the important role of sulphur in the transformation of Cu and the complex microbial processes in soil.

Methane and nitrous oxide emissions

A major contributor to methane (CH_4) and nitrous oxide (N_2O) emissions comes from the production of rice paddies under various agricultural management systems including water regime, crop residue incorporation, and synthetic fertilizer application (Zou et al., 2005). The

N_2O emissions depended on the intensity of waterlogging, but urea application tended to reduce CH_4 emissions and significantly increased N_2O emissions. Relative to conventional rice paddies, organic cropping systems increased seasonal CH_4 emissions by 20%. Under the waterlogged conditions regimes, N_2O-N emissions were lower (10.85µg/m^{-2}/h^{-1}) in conventional rice than in organic rice paddies (13.66µg/m^{-2}/h^{-1}). It is suggested that organic cropping systems might not be an effective option for mitigating the combined climatic impacts from CH_4 and N_2O in paddy rice production (Qin et al., 2010). Estimations of net global warming potentials (GWPs) indicate that water management by flooding with mid-season drainage and frequent waterlogging without the use of organic amendments is an effective option for mitigating the combined climatic impacts from CH_4 and N_2O in paddy rice production (Zou et al., 2005).

Trace elements

Zinc (Zn), Iron (Fe), Copper (Cu), and Manganese (Mn)

Sajwan and Lindsay (1986) indicated that the pH and redox relationships associated with various soil moisture conditions increased the incidence of Zn deficiency of rice in submerged soils through greater solubilization of Fe and Mn. They found that Zn deficiency observed in the submerged paddy rice can partially explain the increased reduction and solubilization of Fe and Mn which had an antagonistic effect on the availability and uptake of Zn. Furthermore, increased HCO^{-3} may also contribute to increased Zn deficiency. The Fe dissolved at reduced microsites and subsequently reprecipitated as ferrosic hydroxide ($Fe_3[OH]_8$) in more oxidized zones. Also, the higher solubility of Fe maintained by $Fe_3(OH)_8$ could depress Zn^{2+} solubility through the formation of $ZnFe_2O_4$ or a similar franklinite-like solid material. Zinc is the most common micronutrient fertilizer applied to rice and can limit yield. Growers apply Zn fertilizer solutions or granules to the soil surface without incorporation before emergence, with recommended rates (11kg /Zn /ha^{-1}) of granular Zn preferred for alkaline, Zn-deficient soils.

Cadmium (Cd) and Arsenic (As)

Rice cultivated under flooded conditions has higher concentrations of arsenic (As) but lower cadmium (Cd) compared to rice grown in unsaturated soils (Moreno-Jiménez et al., 2014). This suggests that methylation is favored under waterlogging. However, irrigation can increase Cd transfer to grain by a factor of 10. Controlled irrigation as opposed to flooding as in paddy fields can mitigate against excessive arsenic (As) accumulation, as evidenced in an increased Cd load in rice grain which may result.

Morphology and growth adaptation physiology

Waterlogging affects several biological and chemical processes that can impact crop growth in both the short and long term. Germinating rice seeds are very sensitive to waterlogging and drought as their level of metabolism is high. However, even though the seeds germinate under both extreme conditions, it cannot tolerate flooding after it has emerged on dry soils for an extended period during this stage (Bridgemohan & Bridgemohan, 2014b). There are many ecotypes of *O. sativa* ranging from those adapted to arid/semi-arid soils to those in deep-water and floating ecotypes (Bridgemohan & Bridgemohan, 2014c).

Molecular genetics has demonstrated that a region on chromosome 9 controls tolerance anaerobiosis, anatomical elongation, retardation of senescence and ethylene insensitivity. The DNA marker is fine mapped to this locus, and has proven to be inextricably linked with the inheritance of the tolerance trait. Plant breeders and agronomists have been successful in breeding and selecting submergence-tolerant varieties by manipulating these traits. Under

these anaerobic conditions, the plant under genetic influence modifies its anatomical and morphological structures at the cellular, tissue and organ level so that it can better adapt to the ecological changes and variations.

Aerenchyma and sclerenchyma cells

Feng et al. (2006) observed differentiation in the root anatomical structures of rice genotypes under inundatory and aerobic conditions, especially on the aerenchyma and sclerenchyma cells. The aerenchyma in hybrid Japonica root developed the latest, whilst the cortex sclerenchymatous cells in conventional Indica root were different from those in conventional Japonica root in terms of morphological traits. Compared with inundatory conditions, aerobic conditions retarded the formation of aerenchyma of hybrid rice roots and made the cortex sclerenchymatous cells array loosely in conventional Japonica roots. However, Fagerstedt (2010) observed a novel sequence of activities that led to the lysigenous aerenchyma formation in wetland crops. The cell was induced into a strictly programmed cell death (PCD) in the mid-cortical parts of the root. This subsequently resulted in hypoxia, and N_2 and S deficiency. The lack of O_2 caused a lowering of the cytoplasmic energy which affected the cellular redox balance.

Epidermal and exodermal cells

The efficacy of aerenchyma is increased due to gas-tight barriers formed in the epidermal and exodermal layers of the roots to the surrounding oxygen-deficient soil (Colmer, 2002). However, under severe inundation of the crop shoots and roots, abiotic stress on the plant is magnified as aerial carbon dioxide for photosynthesis is prevented. Underwater photosynthesis, enhanced shoot elongation, adventitious roots, and aerenchyma formation are typical adaptive responses which are believed to improve the oxygen status of submerged plants (Voesenek et al., 1992). In addition to the extensive lysigenous aerenchyma system in the rice roots, the plant has developed an intricate barrier to radial O_2 loss (ROL) in the basal zones (Visser et al., 2003; Nishiuchi et al., 2012). This synergistically enhanced the O_2 diffusion to the root tip and enabled an aerobic rhizosphere around the root tip. The aerenchyma is a low resistance network for the transport of aerated aerial shoots to submerged plant organs under anaerobic conditions.

Adventitious roots

In deep-water rice (*Oryza sativa*), adventitious root primordia initiate at the nodes as part of normal development. The emergence of rice roots is dependent on flooding and is stimulated by ethylene action (Mergemann & Sauter, 2000). Root growth is preceded by the induced death of epidermal cells of the node external to the tip of the root primordium. The cell death proceeded until the epidermis splits open from which root eventually emerged. Induced death was confined to nodal epidermal cells covering the tip of the primordia. This process facilitated adventitious root emergence and prevented injury to the growing root. Root cell death was stimulated by submergence and application of 1-aminocyclopropane-1- carboxylic acid (ACC). This is a natural precursor of ethylene, but it can be suppressed in the presence of 2,5-norbornadiene (bicyclo [2.2.1] hepta-2,5-diene), which has an inhibitory effect on ethylene production. Adventitious root growth and epidermal cell death are therefore linked to the ethylene signaling pathway, which is activated in response to low oxygen stress (Mergemann & Sauter, 2000).

Growth and development

There are three major growth and development phases in the rice crop: germination, vegetative growth, and reproductive and yield phase and each is affected in different ways by flooding. The crop can acclimatize and adapt to these physical changes to relieve the constraints imposed by the flooded environment.

Germination

There is a decrease in rice seed germination under waterlogging soil. Respiration, electron transport, and ATP formation are a condition of hypoxia which are inhibited during germination (Voesenek et al., 1992).

Vegetative growth

This phase is affected by a growth reduction, low specific leaf area (SLA), ethylene and products of root and bacterial anaerobic photosynthesis declination, stomatal closure, and decrease metabolism (Akhtar & Nazir, 2013). This is manifested in shorter stem length in early growth, but as the duration of flooding extends, there is an extensive and rapid elongation of stem length resulting in lodging (Bridgemohan & Shand, 1995).

Reproductive and yield phase

Generally, the same variety of rice cultivated under rainfed as opposed to irrigated or waterlogged conditions produced a lower crop yield, and also lower biological harvest index (Bridgemohan, 1995). There was a marked reduction in grain size, weight, and percentage filled spikelet in rainfed rice. Mishra and Salokhe (2010) observed that variations in water regime and planting pattern on the growth of rice plant roots and shoots and on yield and found that intermittent flooding improved root length density, root physiological activity, and chlorophyll content of the upper and lower leaves, leading to higher grain yield compared with the other treatment combinations. However, continuous flooding (CF), gave 23% more grain yield. Similarly, Surex et al. (1999) investigated the effects of continuous flooding, water stress on grain and total biological yield, and harvest index on selected rice varieties. The results indicated that the highest values were observed at continuous flooding,

Plant growth hormone

Gaseous plant hormone plays an important role in modifying plant response to oxygen deficiency and these may be induced genes of enzymes associated with aerenchyma formation, glycolysis or fermentation pathway with the rice plant. Plant hormones play a central role in the initiation and regulation of most of these adaptive responses, which permit "escape" from anaerobiosis (Voesenek et al., 1992; Nishiuchi et al., 2012).

The plant encounters various abiotic and biotic environmental stresses, but it has developed sophisticated mechanisms to sense changes in environmental conditions and will modulate their growth and development patterns to mediate with or adapt, accordingly (Bridgemohan & Bridgemohan 2014a). Plant growth-controlling hormones, such as auxin, gibberellic acids (GAs), brassinosteroids (BRs), and abscisic acid (ABA), are actively involved in plant immunity (Bari & Jones, 2009).

Ethylene

The rice plant possesses anatomical, metabolic, or morphological adaptations that make it tolerant to waterlogging conditions (Steffens, 2014). One metabolic response induced by hypoxia is the stimulation of ethylene production in a two-step reaction (Zarembinski & Theologis, 1993):

i. formation of 1- aminocyclopropane-1- carboxylate (ACC) by ACC synthase (ACS),
ii. ethylene formation from ACC by ACC oxidase (ACO).

Ethylene production is and the enhanced activity of 1- aminocyclopropane -1- carboxylic acid (ACC) synthase, which is the key enzyme in the ethylene biosynthetic pathway. Ethylene regulates various growth and developmental processes including seed germination, seedling growth, organ development, fruit ripening, and organ senescence and abscission. It is also involved in responses to stresses, such as salt, drought, cold, flooding, and microbe and insect infection (Yoo et al., 2009). Depending on the pathogen type and environmental conditions, studies have demonstrated that ethylene could act as a positive or negative modulator of disease resistance. It has been shown that flood or hypoxia-induced ethylene biosynthesis was important for field resistance to *Magnaporthe oryzae* in rice (Broekaert et al., 2006). The principal strategy for survival is to shorten the period of total submergence using a strong increase in the shoot elongation rate that reunites the shoot with air. As such, this growth pattern requires oxygen, which is regulated by a build-up of the hormone ethylene and is mediated via expression of expansion genes (Voesenek et al., 1992; Yukiyoshi & Karahara, 2014; Yamauchi et al., 2015).

Abscisic acid (ABA)

Waterlogging increases the production of abscisic acid (ABA) which can influence the growth of rice. After a decrease in growth, the tissue water potential or the rate potential to absorb nutrients, and concentrations of photosynthetic enzymes, and turgor also decreases (Bridgemohan & Bridgemohan, 2014c). Chen et al. (2006) reported a novel function of ABA in rice root growth and development as it affected root morphogenesis changes through a cellular and signal transduction mechanism. The ABA increased 2, 3, 5-triphenyl tetrazolium chloride (TTC) reductase ability in the root tips and the exudation rate of xylem sap.

Gibberellic acid (GA3)

Deepwater rice establishes a 'snorkel' via elongation of aerenchymatous internodes and leaf sheaths. These internodes elongate in response to increasing water levels to keep the leaves above the water surface to avoid anoxia. Ethylene induces the snorkel genes (Snorkel1 and Snorkel2) which encode ethylene-responsive factor (ERF) transcriptional regulators that elicit the action of gibberellin (Colmer et al., 2014). Both Snorkel genes and Submergence-1A encode ethylene-responsive factor-type transcription factors and are connected to gibberellin biosynthesis or signal transduction (Nagai et al., 2010). However, deep-water and submergence-tolerant rice seem to have opposite flooding responses i.e., escape by elongation or remaining stunted underwater until the flood recedes. The submergence tolerance of rice can be substantially improved when underwater elongation is minimized by treatments of paclobutrazol which is a GA3 biosynthesis inhibitor, as GA3 increases root elongation.

Plant biochemistry

There are biochemical responses in the rice plant to flood due to the effects of oxygen shortage and mechanisms of avoiding internal anoxia (Jackson & Ram, 2003). This oxygen deficit shifts the energy metabolism to anaerobic mode forcing the plants to adapt to stress such as increased availability of soluble sugars, greater activity of glycolytic pathway and fermentation enzymes and involvement of antioxidant defense mechanism to cope with the post hypoxia/anoxia oxidative stress.

Enzymes

Fukao et al. (2003) investigated the regulation of anaerobic metabolism during germination in anoxic conditions and the enzymes associated with anaerobic metabolisms such as sucrose synthase, aldolase, enolase, pyruvate decarboxylase (PDC), alcohol dehydrogenase (ADH), and aldehyde dehydrogenase (ALDH). Activities of sucrose synthase, enolase and ADH exhibited the same induction patterns under anoxia. For ALDH, activities were strongly induced to a greater extent under anoxia in anoxia-tolerant families than in anoxia-intolerant families, a trend also exhibited by the parents. This indicated that ALDH may play a role in detoxifying acetaldehyde formed through alcoholic fermentation during anaerobic germination.

Soluble sugars

Soluble sugars are rapidly channeled to fermentative metabolism as soon as oxygen levels decrease. Since the amounts of these sugars are limited, the starch breakdown is highly regulated by interactions between hormonal and sugar signals. Flooding during germination reduced survival but to a lesser extent in tolerant genotypes (Ismail et al., 2009). Starch concentration in germinating seeds decreased while sugar concentration increased under flooding, but more so in tolerant rice genotypes. Amylase activity correlated positively with elongation and plant survival. Tolerant genotypes had higher amylase activity and higher RAmy3D gene expression. Peroxidase activity was higher in germinating seeds of sensitive genotypes and correlated negatively with survival.

Glycolysis and ethanolic fermentation

The biochemical characteristics in response to waterlogging abiotic stresses affect rice crop in 2 ways viz:

i. metabolic utilization of glycolysis and ethanolic fermentation, and
ii. sucrose breakdown through sucrose synthase instead of invertase.

Flux analysis on photo-respiring leaf cells have elucidated the function of plastid-cytosol and mitochondrion-cytosol malate transporters in recycling the ammonia liberated during photorespiration and in exporting the excess redox cofactors, respectively.

Alcohol dehydrogenase (ADH)

Flooding usually reduced shoot and root growth of cereals, but prolonged flooding resulted in increased activity of alcohol dehydrogenase (ADH) in roots of flooding-tolerant than flooding-sensitive cultivars. Rice grown in solutions flushed with gases of different oxygen concentrations showed, high activities of ADH and pyruvate decarboxylase (PDC) when the solutions were flushed with pure N_2 gas. Species differences in the activity of ADH might be mainly related to different oxygen tensions inside the roots, due to differences in the volume of aerenchyma and morphology of roots (Wignarajah et al., 1976).

Anaerobic proteins

Plant species synthesize so-called anaerobic proteins that enabled an oxygen-independent energy-generating metabolism to proceed where fermentable substrates were available. Mujer et al. (1993) found these fermentation pathways can sustain survival underwater for many months, and anaerobic stress resulted in a change in the protein accumulation patterns in rice shoots. Analysis of the protein patterns from rice indicated that under anaerobiosis the plant produces five classes of proteins and a total of at least 9 to 13 anaerobic stress proteins

compared to 4 to 7 "aerobic" proteins. Immunoblotting has further identified two of the major anaerobic stress proteins as fructose-1,6-bisphosphate aldolase and pyruvate decarboxylase.

Phytoglobin

Prevention of the build-up of potential phytotoxins is another mechanism that enhanced rice crop survival under flooded conditions as a reactive oxygen species (ROS). Phytoglobin is a specific type of hemoglobin that can detoxify nitric oxide formed during hypoxia of root tissues, and may also regenerate NAD+, thereby serving as an alternative to fermentation (Dordas et al., 2003). Besides, non-symbiotic hemoglobins and nitric oxide have also been suggested as an alternative to fermentation for maintaining lower redox potential (low NADH/NAD ratio), and thereby played an important role in anaerobic stress tolerance and signaling.

Improvement of rice plant waterlogging tolerance

Flooding conditions are often accompanied by changes in light (duration and timing), carbon availability, and the diffusion rate of gases which subsequently influenced physiological processes including aerobic respiration, photosynthesis, and photochromic photo-equilibrium (Voesenek et al., 1992). Partial or complete submergence of shoots of rice (*Oryza sativa* L.) posed a dual challenge. The roots have to function in anoxic soil and, the gas exchange between shoots and air becomes restricted to a small aerial portion or is abolished during complete submergence (Colmer et al., 2014). Plants tolerant of waterlogging stress particularly in respiration and biomass production and protein synthesis exhibited certain physiological adaptations (Akhtar & Nazir, 2013; Bridgemohan, 2011).

Respiration

Rice is a flood-tolerant plant which can maintain its energy status by using fermentation and lactic acid production. It can germinate in the complete absence of oxygen with an initial decline in cytosolic pH attributed to them and grow in standing water (Bridgemohan, 1995). Alcoholic fermentation (AF) is one of the major metabolic adaptations that the submerged rice plant assumes. Although less efficient it provided energy and sustained plant life. The amount of adenosine triphosphate (ATP) produced by this process is very small (5%) compared to aerobic respiration, but it is still vital for survival. This pathway is important for both under anoxic and aerated floodwater, as the boundary layer limited diffusion of O_2 in water resulting in anoxic conditions. Plants could get only two ATP per aerenchyma and adventitious roots under fermentation, whereas, 36 ATP are produced with the interaction of plant hormones (auxin and ethylene) per glucose molecule in aerobic formation.

Translocation and synthesis

Flooding reduced phloem transport and growth is maintained at lower water potentials. It could also cause a reduction of carbohydrates in roots (Colmer et al., 2014). Oxygen starch accretion may show reduced phloem transport as a deficiency in roots caused a change from aerobic to a consequence of a discard in root metabolism caused by anaerobic respiration, which is much less efficient in low oxygen levels. The low oxygen concentration in soil affected the concentrations in the shoots and a reduction of the root (hypoxia). The complete absence of oxygen (anoxia) affected nutrient uptake, transpiration stream, synthesis of organic compounds, translocation and the partitioning of assimilates (Bridgemohan & Mohammed, 2019).

Chlorophyll (Chl) a fluorescence

Increased duration of submergence of rice seedlings resulted in decreased O_2 concentration of floodwater which concomitantly increased in carbon dioxide in concentration. Extended submergence increased the diminution of total Chl (Panda et al., 2006; Sikuku et al., 2010). Chlorophyll fluorescence, protein, and chlorophyll content of three Nerica rain-fed rice varied under varying irrigation regimes. Quantification of the Chl a fluorescence transient revealed varietal differences in the response of photosystem 2 (PS2) to submergence.

Photosynthesis

Any factor that inhibited root respiration such as insufficient drainage can result in a considerable reduction in energy of root cells. Diffusion of oxygen in the absence of oxygen terminated electron acceptor. During the day, underwater photosynthesis largely determined the O_2 concentrations within submerged rice, whereas, at night, tissue O_2 declined, particularly so in roots (Colmer et al., 2014). The effect of stress is associated with low dry matter production during the flooding (Shao et al., 2014).

In drought stress conditions, the process of physiological metabolism of rice changes greatly. The net photosynthetic rate, chlorophyll content and the activities of photosynthetic enzyme decrease, the contents of free proline, abscisic acid, active oxygen species and malondialdehyde obviously increase, and the activities of antioxidase SOD, POD and CAT are strengthened and excessive active oxygen is cleared out, which lighten the damage to rice. Rice variety with strong drought resistance may be of strong resistant to oxidation (Dai et al., 2006).

Post submergence rice ecophysiology

After the floodwater has receded, rice plants are then exposed to both high light intensity and higher oxygen levels. As a consequence of this rapid ecological shift, the plant manifest visual symptoms of injury caused by the inundation which become progressively apparent after the de-submergence. The post-anoxic injury is due to the generation of reactive oxygen species and toxic oxidative products such as acetaldehyde. This would occur as the O_2 reduced electrons leaked out from the electron transfer system converting it into superoxide anion (O_{2-}), resulting in more active O_2 forms such as hydrogen peroxide (H_2O_2) and hydroxyl radical (OH.). These can oxidize unsaturated fatty acids in cellular membranes and intercellular organelles.

CONCLUSIONS

The rice crop has demonstrated its diverse ecological amplitude to the tolerance and adaptability to anaerobiosis as a consequence of waterlogging and submergence and in the cases the extreme of low soil water availability and deficit. The anaerobiosis conditions influenced not only soil O_2, but pH, mineral elements availability and fixations, and methane emission. The plant at the molecular level has genetically modified its chromosomal arrangement which is manifested in its sub-cellular organelles, resulting in changes in the aerenchyma and sclerenchyma tissues. These structures facilitated the access to aerial O_2 and its diffusion to the root tip enabled an aerobic rhizosphere and acted as an intricate barrier to radial O_2 loss (ROL) in the basal zones.

The crop further mitigated against the inundatory ecological conditions by adjusting its physiological and biochemical pathways by the synthesis of compounds viz., anaerobic proteins, phytoglobins, and alcohol dehydrogenase. Through endogenous hormones, the rice plant has developed certain anatomical and morphological adaptations by the production of

ethylene which is the precursor of the aerenchyma cell network. The review has demonstrated the plant's ecophysiological adaptions to anaerobiosis by modifications of its respiratory pathways, translocation and transpiration streams, chlorophyll (Chl) a fluorescence synthesis, photosynthesis, and partitioning of assimilates.

This adaptability has made the rice plant a most versatile crop that produces a major source of carbohydrates and high energy foods for both the tropical and sub-temperate zones, under conditions from partial arid to extreme waterlogging and submergence. This characteristic and intense plant breeding and agronomic, and ecophysiological selection, has promoted this crop for peasant and large scale commercial production through aerial broadcasting of pre-germinated seeds underwater, regardless of depth, quality, and % silt of the water, including the O_2 levels.

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Conflict of interest

The authors have no conflict of interest to report.

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