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PHYSIOLOGICAL AND MORPHOLOGICAL CHANGES IN RICE DURING DROUGHT STRESS: A REVIEW

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ABSTRACT

Rice is the staple food for about half of the world's population. The rice grain yield and quality are affected by various biotic and abiotic stress conditions. Among all the Asian countries, India is the prominent rice-growing country, it occupies 23.3 per cent of gross cropped area and contributes 43 per cent of total food grain production and 46 per cent of total cereal production (Ashok *et al*., 2022). Among the abiotic stress drought stress is an important water stress condition, as rice crop needs more water supply to grow, among other crops. Water shortage has become a serious ecological problem. This drought causes various changes in the physiological and morphological characters of rice. Weedy rice is important for rice crop improvement as it has high genetic diversity. Drought affects phenotype and photosynthetic parameters in different ways in weedy rice genotypes. Therefore, it is essential to study the effects of drought stress on plant morphological, physiological including the changes in external morphology and internal structure of root, stem, and leaf, osmotic regulation substances, reactive oxygen species, antioxidant enzymes, and stomatal conductance. Morphological and physiological responses in rice include inhibition of seed germination, slower growth rate, low root and shoot length, lower chlorophyll content, stomatal closure, lower rate of photosynthesis, yield reduction and generation of reactive oxygen species which excites oxidative stress in plants.
***Keywords* :** Rice, Physiology, Morphology, Drought stress

Introduction

The demand for food increases with the increase in population and buying power of densely populated countries. Drought is the main factor that affects plant growth. Drought stress is a major constraint to rice production, particularly in water-limited environments (Mishra *et al*., 2015) mainly for upland rice cultivation. Large areas of lowland and upland rainfed rice occupy 31% and 11% of the global rice-growing area, respectively (Korres *et al*., 2017). The event of dry spell can be evaluated by following factors, for example, climate conditions, soil dampness, and yield condition over a specific developing season. In rice, the impact of dry season shifts with the variety, degree, and length of stress and its fortuitous event with various development stages (Ashok *et al*., 2021). Cell damage, inhibition of photosynthesis, osmotic adjustment, changes in gene expression, and metabolism are the general plant responses to drought stress**.** Under drought conditions, plants sense water stress signals and produce signal molecules, such as abscisic acid, Ca^{2+}, inositol-1, 4, 5-triphosphate (IP3), cyclic adenosine 50-diphosphate ribose, NO, etc... Directly or indirectly lead to the morphological and physiological changes of plants through signal transduction. Changes in morphology and physiology of rice under water stress are dependent on the duration of stress, the condition of rice growth. Morphological and physiological characteristics of the vegetative stage determine rice condition in the reproductive and maturation stage and yield. It is believed that drought stress mainly affects the absorption and transport of nutrients from roots to leaves. In a country like India where many regions lack basic irrigation facilities, severe drought can result in the loss of yield of important crops including rice. Among the abiotic stresses, drought stress is a major limitation to rainfed rice production and yield stability. Droughts have apparent yield impacts, especially if they occur during critical times of the rice growth cycle when plant development is highly sensitive to water requirements. Similarly, drought scans limit the amount of land that can be cultivated, as in the case of delayed monsoon (Sampath *et al*., 2022). Root morphological traits that facilitate growth under flooded conditions may vary under water stress conditions. The healthy growth of rice depends on the results of the collective effort of several environmental factors that affect its life. Plant responses to drought stress are very complex as stress itself involves various climatic, soil and agronomic factors, frequently complicated by variation in timing of occurrence, duration and intensity. Drought management strategies therefore need to focus on maximizing extraction of available soil moisture and the efficiency of its use in crop establishment, growth, biomass and grain yield.

Physiological Changes in Rice

The rice growth cycle has the germination stage, vegetative stage, and reproductive stage. Drought stress influences the physiological characters of rice. The high variability in the nature of drought stress made it difficult to identify specific physiological traits required for improving the crop performance under the drought condition, consequently limiting plant breeding efforts to enhance crop drought tolerance.

Seed Germination and Seedling Growth

The principal impact of drought stress is blighted germination and reduced growth. Seed germination needs appropriate temperature and soil humidity. Drought negatively affects germination process through inhibition of water uptake and reduces the strength of seedling. Drought stress causes trouble of water balance, and damages metabolic process at cell level impairment of membrane transport, and decreases ATP production and respiration, leading to poor seed germination.

Reproductive stage

Drought during vegetative growth, before the onset of flowering, can reduce yield by reducing the growth of photosynthetic and storage organs. Drought incidences during flowering will limit the viability of pollen, the receptivity of stigma, and the seed set (Barnabas *et al.,* 2008). Although drought affects all stages of rice growth and development, water stress during the flowering stage depresses grain formation (Boonjung and Fukai, 1996). The effects of drought on grain yield are largely due to the reduction of spikelet fertility and panicle exertion. The drought-induced inhibition of panicle exertion is due to a reduction in peduncle elongation, which usually accounts for 70% to 75% spikelet sterility under water deficit (Namuco, 1983). Drought stress during panicle emergence prevents peduncle elongation, obstructing exertion of spikelet and causing sterility. Relative water content decreases and abscissic acid (ABA) content increases during drought, which also results in the down-regulation of gibberellic acid (GA) biosynthesis genes. The ABA-GA antagonism is supposed to play a role in the failure of panicle exertions during drought (Muthurajan *et al*., 2011).

Grain Filling Stage

The rice quality is determined both genetically and environmentally (Krishnan and Rao, 2005). There is an increase of the head rice ratio in moisture stress condition. Therefore, the occurrence of drought during grain ripening stage could be considered as a useful factor that helps to reduce broken grain in milled rice with high level of head whole. The amylose content generally becomes lower in water stress conditions, but it may increase if the amylose content is very low. A negative correlation is present between amylose content and protein content in stress conditions. Protein content is also associated with grain quality traits such as head rice ratio, milled grain dimensions, milled grain appearance, viscosity parameters. The increase of protein content can improve the nutritional status of people. The protein content should be taken with care since it negatively correlates to rice taste (Ishima *et al*., 1974). Basmati rice grown under poor water supply conditions during grain filling time shows excessive abdominal whiteness in grains whereas these factors adversely affect cooking qualities. However, diminishing soil moisture at the time of grain filling is reported to favour the aroma formation.

Table 1: Physiological changes in rice during drought condition

S. No.	Parameters	Status	
		low	high
1.	Metabolism	✓	
2.	ATP production	✓	
3.	Respiration	✓	
4.	Seed germination	✓	
5.	Pollen viability	✓	
6.	Stigma receptivity	✓	
7.	Spikelet fertility	✓	
8.	Amylose	✓	
9.	Protein		✓
10.	Suberin		✓
11.	Stomatal conductance	✓	
12.	Stomatal closure		✓
13.	Gaseous exchange	✓	
14.	Carbon-dioxide	✓	
15.	Abscisic acid		✓
16.	Gibberellic acid	✓	
17.	Proline		✓
18.	Functional proteins (LEA, aquaporin, dehydrins)		✓
19.	Regulatory proteins (small regulatory RNAs, transcription factors, protein kinases)		✓
20.	Osmotic regulation		✓
21.	Osmolytes (sorbitol, betaine, inositol)		✓
22.	Turgor pressure	✓	
23.	Chlorophyll	✓	
24.	Photosynthesis	✓	
25.	Cutinisation		✓
26.	Leaf water potential	✓	
27.	Mesophyll conductance	✓	
28.	Reactive oxygen species (ROS)		✓
29.	ROS scavenging system	✓	
30.	Antioxidant (carotenoids, flavinoids, superoxide dismustase)		✓
31.	Cell membrane transport/stability	✓	
32.	Transpiration	✓	

Stomatal Conductance and Osmotic Regulation

Drought stress leads to stomatal closure leading to limitation of gaseous exchange. The closure of stomata is controlled by phytohormones such as abscisic acid, cytokinnins, etc. Reduction of water content reduces stomatal activity and cell growth. Osmotic regulation is generally considered to be the active regulation of cells to reduce osmotic potential by increasing solute. Organic osmotic regulating substances like amine compounds are usually of small molecular weight, highly soluble, and have little toxicity to cells. Osmotic regulation can maintain stomatal conductance to moderate water deficit by maintaining turgor pressure. It helps to keep the content of CO_2 in mesophyll intercellular space at a high level so as to avoid or reduce the photosynthetic inhibition on photosynthetic organs.

A research was done in Netherland were they have used six cultivars from *Oryza sativa*, one cultivar from *Oryza glaberrima* to analyse the leaf anatomical characteristics under three level of drought stress that is at control, mild and severe. The *Oryza sativa* represents the cultivars grown for lowland and upland cultivation systems. They have done pot experiment with pre germinated seeds. Variations were observed in stomatal conductance among both the species and within *Oryza sativa.* The stomatal conductance was decreased in IR64 than the other cultivars in *Oryza sativa* and CG14 in *Oryza glaberrima* (Wenjing Ouyang *et al.*, 2017). A research done by Farooq *et al.*, with IR64 under drought condition at 2010 has concluded that the leaf area, leaf number were reduced under drought condition so that the broader leaves results in better performance of indica rice in drought stress. Increase in the proline content is the initial response during water stress. Proline can maintain cell turgidity and membrane stability from damage. It can directly or indirectly influence growth and protect cells from oxidative stress. Proline influences osmotic adjustment and increases water uptake under water stress. (Zivcak *et al.*, 2017).

Suberization of Roots

Lowland rice roots have physiological response to drought stress. They have special features for their adaptation to grow in the flooded condition. The path of movement of water from the root surface to the xylem vessel has many potential barriers. The rice roots in well watered condition has a special feature in sclerenchyma layer that is much suberized than in the exodermis as it consists of tightly packed cells with lesser size than other cells in the outer part of the root system. The smaller cells together with the cell layers of the outer part if the root system in rice root form a barrier that reduces the radial oxygen loss (Colmer *et al.*, 1998) but does not restrict the water uptake.

To allow the cellular control of water and mineral ion uptake and transport via specialized transport proteins, plant roots contain a waxy layer of suberin that acts to seal connections between the cells, preventing uncontrolled leakage of water and ions between the cell. Roots actively regulate the creation of these structures, along the length of the root, and in the response to the environment. Suberization of the root system also results from water stress. Suberin is defined as glycerol based aliphatic polyester complex connected with cross linked polyaromatics and waxes. In response to drought there is an increased deposition of suberin which contributes to further decrease in root permeability. In drought, root resistant signaling is carried out based on ABA signaling, trehalose and sucrose sugars are also seen as major indicators of drought stress. The phenomenon of drought tolerance in roots is seen as the formation of suberization and development of roots.

Photosynthesis

Drought stress decreases the rate of photosynthesis by impairing pigments, photosystems, gas exchange, and key photosynthetic enzymes, thus affecting various steps in the photosynthetic pathway and this can ultimately reduce plant biomass and yield. Water is major constituent of plant tissue as reagent for chemical reactions and solvent for translocation of metabolites and minerals as well as an essential component for cell enlargement through increasing turgor pressure (Carlos *et al.*, 2008). The occurrence of soil moisture stress affects many of the physiological processes such as photosynthesis and transpiration resulting in reduced growth and poor grain filling (Samonte *et al.*, 2001). Alterations in various photosynthetic attributes are good indicators of a plant's drought tolerance as they show correlations with growth (Ashok *et al.*, 2022). Stomatal limitation was the main factor of photosynthetic rate decrease under mild drought. When water is deficient, it will lead to the decrease of photosynthesis directly through decreasing CO_2 availability resulted in diffusion limitations of the stomata and the mesophyll. Hydroponics experiments were done by Lei ding *et al.*, at 2017 to compare photosynthesis and water status in rice leaves under normal condition and drought stress stimulated by addition of 10%, 20% and 30% polyethylene glycol. The results show that there was a positive correlation with photosynthesis, stomatal conductance, mesophyll conductance, total conductance and chloroplastic CO_2 concentration. Under severe drought tress leaf water potential and water content were decreased and leaf water potential was positively correlated with stomatal conductance, mesophyll conductance and total conductance. Therefore, the stomatal closure during drought stress have led to reduced CO_2 concentration and the decreased leaf water potential will increase the internal CO_2 transport resistance, which are considered as the major limitations of photosynthesis.

Increasing chlorophyll will keep photosynthates rate to maintain growth rates (Kumar S *et al*., 2020). The increase in chlorophyll is due to the active nutrient uptake under water stress to support chlorophyll formation. Chlorophyll content in plants depends on availability of Nitrogen, Magnesium, ferrous, and Potassium to accelerate forms of chlorophyll (Taiz *et al.,* 1991). So there is a need to increase N, Mg, Fe and K in fertilizer management in water stress condition.

Drought induced proteins

Drought-induced proteins are synthesized in plants under drought which play a protective role in plant adaptation to stress and can improve plant drought tolerance. Drought-induced proteins can be divided into two categories according to their functions: (1) functional proteins, which play a direct protective role in cells, mainly include ion channel proteins, LEA proteins, OSM proteins, and metabolic enzymes (2) Regulatory proteins, including protein kinases, phospholipase C, phospholipase D, G protein, calmodulin, transcription factors, and some signaling factors, are involved in signal transduction in water stress and play indirect protective roles.Three important drought-inducible proteins are, Late Embryogenesis Abundant Protein, dehydrin and aquaporin.

Reactive Oxygen Species

When oxygen is not completely reduced in the metabolic process, a series of metabolites and their derivatives with more active chemical properties were produced, called reactive oxygen species (ROS). ROS include superoxide radical O_2^-, H_2O_2, singlet oxygen, hydroxyl radical ·OH, and organic oxygen radical (RO·, ROO·). Under normal conditions, the ROS produced in plants maintains a balance with its scavenging system. Drought can cause the increase of reactive oxygen free radicals and make plant cells suffer oxidative stress. When

ROS exceeds the capacity of the ROS scavenging system, it will cause the accumulation of ROS and oxidative damage.

In order to protect plants from ROS damage, there are endogenous antioxidant protection systems that are non-enzymatic antioxidants and antioxidant enzymes. The non-enzymatic scavenging systems of ROS in plants mainly include ascorbate, reduced glutathione, vitamin E, mannitol, carotenoids, and flavonoids. These substances can react as substrates of enzymes in the ROS scavenging mechanism. In addition, some small molecules such as vitamins are also involved in scavenging oxygen free radicals and preventing lipid peroxidation. Enzymes involved in antioxidant protection in plants mainly include SOD. The main function of SOD (superoxide dismustase) is to remove O_2^-, and can convert O_2^- to H_2O_2. SOD plays a key role in the enzyme system and is the first line of defense against ROS elimination system in plants.

Water deficit is the one of the most limiting factor that completely affects the crop productivity. Oxidative stress is regarded as a major damaging factor in the plants exposed to drought stress (Sgherri *et al.,* 1996). Research was carried out by Pallavi sharma and Rama Shankar Dubey at 2004 on drought induced oxidative stress and the activities of antioxidant enzymes in growing rice seedlings. Seedlings of two commonly grown rice namely Malviya 36 and pant 12 were taken, which were grown in pot culture in nutrient solution for 20 days. Due to application of mild as well as high drought stress there was a significant increase in superoxide anion production in roots and shoots of both the rice cultivars. The concentration of H_2O_2 was declined in the seedlings of mild drought stress. A decline in the H_2O_2 concentration of between 12 to 40% was observed in 20 days grown mild drought stressed rice seedlings compared to control seedlings.

Phytohormones

Phytohormones play a vital role in plant growth and metabolism. Drought stimulates abscisic acid (ABA) production in different plant organs, especially in the root, which can reach leaf guard cells and send signals through xylem transport and transpiration. ABA combines cytokinin (CTK) and jasmonic acid (JA) to regulate stomatal movement. They reduce the leaf transpiration rate and guard cell turgor pressure, which causes stomatal closure to adapt to external environments stress and ABA accumulation, also activates downstream signal components and enhances root antioxidant capacity to improve stress resistance. These results indicated that ABA could play an important role in plant cells receiving drought signals.

Rice variety MR219 from Malaysia was used for an experiment conducted on rice research centre at 2014, Serdang, Selangor, Malaysia which was treated with five phytohormone regimes they were control (without hormones), commercial products, Epibrassinolide, spermine, pyroligenous acid and three foliar sprays under drought condition. As a result the plant height, leaf area, root length, photosynthesis and yield were increased. Spermine shows better result in plant height, tiller and leaf number as well as grain yield which shows the rice variety MR219 is susceptible to spermine under drought. Efficient utilization of water and greater biomass production was enhanced by spermine treatment. Better plant growth and biomass allocation in spermine possibly involving physiological plasticity to drought (Shimzu *et al.,* 2010). Epibrassinolide and spermine cause better surface area, length and volume of root which improves the drought resistance capacity of the crop.

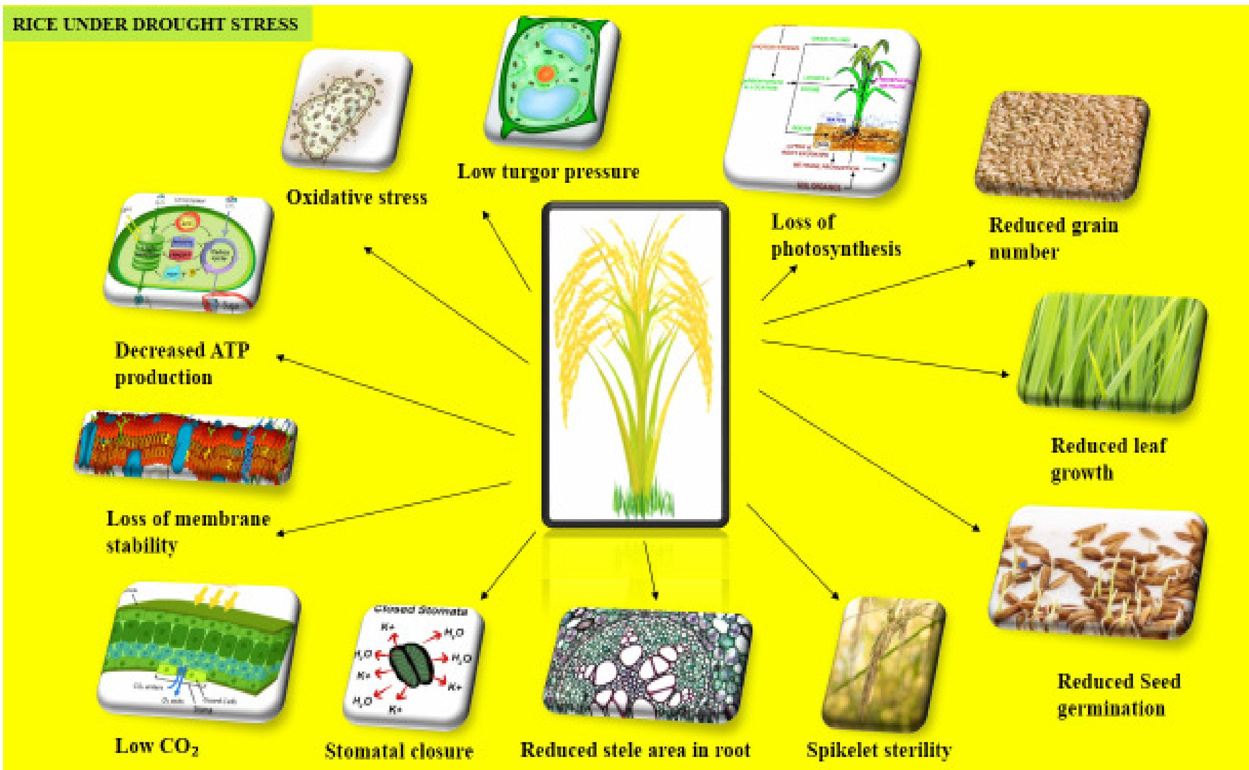

Fig. 1 : Changes in rice under drought stress

Morphological Changes in Rice

Drought stress is very important factor for plant growth and affects both elongation and expansion growth. Water deficit is one of the most environmental stresses affecting agricultural production and productivity around the world and may result in considerable yield reduction. Among the crops, rice is probably more susceptible to drought as compare to other crops. When plants are subjected to drought stress, they will first respond to changes in external form and internal structure. The most significant effect of water loss is that the plant grows slowly and even dies. The response of plants to water stress is mainly reflected in leaves and roots, and their external morphological characteristics and internal anatomical structure can best reflect the adaptability to adverse environments.

Table 2 : Morphological changes in rice during drought condition

S. No	Parameters	Status	
		low	high
1.	Plant height	✓	
2.	Leaf growth	✓	
3.	Leaf area index	✓	
4.	Tiller count	✓	
5.	Panicle exertion	✓	
6.	Peduncle elongation	✓	
7.	Grain filling	✓	
8.	Grain weight	✓	
9.	Grain number	✓	
10.	Head ratio of milled rice grains		✓
11.	Production of secondary roots		✓
12.	Thickening of leaves		✓
13.	Root length		✓
14.	Leaf rolling		✓
15.	Senescence		✓
16.	Shoot length	✓	

Plant Height

Drought can limit plant growth by inhibiting the cell division of leaf meristematic tissue and cell expansion in elongation areas, as well as inducing complex changes in leaf thickness, palisade tissue and spongy tissue during adaptation. Drought can affect soil chemical, physical and biological activities that are essential for plant and soil health. Impacts may include lack of nutrients uptake by vegetation, increased soil temperatures, altered microbial activity, changes in organic matter decomposition, and increased release of carbon-dioxide.

A research with a high yielding cultivar Neda from North Iran which was mutagenized with Ethyl Methyl Sulfonate, with two mutant lines MT58 and MTA one from M2 population with dwarfism and another a high yielding mutant line were evaluated for drought stress was done by Asodollah *et al*., 2016. The research shows that water stress significantly affected the plant height and plant yield. Severe water deficit compared with normal irrigation significantly decreased plant height (8 cm), total kernels per panicle (18 kernels), tiller number (2 tillers), and plant yield (12 g/plant).

Root

The root is an important organ for plants to fix and absorb substances from the soil. Drought stress reduces the stele area, vessel diameter and secondary root cortex cells and increases the number of vessels in the stele to facilitate water flow. To improve water retention and drought resistance, plants not only extend the root system by increasing the number of functional roots, but also increase the water-absorbing capacity of the root sheath. In tropical or subtropical regions when drought occurs after a rainy season, water saving strategies are required, whereas the use of deep rooting cultivars is suggested during summer dry storage to avoid an intermediate to high severity drought stress (Bodner *et al*., 2015)

Leaf Growth

Leaf growth is reduced due to limited water potential under drought stress. Disrupted flow of water towards another cell from xylem, including lower turgor pressure due to water deficiency, responds in form of poor cell development and diminished leaf area in crops. The anatomy of leaf and its ultra-structure are changed in drought stressed conditions. These changes are shrinkage of leaf size, reduction in number of stomata, bulky cell wall, cutinisation on leaf surface, and poor development of conducting system.

Table 3 : Internal changes in rice during drought condition

S. No	Parameters	Status	
		low	high
1.	Number of stomata	✓	
2.	Cell damage		✓
3.	Cell expansion	✓	
4.	Cell division	✓	
5.	Stele area in root	✓	
6.	Vessel diameter in root	✓	
7.	Number of vessels in root		✓

The leaf area development is considered to be more sensitive to water deficits than transpiration rate due to inhibition of leaf cell expansion or division by water stress. This is the consequence of the critical role of the turgor in the leaf cells expansion process (Hsiao *et al*., 1976). It significantly attributes to reduction in Leaf Area Index by the effects of translocation via altered source-sink relationships for assimilate. Large decline in leaf area under mild water stress is disadvantageous to plants because it leads to reduced nutrient uptake, because of reduced transpiration (Toole and De Datta, 1986). Reduced leaf area also decreases carbon assimilation per unit land area (Schulze, 1986)

Rolling of leaf and initiation of early senescence are other important characteristics seen under drought stress. Usually, senescence induced by water deficit shortens grain-filling period and can result in reduction in grain weight. When leaf temperature increases, the stomata become close and transpiration rate decreased sharply with leaf rolling. Leaf rolling scored visually in rice either in the morning or mid-day. Rice can anticipated water stress through the mechanism of escape, avoidance and tolerance. Avoidance is done by rolling the leaves to minimize the area of sun exposure to reduce transpiration (Kumar *et al*., 2020).

Yield reduction

Drought in general reduces the dry weight accumulation in all plant organs and shortens the life cycle of plants causing yield reduction (Blum, 2005; Kamoshita *et al*., 2008). Under drought stress, water use efficiency was strongly negatively correlated with tiller number. Water deficiency during flowering stage will drastically reduce the grain filling which gradually leads to yield loss. Yield loss has been attributed to the reduction in photosynthetic activity and lower supply of assimilates that support reproductive development and seed growth.

A pot experiment was conducted with rice genotypes swarnasub1, Nagina 22, NDR 102, NDR 97 and susksamrat during kharif season at UP, India by Sonamsingh *et al*., The results shows that the drought stress reduces the tiller number per plant in all rice genotypes. Maximum reduction in tiller number is recorded in Swarna Sub 1 (25.82%) while minimum in Nagina 22(8.76%).The number of tillers reduces due to reduced growth and photosynthesis processes of plant (Quampah *et al*., 2011).

Rice is more sensitive to drought with a larger reduction in yield. Molecular genetics have discovered many quantitative trait loci that affect yield under drought condition. The most important component responsible for biomass reduction of rice was the decrease in grain yield, which was followed by decrease in pH. Drought has an extremely adverse effect on meiosis and anthesis, which directly affects grain number. This causes a substantial reduction in grain yield. Moreover, pollen becomes sterile when drought occurs during the early microspore stage of pollen development, which would reduce the grain number. The grain yield of some rice varieties was reduced by up to 81 % under drought condition and thisreduction depended on timing, duration, and severity of the plant water stress (Pantuwan *et al*., 2000). Drought stress decreases the rate of photosynthesis by impairing pigments, photosystems, gas exchange, and key photosynthetic enzymes, thus affecting various steps in the photosynthetic pathway and this can ultimately reduce plant biomass and yield (Asharf and Harris, 2013).

Conclusion

Drought stress is the foremost and main constraint that severely causes the yield loss in the rice crop. It leads to many Morphological, Physiological, Biochemical, and Molecular changes in the crop. It greatly affects the Plant height, Leaf growth, Root anatomy, reducing the Panicle elongation, which gradually affects the grain number and causes yield loss. It also reduces the Stomatal conductance, Chlorophyll content which affects the Photosynthesis, increasing the rate of Reactive Oxygens species etc., Even though there are some adaptive measures in the crop to tolerate the drought stress, it is not supporting in eliminating the yield loss.

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