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RESEARCH ARTICLE

DROUGHT STRESS IMPACTS ON WHEAT AND ITS RESISTANCE MECHANISMS

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ABSTRACT

Scarcity of water has been a serious agricultural hindrance to crop productivity since antiquity. Drought-stressed loss in wheat yield likely exceeds losses from all other causes, since both the severity and duration of the stress are censorious. Here, we have reviewed the effects of drought stress on the morphological, physiological, and biochemical attributes along with the growth impacts, water relations, and photosynthesis impacts in wheat. This review also illustrates the mechanism of drought resistance in wheat. Historical drought years in Nepal have been identified and the yield losses were assessed. Wheat encounters a variety of morphological, physiological, biochemical responses at cellular and molecular levels towards prevailing water stress, thus making it a complex phenomenon. Drought stress affects leaf size, stems elongation and root proliferation, imbalance plant-water relations and decline water-use efficiency. Different types of physiological research are ongoing to find out the changes occurs in the wheat plant as a result of drought stress. Morphological changes can be looked through two ways: changes in root system and changes in shoot system such as effects on height, leaf senescence, flowering, and so on. Physiological changes involve changes in cell growth pattern, chlorophyll contents, photosynthetic disturbances, plant-water relations, etc. Biochemical changes occur in different chemical, biomolecules, and enzymes. Plants portray several mechanisms to withstand drought stress which can be classified as Drought escape, Drought avoidance, and Drought tolerance. Selection of wheat genotype that can tolerate water scarcity would be suitable for the breeding program aiming to development of drought tolerant variety under water limited regions.

KEYWORDS

Agronomic changes, Drought, Nepal, Resistance, Wheat.

1. INTRODUCTION

Wheat, *Triticum aestivum,* is one of the most widely cultivated cereals, particularly in the mediterranean region and other semi-arid regions from temperate to subtropical areas of the world (Ahmed et al., 2019). Most of the areas of land in which wheat is cultivated lie in arid and semiarid regions. A key determinant in the favorable outcome of wheat is its adaptation to a broad range of climatic conditions. Approximately, one-third of the global population uses wheat as a staple crop and also the first cereal crop in majority of the developing countries (Bayoumi, 2009). It serves as an essential food source, as it contains carbohydrates, dietary proteins, fiber, calcium, zinc, fats, and energy. However, in many countries, including Nepal the attainable yield hasn't been achieved through there is high potential of enhancing the average yield.

Wheat is mostly cultivated under rainfed conditions where fluctuations in rainfall pattern have caused water insufficiency to act as a determining factor for declining the crop yield, especially when water deficit stress occurs during the flowering and grain filling period stages (Bassi et al., 2017). The likeliness of drought stress in the coming days is high owing to global climate change and declines in availability of underground water resources for agriculture. It has been proved through many researches that wheat production is drastically affected by abiotic stresses. A study reported that for every 1-degree centigrade increase in temperature, there is a yield loss of about 4.1% to 6% (Liu et al., 2016). Salinity contributes to the reduction of wheat yield (Mujeeb-Kazi et al., 2019). On the other hand, drought is considered as major menace to wheat yield and is gaining much attention nowadays. By 2025 it is anticipated that nearly 1.8 billion people will face absolute water shortage and 65% of the world's population will face water-stressed environments (Nezhadahmadi et al., 2013b).

The factor limiting the wheat production in many regions is primarily due to erratic rainfall, reducing average yield up to 50% and often over. Wheat can be produced in a varied range of agro-climatic environments; nevertheless, most of these environments have drought stress as one of the major constraints to their production and yield. The predicted global warming and climatic fluctuations will increase the frequency of drought, therefore leads to the losses of the wheat yield. The increase in annual average temperature accompanied with fluctuations in rainfall patterns and arising drought risks in many regions have impacted agricultural

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productions, globally, which has brought limitations on crop yield potential. Declining underground water availability and rising temperature is assumed to worsen in coming decades (IPCC, 2013). Drought stress along with high temperature at reproductive stage (terminal growth phase of wheat crop) is prime contributing factor towards low wheat yield in tropics and subtropics.

Drought is a leading environmental stress declining the global cereals productivity, with up to half of the agricultural land prone to frequent drought (Ashraf and Fooled 2007). A rising problem of global warming is predicted to amplify the frequency and severity of drought in the near future (Yu et al., 2017). It can bring to the lack of water resources which influences morphological, biochemical, physiological, and molecular attributes of the plants. All of these changes retard the plant growth and the crop yield. Drought stress unfavorably alters the physiological and morphological parameters of crops. Along with the complexity of the drought itself, crop response to water shortage is even more complex because of unpredictable components in the environment and the interaction among biotic and abiotic factors (Nevo and Chen, 2010). Such stress leads to significant reduction in photosynthetic efficiency, stomatal conductance, leaf area and water-use efficiency of wheat (Farooq et al., 2019; Hussain et al., 2016).

Different researchers have performed study on drought resistance mechanism in many cereals, but the improvement of wheat for drought tolerance is limited for many constraints. There is a need to assess the response mechanism of the plants in response to drought stress. The objectives of the current study are to assess the possible changes in the morphological and physiological attributes of the wheat crop due to the drought stress and plant tolerance mechanism to the stress.

2. Drought Stress

Faced with inadequacy of water resources, drought is the distinct perilous hazard to global food security. It was the impetus of the great famines of the past. As the water supply is limiting worldwide, future food demand for rapidly increasing population pressures is likely to further aggravate the impacts of water stress. The severity of drought is uncertain as it relies on various factors such as quantity and quality of precipitation, evaporative demands, and soil moisture contents (Wery et al., 1994). There are various types of stress factors responsible for the reduction of wheat cultivation among which drought stress plays significant role for reducing the yield in wheat. About 50% of the cultivated land in the developing country is under rainfed condition (Paulsen, 2002). The scarcity of water which induces gradual morphological, biochemical, physiological and molecular changes is called as drought stress (Sallam et al., 2019). Due to drought stress, plant transpires less and in order to do so stomata of the wheat plant close to prevent water loss. And if stomata close for a long time there occurs an oxidative damage to the plant leaves tissue which affects the different physiological and biochemical activity of wheat plant.

Approximately 65 million ha of wheat production was affected by drought stress in 2013 (Nations, 2020). Different development stages of plant from germination, vegetative and reproductive stage to grain filling and maturation of crop are disturbed when the plant suffers from drought stress. Drought reduces the nutrient uptake efficiency including nitrogen as a main factor and nutrient utilization by plants. The reduction in nutrient uptake capacity is due to impaired membrane permeability and active transport and reduced transpiration rate resulting in decreased root absorbing power (Ahmad et al., 2018). Different types of research show that plant height, biomass and yield are more susceptible traits to drought stress in comparison with number of spikes and 1000 grain weight (Nouri-Ganbalani et al., 2009). For the development of stress tolerant plants, we have to know the adaptation methods used by the plant for surviving during drought stress. Knowing the importance of drought in wheat yield reduction, a number of researchers have been studying about the effect of drought and the number of problems caused by it. They are continuously trying to develop new drought tolerant genotypes which can perform well under stress conditions.

Drought (water stress) is one of the most crucial environmental stresses and occurs for various reasons, including erratic rainfall, salinity, fluctuating temperatures, and high intensity of light. It is a multidimensional stress and bring alteration in the physiological, morphological, biochemical, and molecular attributes in plants. Prolonged drought is a severe curb in landscape restoration in both arid and semiarid regions. There are numerous kinds of drought; meteorological, caused by a prolonged lack of rainfall; hydrological, caused by a scarcity in river flow; pedological, ascribed to a scarcity of water in the soil structure; agronomic, caused by a insufficiency of water available to plants in order to balance the physiological needs of evapotranspiration; and sociological, caused by competing consumptions to meet human and social needs. Landscape restoration can be drastically affected by all kinds, but notably by agronomic droughts, which negatively affect seedling establishment and crop stand establishment. Three major processes decline crop yield by soil water-deficit; decreased canopy absorption of photosynthetically active radiation, reduced radiation-use efficiency, and decreased harvest index (Earl and Davis, 2003).

Wheat has improved its tolerance mechanisms to withstand drought stress; however, these mechanisms are different and rely on the crop varieties and the cultivars. It is important to enhance the drought tolerance of wheat crops under the changing climatic conditions. To date, there are no efficient feasible technological mechanisms to promote crop production under drought stress environments. Yet, improvement of crop plants tolerant to drought stress might be a hopeful approach, which helps in maintaining the food security. Development of crops for increased drought resistance needs the sound knowledge of physiological and genetic mechanisms of the contributing traits at different plant developmental stages. Relevant research has been carried out on drought tolerance in wheat crops. Ingram and Bartels, more than a decade ago, excellently reviewed those appreciable efforts (Bartels, 1996). Similar reviews have been done by which deal with specific aspects of plant drought tolerance (Penna, 2003; Reddy et al., 2004; Agarwal et al., 2006).

3. Drought in Nepal

In regards to irregular climate change and higher temperature in recent years than that of global average, Nepal is considered to be among the most vulnerable countries. From 1975 to 2005, the global mean surface temperature rises by 0.6 ^{0}C while Nepal experienced a significantly higher temperature rise of 1.5 ^{0}C during similar duration of time, from 1982 to 2006 (Biwa et al., 2012). Likewise, rainfall pattern is also becoming more unpredictable (Wang et al., 2013). Consequently, average rainfall has been declining by 3.7 mm (−3.2%) monthly, per decade (Ministry of Education, 2010). These ultimately created drought condition particularly for the rainfed farming, where farmers depend on monsoon rainfall for their major agricultural activities (Ghimire et al., 2010). Furthermore, the mean annual temperature is estimated to be rose between 1.3 ^{0}C to 3.8 ^{0}C by the 2060s, and 1.8 ^{0}C to 5.8 ^{0}C by the 2090s and annual precipitation declination could be within the range of 10% to 20%, across the country (Ministry of Education, 2010).

In Nepal, drought usually happens from March through June, which is the onset of monsoon and winter precipitation has almost declined to zero, also groundwater has hardly been replenished (Joshi, 2018). Some areas of the trans-Himalayan regions are intensely dry tall through the year and droughts occur often in the lowland of Terai and in the western hill of Nepal. Nepal faced drought in 1972, 1977, 1982, and 1992. The country has tackled incessant dry spells since 2002, particularly during the years 2002, and from 2004 to 2006—in monsoon (Joshi, 2018). Different incidences of drought were also noticed during 2012, 2013, and 2015. Drought in Nepal have created panic in the hill farming system, generally for crop production and the livelihood support of farmers dependent on it. However, droughts can generate opportunities to learn different adaptations strategies that are appropriate in such changing circumstances (Dulal et al., 2010).

Table 1: Major cereal loss in different drought years

S.N	Drought years	Causes of Drought	Major cereal loss (in Metric Ton)	Affected regions
1	1972	Late onset of monsoon/rainfall	333,380	Eastern and Central
2	1976	Poor distribution of rainfall	218,480	Western
3	1977	Late onset of rainfall	322,320	Eastern and Central
4	1979	Late onset of rainfall	544,820	Western
5	1982	Late onset of rainfall	727,460	Eastern
6	1986	Poor distribution of rainfall during August and September	377,410	Western
7	1992	Late onset of rainfall	917,260	Eastern
8	1994	Poor distribution of rainfall	595,976	All regions
9	1997	Poor distribution of rainfall	69,790	Eastern
10	2002	Poor distribution of rainfall	83,965	Eastern and Central
11	2008	Poor distribution of rainfall during November 2008 to February 2009	56,926	All regions
12	2009	Late onset of rainfall	499,870	Eastern and Central
13	2012	Summer monsoon late onset and long dry spell	797,629	Eastern and Central
14	2013	Inadequate rainfall that affected wheat plantation	56,000	Eastern and Central Terai districts
15	2012	Delayed monsoon and weak at the onset, which delayed paddy transplantation	not available	Eastern Terai
16	2015 to 2016	Poor monsoon and drought	30,000 people highly insecure	Mid and Far-Western hills and mountains

Source: (Joshi, 2018)

Table 1 depicts the major drought years in Nepal, main causes of drought, and damages on chief cereal crops. But this is not the comprehensive data, and many of the database are still be missing. The major elements determined for the drought are delayed onsets of monsoon, irregular rainfall pattern, and decreased intensity of rainfall. For example, late onset of monsoon likely led to a delay in the sowing of rice, impacting the growth of wheat, along with reducing the volume of underground water (Joshi, 2018).

4. Effects of Drought on Wheat

The impacts of drought stress may range from morphological to molecular levels and are detrimental to all physiological performances of plant. An account of various drought stress effects and their extent is elaborated below.

4.1 Morphological Changes

As a response of drought there occur various morphological changes in wheat crop which can be directly observed throughout the different stages of plant growth. Generally, the morphological response of wheat can be categorized into two parts i.e. shoot part and root part. The shoot part contains changes in leaf shape, leaf expansion, leaf area, leaf size, leaf senescence, leaf pubescence, leaf waxiness, cuticle tolerance and reduction in shoot length. And the lower root part includes changes in root dry weight, root density, and root length (Denčić et al., 2000). Several studies have shown that the correlation between morphological traits such as grain yield per plant, grain spike per plant, spike fertility and plant height were considered as a reliable indicator for screening drought tolerant wheat cultivars. Researchers found the positive correlation between leaf area, plant height and grain yield. In conclusion we came up with the various morphological changes like decreased plant size, early maturity, decreased leaf area, reduced yield, limited leaf extension, small leaf size, reduced number of tillers, reduced leaf longevity, reduced total shoot length, decreased plant height, increased in leaf rolling and reduction in plant biomass in wheat as a response to drought stress. Among these various morphological responses some of major responses are discussed below.

4.1.1 Changes in Plant Height

The most common effect of water stress is defective germination and poor crop establishment (Harris et al., 2002). Drought has been proved to immensely impaired germination and seedling stand. The quality and quantity of crop stand rely on these events, which are affected by water deficit (Figure 2). Cell growth is an important drought-sensitive physiological process due to the decline in turgor pressure (TaizandZeiger, 2006). Under serious water shortage, cell elongation of wheat can be altered by interruption of water flow from the xylem to the surrounding elongating cells (Nonami, 1998). Drought affects the growth of wheat plant. Wheat is a plant which is very sensitive to water stress condition and shows drastic change in growth of plant when exposed to these types of situations.

However, the duration, time, magnitude of drought and stage of wheat plant also determines the effect of drought stress. Different experiments have been carried out at different developmental stages like stem elongation, booting, grain filling of wheat plant and results shows that the plant facing drought stress start from stem elongation stage suffered more as compared to others. Plant height was reduced by 35% and 23% at stem elongation stage and booting stage respectively while the plant height was only reduced by 7% at grain filling stage (Caverzan et al., 2016a). Similarly, reduction in the root and shoot growth of wheat when exposed to drought conditions is reported by many other researchers also (Azooz and Youssef, 2010; Farooq et al., 2013). Hence drought is one of the major factors responsible for overall decrease in growth of wheat plant.

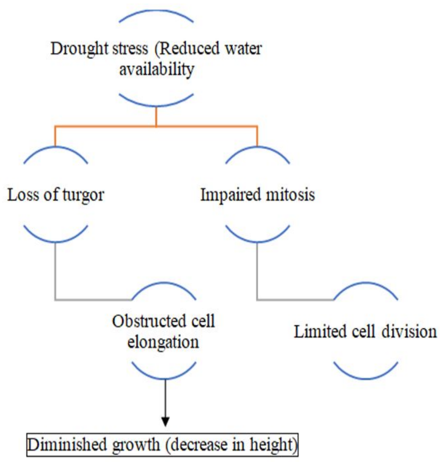

Figure 1: Drought effect on growth of wheat

Figure 1 illustrates the mechanisms of growth impact under drought stress. Under water stress conditions, cell elongation in wheat is retarded by fall in turgor pressure. Less water uptake leads to a decrease in tissue water contents. Consequently, turgor is lost. Similarly, drought stress also lowers down the metabolites required for cell division. As a result, impaired mitosis, cell elongation and expansion result in reduced growth.

4.1.2 Leaf Senescence

A study reported that if drought occurs during reproduction stage, the rate of senescence increases as a result of drought stress which causes the remarkable reduction of grain yield (Nawaz et al., 2013). There occurs a change in leaf color due to breakdown of chlorophyll membrane and water content when the function of leaf deteriorates. Chlorosis leading to decrease in photosynthesis is one of the vivid signs of leaf senescence (Ali et al., 2020). Wheat growing in extreme drought conditions can cause senescence to the whole plant but it also enhances the mobilization of stored carbohydrates during parenthesis from the stem and leaves to developing grains and help in compensating the loss of yield caused by senescence during drought stress (Farooq et al., 2014). The amount of total protein content, glutamine synthetase and rubisco (Ribulose Bi-Phosphate Carboxylase) was used to indicate the beginning and stages of senescence in wheat. In most of the cases senescence occurs first in older leaves and then in younger leaves. But in some sensitive varieties, the sequence of senescence is disturbed due to drought and first occurs in flag leaves and later on older leaves. It is found that in younger leaves the amount of glutamine synthetase isoenzyme declined considerably and the sequence of senescence were disturbed slightly as compared to plants growing in sufficient water conditions (Nagy et al., 2013). In conclusion, the leaf senescence of wheat is correlated with drought and by monitoring the carbon and nitrogen metabolism, we can achieve progress in making drought sensitive genotype of wheat to make them tolerant.

Figure 2: Impacts of drought on leaf (Source: Agrilife, 2015)

4.1.3 Changes in Root System

Plant root obtains nutrients and water from the ground and plays an important role during the condition of drought also. When there is scarcity of water resources plant root goes deep into the soil in order to absorb water from the soil. Many researchers have reported that the volume, weight, length and density of root are interrelated with resistance of water scarcity in crops. In order to survive against drought conditions, the architecture of the root system is considered very important as the good architecture of wheat extracts maximum soil water under drought stress and also improving the yield of the grain (Dodd et al., 2011). The adaptive mechanism shown by wheat in order to fight against drought stress are osmotic adjustment of root, increase root penetration to the soil, increased root density and root increase root to shoot ratio (Ali et al., 2020).

When there is scarcity of water root growth is favored over shoot growth. If there is reduction in the water potential, osmotic adjustment in the root helps to maintain level of turgidity up to some level and the water potential gradient is re-established for water uptake. The formation of lateral root also increases during drought stress in order to increase surface area for water absorption. Similarly, there is increase in cross-section diameter which helps in maintaining water retention in vascular bundles of wheat. Also, there is increase in sclerenchyma cell diameter and decrease in aerenchyma cell formation during drought stress (Henry et al., 2012). So, during breeding programs, genotypes with improved root systems are used for increasing yield because they can utilize the deep underground water more properly to survive against drought stress.

4.2 Physiological Changes

Numerous physiological responses have been determined in response to drought stress. There are many physiological attributes that reduces the effect of drought stress on wheat crops. There is a direct relationship between the availability of water and performance of different physiological processes of plant. When there is reduction in the water availability, these physiological processes are disturbed and plants are unable to produce sufficient amount of dry matter. Studies have shown that during drought condition there is reduction in the plant nutrient uptake, plant growth rate and height as well as photosynthetic activities and dry matter production (Todaka et al., 2015; Barbeta et al., 2015; Ashraf and Harris, 2013). Deficiency of water also leads to decrease in chlorophyll contents, reduction in the water content and membrane stability (Sallam et al., 2019).

Due to the drought stress, there is a need to make some physiological changes in the plant in order to alleviate the effect of drought stress (Vinocur and Altman, 2005). For surviving the drought situations, plant have to adapt itself in this situation and for this there is a development of many tolerant genotypes which helps to maintain the soluble sugars, proline content, amino acids, chlorophyll content, enzymatic and non-enzymatic antioxidant activities as well (Abid et al., 2016). The modifications done during the breeding process of these tolerant variety help to alter the normal physiological process of wheat and performs its normal functions on water deficit conditions. For obtaining this, wheat plant undergoes different adjustments like change in amount of antioxidant production, proline content, osmotic adjustment, hormone composition, opening and closing of stomata, cuticle thickness, root depth, loss of chlorophyll and decrease in transpiration (Rosenberg et al., 1990; Zhu, 2002).

Different types of research have been done so far in order to understand the physiological response of wheat to drought stress. A group researcher observed that transpiration decreased significantly due to drought stress and then heat can slowly be lost from the leaves and leaf temperature can be increased (Rosenberg et al., 1990). And due to this, there is increase in CO_2 concentrations and photosynthesis which affects plant growth and finally water use efficiency can be improved. These different types of drought tolerance mechanism of plant help in understanding the physiological response that helps to maintain the growth and productivity during stress period. Similarly, these traits are also responsible in breeding programs in order to develop drought tolerant varieties which can perform well under those regions of the world which have scarcity of water resources.

4.2.1 Changes in Cell Growth Pattern

Wheat is very sensitive to water stress condition and shows drastic change in growth of plant when exposed to these types of situations. However, the duration, time, intensity of drought and stage of wheat crop also determines the effect of drought stress. Different experiments have been carried out at different developmental stages like stem elongation, booting, grain filling of wheat plant and results shows that the plant facing drought stress start from stem elongation stage suffered more as compared to others. Plant height was reduced by 35% and 23% at stem elongation stage and booting stage respectively while the plant height was only reduced by 7% at grain filling stage (Caverzan et al., 2016a). Similarly, reduction in the root and shoot growth of wheat when exposed to drought conditions is reported by many other researchers also (Azooz and Youssef, 2010; Farooq et al., 2013). Hence drought is one of the major factors responsible for overall decrease in growth of wheat plant.

Moreover, the duration, type, and magnitude of drought and the stage of plant growth also regulate the possible changes. A large body of literature is available on the growth stage and tolerance level of wheat cultivars under drought stress. Plant growth is also varied with duration and type of drought. Shamsi and Kobraee conducted a two-factor experiment with three wheat cultivars and three different stages of wheat growth (Shamsi and Kobraee, 2011). Drought stress was imposed at stem elongation, booting, and grain filling stages and continued up to harvest.

Results showed that plants facing water stress from stem elongation stage suffered more compared to other two stages of plant growth. Plant height was reduced by 35% and 23% in plants facing drought from stem elongation stage and booting stage, respectively, but only by 7% in plants exposed to drought at grain filling stage. Almost similar findings were reported, by who initiated drought at Moreover, the duration, type, and magnitude of drought and the stage of plant growth also regulate the possible changes (Akram, 2011). A large body of literature is available on the growth stage and tolerance level of wheat cultivars under drought stress. Plant growth is also varied with duration and type of drought. Some researchers conducted a two-factor experiment with three wheat cultivars and three different stages of wheat growth (Shamsi and Kobraee, 2011). Drought stress was imposed at stem elongation, booting, and grain filling stages and continued up to harvest. Results showed that plants facing water stress from stem elongation stage suffered more compared to other two stages of plant growth.

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4.2.2 Change in Chlorophyll Content and Photosynthetic Rate

With reduction in the volume of available water, plant closes their stomata (plausibly via ABA signaling), which reduces the CO_2 influx. Reduction in CO_2 not merely decreases the carboxylation directly but also directs more electrons to form reactive O_2 species. Serious drought stress restrict photosynthesis due to the reduction in the activities of ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase (PEPCase), NADP-malic enzyme (NADP-ME), fructose-1, 6-bisphosphatase (FBPase) and pyruvate orthophosphate dikinase (PPDK). Lowered tissue water contents also enhance the activity of Rubisco binding inhibitors. Chlorophyll is a green pigment and is responsible for the photosynthetic process. Mainly there are two types of chlorophyll found in wheat i.e. chlorophyll a and chlorophyll b. The ratio between chlorophylls a and b is generally 3:1 depending upon cultivars, plant growth, and various environmental factors (Ahmad et al., 2018). Many researchers and scientists have reported that whenever wheat plant goes through drought stress, there is significant reduction in the leaf chlorophyll content (Fotovat et al., 2007).

The effect of this stress is more in the chlorophyll b and the number of chlorophyll b has decreased to more extend as compared to chlorophyll a. This is explained by the fact that the part of the decrease in chlorophyll a could be because of conversion to chlorophyll b (Fang et al., 1998). Scientists have found that when wheat plant is exposed to light there occurs enzyme activation reaction of chlorophyll synthesis which increases the chlorophyll content in young leaves but the chlorophyll content decrease by 13-15% in older leaves due to activation of chlorophyllase and inactivation of enzyme under drought condition (Nikolaeva et al., 2010). As the drought stress damages the chlorophyll components there occurs change in the photosynthetic machinery which resists the photosynthesis. Different studies have shown that there is decrease in the photosynthesis of cereal crops because of the drought stress. Electron transport chain is also affected by drought stress which ultimately results for the production of ROS that are harmful for plant cells and organelles like mitochondria, chloroplast and perioxisomes (Farooqi et al., 2020).

ROS is also responsible for reduction of chlorophyll from the leaves. This changes the inner structure of chloroplast, mitochondria, chlorophyll content and minerals. As a result of imbalance between the light capture and its utilization there is metabolic distortions of photosynthetic activities, decrease in Rubisco activity, reduction of chloroplast membranes, degradation of chloroplast structure and photosynthetic apparatus, chlorophyll photo-oxidation, loss of chlorophyll substrate, inability of chlorophyll biosynthesis, and the increase of chlorophyllase activity (Kabiri et al., 2014; Kingston-Smith and Foyer, 2000). Some of the major components limiting photosynthetic rate is CO_2 diffusional limitation due to early stomatal closure as a response to the drought induced loss of turgor, reduced activity of different photosynthetic enzymes, decrease of biochemical components which help in the formation triose-phosphate and most of all there is reduction in the photochemical efficiency of photosystem II (Pandey and Shukla, 2015). The decrease in photosynthetic amount under drought condition is a result of inhibition of RuBisCO (ribulose-1, 5-bisphosphate carboxylase/oxygenase) enzyme activity and development of ATP (Dulai et al., 2005).

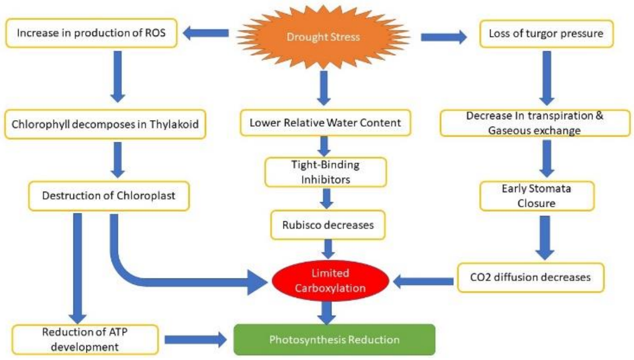

Figure 3: Effect of Drought on Photosynthetic activity.

4.2.3 Membrane stability

Biological membranes are the first and foremost target of different abiotic stresses. It is assumed that the maintenance membranes stability under water stress is a major element of drought resistance in crops. The membrane integrity is changed by drought stress. A plausible explanation of this is the rise of the cell permeability accompanied by electrolyte leakage from the cell. Drought has a huge effect on the plant cell, damaging the selective permeability of the plasma membrane. As a result of drought stress cell membrane stability (CMS) depicts the ability of plant tissue to prevent electrolytes leakage by keeping the cell membrane in safe mood (Larson et al., 1971). Measurement of solute leakage from the plant tissue was used to estimate the damage to the cell membrane caused by drought and heat under field conditions. The MSI (Membrane Stability Index) is highest i.e. 82.1% in drought susceptible varieties compared to moderately tolerant i.e. 79.4% and tolerant one i.e. 80.4% at vegetative stage, however no differences were recorded between tolerant and moderately tolerant varieties but at anthesis stage moderately tolerant varieties showed lowest MSI values i.e. 75.7% and the highest value were recorded in drought tolerant varieties i.e. 78.8%, in general MSI decreased as plant advanced in age (Almeselmani et al., 2012). Due to the drought stress, there is loss of water from plant tissues which affects the both membrane structure and function. A group researcher found that there is a correlation between electrolyte leakage and drought and the leakage was caused due to damage of cell membranes which becomes more permeable (Martin et al., 2006). Drought stress affects the plant more having lower CMS value than those genotypes which have higher CMS values (Mehraban and Miri, 2017). The genotypes having less than 50% values are highly susceptible to drought while the genotypes with 71-80% values are considered to grow with full potential under drought condition (Mehraban and Miri, 2017). A group researcher reported that under drought condition cell membrane stability (CMS) have positive relationship with tiller per plant, grain yield but negative relationship with 100 kernel weights (TGW) (Farshadfar et al., 2011).

4.2.4 Relative Water Content (RWC)

Relative water content, leaf water potential, stomatal tolerance, transpiration rate, and leaf temperature are important attributes that influence plant-water relation. Relative water content in leaves of wheat was more initially during leaf development and reduced as the leaf matured (Siddique et al., 2001). Undoubtedly, drought stressed wheat crops had lesser relative water content than non-stressed ones. Exposure of these crops to drought stress significantly reduced the leaf water potential, relative water content and transpiration rate, with a substantial rise in leaf temperature (Siddique et al., 2001). Among the different types of water potential leaf RWC is considered as more important parameter under water deficit conditions. Due to the drought stress, there is significant reduction in the RWC of wheat during its development stages.
The effect of drought is more in later stage (after 6 weeks of emergence) and effects on water relations, nutrient uptake, growth, and yield than in early stage (after 3 week of seedling emergence) in wheat (Nawaz et al., 2014). As a result of drought stress there is reduction in water status during crop growth, soil water potential and plant osmotic potential for water and nutrient uptake which ultimately reduce leaf turgor pressure which results in upset of plant metabolic activities (Mehraban and Miri, 2017). Excised leaf water retention (ELWR) is enhanced by drought stress which reflects the water retention mechanism in the leaf under stress that may cause leaf rolling or decrease in exposed leaf surface area. Many researchers have found that there is continuous variation in the relative water content during drought stress because it is controlled by multiple genes with additive effect.

High turgor potential and relative water content is maintained by drought tolerant genotypes to signify water had a little effect on their protoplasmic structures as compared to sensitive genotypes which represent a highly positive correlation between water content and photosynthetic rate (Moayedi et al., 2010). The final impact of lower relative water content is reducing in water status and osmotic potential in plants. Under water deficit conditions, maintenance of leaf turgor pressure is a crucial adaptive mechanism that plays a remarkable role in stomatal regulation and photosynthetic activities. For the preservation of turgor pressure osmo-regulation plays an important part which help in the absorption of soil water and helps in plant metabolic activities for its survival (Mehraban and Miri, 2017). Total grain yield per plant, biological yield per plant and harvest index of wheat has a positive correlation with relative water content (Abdul et al., 2010). Hence relative water content is a useful parameter for selecting drought tolerant wheat genotypes (Hasheminasab et al., 2012).

4.3 Biochemical changes

Wheat crops are provided with internal defense mechanism equipped with antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POX) for ROS scavenging under stressed conditions (Chen et al., 2012). Therefore, water stress contributed to the drastic changes in the biochemical attributes of the wheat plants as described below:

4.3.1 Proline Content

Proline can be defined as one of the major amino acids which is used in the biosynthesis of proteins. The response of wheat to water stress by accumulating proline is a useful tool to understand the mechanisms of drought tolerance. The accumulation of some organic compatible solutes in wheat which adjust the intercellular osmotic potential is highly affected by drought stress. As there is accumulation of organic compatible solutes it increases the solute potential of plant which prevents loss of water (Naeem et al., 2015). Due to the lack of water, wheat plant accumulates proline content in larger extend than any other osmoregulators (Maralian et al., 2010). It is reported that there is increase in the proline content of wheat plant after it had been subjected to drought stress (Vendruscolo et al., 2007). It is found that the maximum amount of proline increases in heading stage of wheat when it is under water stress condition (Maralian et al., 2010). The genotypes of wheat which have more accumulation of proline under drought have the ability to bear drought stress and it is different for different wheat genotypes because different genotypes have variable water stress threshold. Hence the estimation of proline content of wheat can be a useful trait for selecting drought tolerant wheat genotype.

4.3.2 Antioxidant Properties

Due to the drought stress, there is accumulation of reactive oxygen species (ROS) in the cells, which can cause severe oxidative damage to the plants which inhibits the growth and grain yield of wheat plant. The equilibrium between the production and scavenging of ROS is knows as redox homeostasis (Caverzan et al., 2016a). However, if the production of ROS exceeds the cellular scavenging capacity, it creates the unbalancing of the redox homeostasis which results in rapid and transient excess of ROS, known as oxidative stress (Sharma et al., 2012). Therefore, plants have antioxidant mechanisms for scavenging the excess ROS and prevent damage to cells. Enzymatic and non-enzymatic antioxidants are responsible for maintaining the equilibrium between the production and detoxification of ROS (Mittler, 2002). In wheat, several studies have showed that there is change in the activity of the antioxidant defense system in plant to control the oxidative stress induced by many environmental factors like drought.

There is activation of both enzymatic and non-enzymatic system which is used to detoxify the toxic levels of ROS which is harmful to plant produced as a result of drought stress (Caverzan et al., 2016b). Different studies have showed that the responses of these enzymatic and non-enzymatic systems vary with different genotypes, Different genotypes shows different responses under same condition. Generally tolerant genotypes show higher antioxidant capacity resulting in lower oxidative damage to the plant. This response also depends upon several others factors like tissue type, length, and intensity of the stress as well as on developmental stage proving the complexity of the mechanism of production and detoxification of ROS and the effect of ROS on antioxidant system (Caverzan et al., 2016a). Hence having the information about the antioxidant response of wheat during drought stress, it helps us to develop different improved genotypes having more antioxidant properties.

5. RESISTANCE MECHANISM OF DROUGHT STRESS

Through the induction of different morphological, biochemical, and physiological responses, wheat crops respond and adapt to and survive under severe drought stress conditions. Drought stress disturbs the water circulations at different levels, causing unwanted reactions and finally adaptation reactions (Beck et al., 2007). To survive under such conditions, susceptible plants have defense mechanisms against drought stress, which need to be studied comprehensively. As a result of drought stress, there occurs a rapid loss in the yield and yield performance of wheat. The different process which occurs in plant in order to suppress the stress in the given condition and producing the higher yield as compared to normal water availability conditions is known as drought resistance. According to the agriculture point of view drought resistance can be defined as the process in order to minimize the loss of economic yield under limited water availability conditions (Bohnert et al., 1995). Generally, there are 3 different forms of drought resistance i.e. drought escape, drought avoidance and drought tolerance (Bohnert et al., 1995).

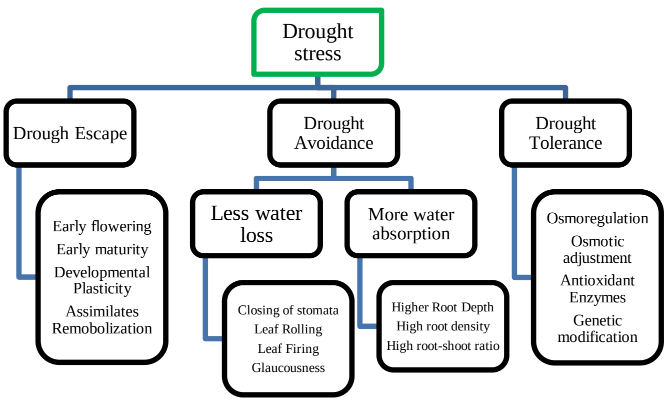

Figure 4: Resistance mechanism of Drought Stress

5.1 Drought Escape

The process of shortening the life cycle or growing season of plant in order to avoid the dry environmental conditions is known as drought escape. The condition required for drought escape is, when the phenological development is successfully matched with periods of soil moisture availability and it occurs when the growing season is reduced and terminal drought stress prevails (Araus et al., 2002). In order to achieve drought, escape we can use different process like early maturity, developmental plasticity, assimilate remobilization (Vani et al., 2017). Among these various factors, early maturity of wheat is considered as one of the major aspects for escaping the drought stress. For obtaining early maturity we have to reduce the developmental time at different growing stages of wheat. Among different stages, shortening of time at flowering stage is considered as one of the most effective time for escaping drought (Shavrukov et al., 2017). Through selection of different genotypes of wheat having early flowering behavior, their vegetative growth can limit and enables the reproductive growth to occur before the terminal stress (Bodner et al., 2015). Early flowering and maturity can be considered as an effective mechanism for drought escaping however it has some drawbacks and can limit the grain yield potential due to reduction in time for photosynthesis and seed nutrient accumulation required for higher grain yield (Bidinger and Witcombe, 1989; Radhika and Thind, 2014).

5.2 Drought Avoidance

There are numerous ongoing physiological and metabolic activities on the plant which are not exposed to drought stress and are continuously performing their normal functions even in the water deficit conditions. The ability of plant to maintain relatively higher content of water in tissue of plant despite the fact of having lower water content in the soil is known as drought avoidance (Levitt and others, 1980). It helps to control the water loss by controlling stomatal transpiration and also maintain water uptake through an extensive and deep root in the soil. During the drought condition wheat maintains its water status by closing their stomata. In contrast, there are some negative effects on photosynthesis and respiration as a result of stomata closing. Moreover, there occurs a leaf rolling in response to drought in order to save water content in plant which later unrolls when the leaf-water relations of plant improve (Sirault et al., 2015). It has been reported that the epi-cuticular wax layer of wheat also called as glaucousnessis also responsible for maintaining the leaf-water relations during the drought stress and is considered as important trait for drought avoidance (Richards et al., 1986). Drought avoidance is also influenced by several root characters like root length, root density and root biomass (Kavar et al., 2008). Greater thickness of root, higher root depth and higher root density are responsible for excessive water uptake during drought stress (Aina and Fapohunda, 1986). Hence there are various characters of plant like stomatal transpiration, glaucousnessis, leaf rolling and different structural and functional aspects of root are responsible for avoidance of drought under stress conditions.

5.3 Drought Tolerance

The ability of plant to maintain their growth and development during water deficit conditions is known as drought tolerance. Drought tolerance is a complex mechanism and plants modify its different physiological and biochemical factors to fight against the water deficit conditions in order to maintain its normal growth and yield capacity. Different studies have shown that osmoregulation, osmotic adjustment and activity of antioxidant enzymes plays a vital for dealing with the drought stress situation in plants (Nemeskéri and Helyes, 2019). In order to fulfill the increasing demand of food for growing population it is must to develop the more advanced wheat tolerant genotypes. Thus, the main aim of the drought related research program is to identify such genes which can be used in the breeding program in order to develop new more drought tolerant genotypes of wheat. Drought tolerant variety of the wheat have some modifications over the normal physiological and biochemical processes in order to survive in the water deficit conditions. Drought tolerance mechanism involves the activation of different physiological and biochemical processes at cell, tissue, organ and whole plant level. Some of the major fields for genetic modifications of wheat in order to obtain drought tolerant variety are in table 2.

Table 2: Modification field for improving wheat resistance

S.N	Field for genetic modifications
1	Drought-Induced Gene Expression/Single Action Gene
2	Osmo-protectants, Metabolites and Protective Genes
3	Transporter Genes
4	Carbon Metabolism
5	Transcription Factors
6	Post-Translational Modification
7	Protein Kinase
8	Nuclear Factor

Source: (Khan et al., 2019)

Until now, different studies have been done in order to exploit the genes that are responsible for drought stress and have been categorized through RNA sequencing and the Affymetrix GeneChip technology (Dugas et al., 2011). Researchers found that different types of kinase likeCDPKs (calcium-dependent protein kinases), CIPK (CBL interacting protein kinase), and SnRK2 (sucrose non-fermenting protein-related kinase 2) and MAPKs (mitogen-activated protein kinases) also shows some response to drought stress (Malone and Oliver, 2011). There is a correlation between the drought and antioxidant system and shows positive response towards it. Reports suggested that reactive oxygen species (ROS) like OH (Hydroxide), H_2O_2 (Hydrogen Peroxide), SOD (Super Dioxide) and oxygen which is singlet are created in drought conditions (Nezhadahmadi et al., 2013a). Some of the studies shows that wheat genotype having lower malondialdehyde (MDA) content and greater osmotic regulator has helpful for obtaining tolerance against drought (Nezhadahmadi et al., 2013a). All these parameters have important role in drought tolerance and it can be useful for selecting drought tolerant varieties and lines particularly at reproductive stage (M. Almeselmani, 2012).

6. Conclusion

Different years of drought in Nepal have been identified and the impacts of those stresses on crop production have been assessed. Historical evidences have shown that there was a huge loss in crop yield in the past. Drought stress retards crop growth and development, leading to the changes in morphological, physiological, and biochemical attributes of the crop. Since majority of the global wheat cultivation area lies in arid and semi-arid regions, drought is one of the major problems for obtaining the potential yield. It reduces the proper growth and development of plants hampering fruiting and grain filling which eventually leads to reduced size and number of wheat grains. Injury biochemical reactions under drought stress are among the major deterrents to growth. Due to this reason, there is great economic loss in the production of wheat all around the world. For improving yield under drought condition, it is essential to understand the physiological response of wheat under these situations. Various resistance mechanisms have been developed in the plants to cope with drought stress. CO_2 assimilation by leaves is decreased primarily by stomatal closure, membrane damage and disturbed activity of various enzymes, especially those of CO_2 fixation. By understanding the physiological, morphological, and biochemical responses of wheat under this situation, it helps us to identify drought tolerance mechanism and develop drought tolerant varieties of wheat.

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