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Impacts of water-logging in maize and mechanisms of water-logging tolerance

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ABSTRACT

Maize is a major cereal crop and staple food crop in the mid-hills of Nepal and majorly grown as a rainy season crop. The crop experiences water logging resulting in hypoxia and anoxia. A few varieties of maize is seen tolerant to water logging. Thus, a pot experiment was performed to study the effects of water-logging on the different stages of different maize varieties in a Completely Randomized Design. Varieties used in the experiment were Hybrid (PAC-781), Rampur Composite and Water Maize (local water-logging tolerant cultivar) and water-logging treatments were done at four leaf stage, knee high stage and tasseling stage. Leaf area index, root volume, root length and root dry weight were reduced after the water-logging, more pronounced effects observed with early water-logging indicating marked impact on the growth of maize. The anatomical study suggested damaged internal structure, especially disintegration of cortical parenchymatic tissues and formation of aerenchymatic tissues as a mechanism of water-logging tolerance. This mechanism was higher in Water Maize, therefore, exhibited lower variability of the observed morphological and growth attributes from early water-logging to the controlled conditions as compared to Hybrid and Rampur Composite. Moreover, brace root formation and lateral roots were observed more in the Water Maize. The study indicated early water-logging to have higher negative impacts on overall growth and development of maize threatening its survival and water maize showing various tolerance mechanisms as compared to other varieties used in the study.

Keywords: Aerenchyma, Anoxia, Hypoxia, Water-logging, Water Maize

1. INTRODUCTION

In Nepal, maize is the second most important cereal crops after rice in terms of total production, area and productivity. Maize is grown in rain-fed condition or either in the flooding irrigation system. Maize cultivation is subjected to the water-logging stress which creates hypoxia or anoxia that affects crop growth and development. Maize is the source of food in hills of Nepal. Sapkota and Pokhrel, 2010, reported that the maize demand is growing by about 5% annually in the last decade. The total production of the maize in 891583 ha of the total area of production in Nepal is 22311517MT in 2015/16 which is significantly increased compared to 1716042MT production in area of 849892ha in 2005 (MOAD, 2016). There are some traditional landraces that has shown the potential to tolerate the water-logging stress. This research deal with one of such landraces to understand their mechanism for water-logging tolerance and detect the most susceptible growth stages of maize for water-logging severity.

The crops grown under the flooding irrigation or rain-fed system are more prone to the biotic and abiotic stresses. The biotic and abiotic stress that crop has to deal affects the growth and development directly or indirectly that consequently reduces the yield of the crop. Among the abiotic stress, maize production is severely affected by the excessive soil moisture. Excessive soil moisture is often created due to heavy rainfall, flooding irrigation, raised water table and lack of drainage from field. The excessive soil moisture in field is main reason for the reduced maize production and productivity in Asian region. In South-East Asia only, about 15% of total maize growing areas are affected by waterlogging, which accounts for the 25-30% annual loss in maize yield (Zaidi et al., 2005). The success or failure of the maize cultivation is determined several factors including soil characteristics, timing of waterlogging in relation to stage of development, frequency and duration of waterlogging and air-soil temperatures during waterlogging (Lauer, 2001). Maize requires the higher amount of water for the growth and development but it is most susceptible to the water-logging stress. Water-logging influences the every stages of maize production; difference is only the level of severity. Seeds sown during the water-logging may not germinate in most conditions or even if they manage to do so, they might fail to grow into the robust plants. Excessive soil moisture restricts the growth of roots, provides the base for the crop disease development and also hinders the nutrient availability and uptake by the roots. The crops under water-logged conditions experience the anoxia and hypoxia. Anoxia is complete absence of oxygen in the root surroundings under water-logged conditions whereas hypoxia is temporary or partial absence of the oxygen. Absence of the oxygen in the rhizosphere is very critical from the view point of root respiration and uptake of the nutrient required for the survival of the plant. Similarly, the excess moisture in the soil triggers the leaching of soluble nitrogen from the soil, which causes the denitrification of the soil. Accumulation of many toxins is initiated due to the absence of the oxidizing agent i.e. Oxygen. This eventually retards the root growth and reduces the leaf emergence rate (Margret, 2013).This also leads to the root physiological dysfuctioning which results in alternation of plant hormone balance and nutrient shortage (Margret, 2013; Pezeshki, 2001). The anchorage property of the soil is also affected. The plant fails to stand upright in the water-logged soil for the longer duration of time. Thus both the soil physical and chemical properties is influenced by the water-logging of soil. The change in the soil property leads to the decline of maize yield in considerable amount (Zaidi et al 2003). Water-logging also disturbs the physiological properties of the soil by changing water and nutrient uptake, preventing shoot and root growth (Liao et al 1995 & Pang et al 2004).Carbon assimilation is influenced during waterlogging as waterlogging decreases the soluble protein content. This results in the decline of photo assimilation (Yordanova, Popova; 2007).Jensen *et al* 1967 also reported that the changes brought by the waterlogging in maize are reduction in leaf growth and root growth in their study. Maize roots undergo the different changes during water-logged conditions for their survival. There is significant structural changes in the roots of maize due to the water-logging stress to the crops. This leads to the modification in the cellular and tissue level to cope with the changed rhizosphere situation. Soil waterlogging reduces plant growth as oxygen availability in the root zone decreases (Armstrong 1979; Jackson and Drew 1984). According to the studies of Laan et al. 1989; Visser et al. 1996 & Huber et al. 2009, plant usually cope with waterlogging by developing the new roots with aerenchyma. Aerenchyma is the soft spongy tissue that is porous in nature that allows the exchange of the gases between the shoot and roots. The development of the aerenchyma may be a response to flooding in both flood tolerant and flood intolerant species (Vartapetian and Jackson 1997, Schussler and Longstreth 2000, Chen et al 2002, Evans 2004). While some other authors like Kludze et al 1994 & Pezeshki 1996 pointed out that the aerenchyma formation is an adaptive response in flood tolerant species only, specifically in bottomland woody species. Laan *et al* 1991 and Evans 2004 reported that the increase in porosity enhances the longitudinal diffusion of gas in roots, thus increasing their aeration. The waterlogging condition of soil leads to the suberisation of the exodermis layer of the roots in maize (Enstone and Peterson 2005) and is associated with a decline in radial loss of root oxygen (Visser *et al* 2000, Armstrong and Armstrong 2005). Such a barrier on the periphery of the cortex may not only reduce the loss of oxygen to rhizosphere but could also protect the plant for the phyto-toxins produced by the microorganisms in the rhizosphere (Soukup *et al* 2002, Armstrong and Armstrong 2005, Soukup *et al* 2007).One of the most important responses to waterlogging is the disintegration of the cortical parenchymatic tissues in the roots of maize and development of aerenchymatous tissues. There are two development processes of aerenchyma in nature. First is the constitutive development of aerenchyma as it occurs whether the plant is in flooded conditionsor not. It is formed during the tissue development through the cell separation, also known as the schizogeny. It is independent of the external stimuli as it is the part of the plant development. And the other type of the process is the lysogeny which is formed by the partial break down of the cortex. When the plant has to grow in the waterlogged condition, biosynthesis and accumulation of ethylene around the rhizosphere of the roots is high. This affects the cortex of the root where the parenchymatic or cortical cells are subject to the death and lysis. The cells death and disintegration is the sacrifices for the formation of aerenchyma. Aerenchyma formed in roots helps in the increment of the oxygen storage within the roots. The stored oxygen is then transported to other parts of roots and shoots as per the need. During the aerenchyma formation, their disintegration provides the necessary energy to the adjacent cells for survival (Kono, 1972).The important morphological adaptation of the maize root to the waterlogging is the development of the adventitious roots. These roots functionally replace the basal or primary roots (Bacanamwo and Purcell 1999, Gibberd et al 2001, Malik et al 2001). The formation of these specialized roots takes place when the original root system becomes incapable of supplying the shoot with required water and minerals (Mergemann and Sauter 2000). Furthermore, decay of main root system may be considered as a sacrifice to allow a more efficient use of energy for the development of a more adopted root system (Folzer *et al* 2006).Adventitious roots are commonly formed at the end of the shoot region and grow laterally parallel to the water or soil surface. Sometimes they emerge out of the flooded surface. Armstrong, 1979 explained that the root needs oxygen at its apex for the elongation in waterlogged soil. The ability of the plants to produce the adventitious roots is commonly been associated with the ethylene production (Voesenek et al 1993, Mergemann and Sauter 2000, Steffens et al 2006). Water-logging tolerant varieties like rice produces the ethylene is very slower rate than the crops varieties like maize, mustard etc. which has higher ethylene production rate under water-logging condition. Under water-logging condition, this growth inhibiting substance is trapped around the roots of the maize. This leads to slower extension of the roots. Ethylene inhibits the growth of roots and cause senescence of the older roots. Ethylene also inhibits the geotropism of roots that is why the adventitious roots of flooded plant is in parallel to the water surface. Those roots can sometimes be outside of water and absorb the oxygen from the atmosphere and then transport to the oxygen deficient cells of other roots inside the water. Zaidi and Singh, 2003 reported that the development of brace roots was found at fifth nodes under waterlogging condition. Adventitious roots helps in the utilization of assimilates in the plants through the anaerobic conditions in spite of the water-logging condition because of high presence of alcohol dehydrogenases. Similarly cultivars that have ability to produce early adventitious roots with presence of aerenchymatous tissues have successfully grown and survived under waterlogging condition. This was the result of the study done by the Lizaso and Ritchie in 1997. Likewise Wenkert et al 1981 explained that the cultivars which can replace the primary root system by newly developed adventitious root system are found to survive longer in the water-logging condition.

2. MATERIALS AND METHODS

Experimental location

The pot experiment was conducted in 2016 at IAAS, Lamjung, Nepal (28’12’’N, 84’42’’E and altitude of 750m asl). Lamjung district lies in the sub-tropical condition of Nepal which comprises of cold winter, hot summer and distinct rainfall with average annual rainfall of 2000mm (Adhikari, 2013).

Planting materials

The landraces that is considered to be water-logging tolerant was used in the research, termed as Water Maize. Other varieties like Hybrid maize (PAC781) which is considered to be high yielding variety was used and Rampur Composite variety of maize was used for its composite nature.

Experimental design

The experiment was conducted under Completely Randomized Design with two factors. The three cultivars of maize viz. water maize, Rampur composite and hybrid maize were used as the first factors and growth stages of maize viz. four leaf stage, knee high stage and tasseling stage along with control were used as the second factors in the experiment. The treatments were replicated three times.

Preparation of growing media and seed sowing

Sandy loam soil was mixed with the well decayed farm yard manure. No chemical fertilizer was added to the mixture. The soil was filled in pot with plastic bag inside it so as to prevent the water leakage during our experiment. The soil was filled up to the level leaving 5cm to the top as that space would be necessary for the flooding the plants. Water used in flooding was same that is used for irrigation in the field. The seed was soaked in plain water overnight prior to sowing. Each pot was sown with two seeds of maize of particular variety. This was done to ensure the germination and when both seeds germinated we uprooted the week seedling from the pot.

Measurements of parameters

Parameters observed were leaf length and largest leaf width during the growth stages at different intervals of 5, 15 and 25 days after water-logging at four leaf, knee high, tasseling stages and controlled conditions. The leaf length and leaf width was used in the calculation of the Leaf Area Index. Similarly, SPAD reading was taken at 5 days after waterlogging.

Calculation of Leaf Area Index

The leaf area index was calculated from the data of leaf length (L) and maximum width (W) of maize at four leaf stages, knee high stage, tasseling stage and control stage according to the method of Montgomery.

$$\textbf{Leaf area} = L \times W \times 0.75$$

$$\textbf{Leaf Area Index} = (\text{leaf area per plant} \times \text{number of plants per pot}) / \text{area of pot}$$

Calculation of root length, volume and dry mass

The root parameters were calculated after the uprooting of the dead maize plant. The length of root was measured with scale and volume was measured with the help of measuring cylinder. The dry mass of root was taken by keeping the root in the oven at 72^0 C for 4 days.

Anatomical observation of maize root

Before keeping the roots in the oven, transverse section (TS) of the roots was observed under the light microscope. For proper TS of roots, roots were sliced with the help of the sharp razor blade and for the support; roots were held inside potato pith during slicing procedure. Best observed TS of roots was selected for the comparison.

3. RESULTS AND DISCUSSION

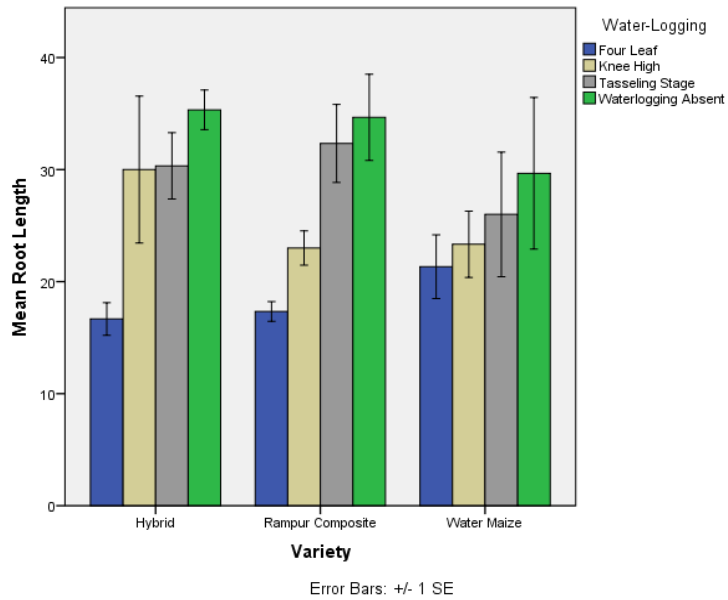
Results

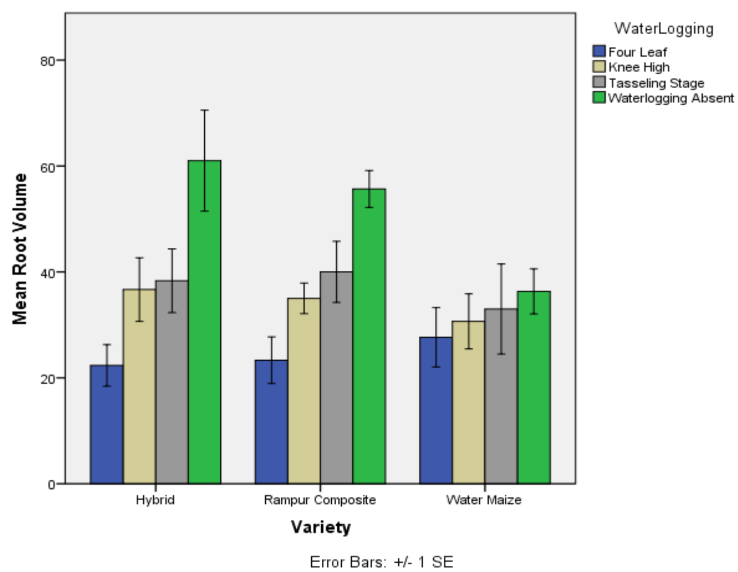
The controlled condition or water-logging absent condition has higher root length for every varietal treatments. When the water-logging was imposed, the root lengths were reduced in each variety. The decrease in the root length in Water Maize was found to be statistically insignificant. The root was already shorter in controlled condition compared to other varieties and upon waterlogging the reduction in root length was minimum compared to other varieties. While other varieties were very much affected by the waterlogging at earlier growth stages than later stages.

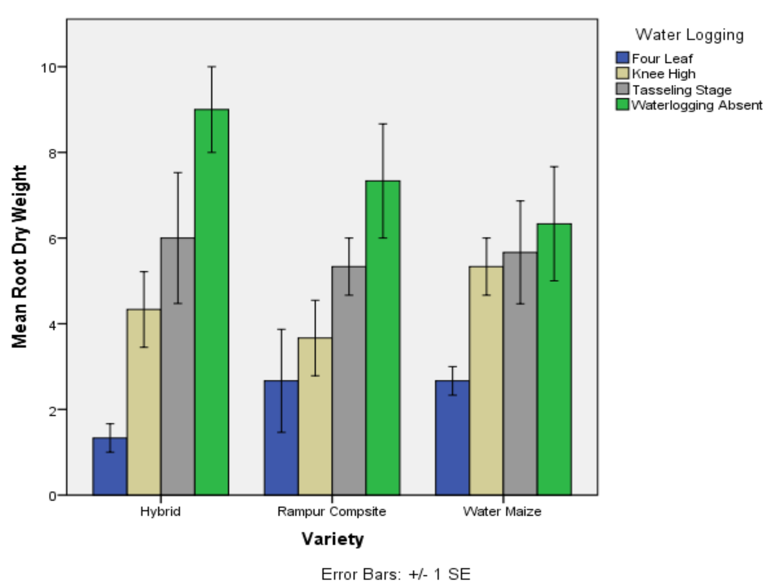
The ethylene concentration is increased in the water-logged condition which inhibits the root growth and decreases the rate of root extension.

Similar trend as in the root length was observed for the root volume. The volume of the maize root decreased due to water-logging condition where the decrease in root length was found to be statistically at par for Water Maize. The root volume was found to be highest for controlled condition than water-logged condition for Hybrid followed by Rampur Composite and then water maize. As water-logging condition arises, root volume was found to highly affected in Hybrid and Rampur Composite than in water maize. The severity of water-logging was found higher when it is imposed during earlier stages.

Root dry matter of maize was significantly decreased after waterlogging. The negative effects varied with growth stages and duration of water-logging. The dry weight of the maize root was most susceptible to damage when water-logging occurred at four leaf stage, followed by other growth stages. The damage increased with the increase in the waterlogging duration or the earlier stages of water-logging showed the higher severity for loss in root dry weight. The root dry weight was found highest in the hybrid maize when no water-logging was imposed.


Water-Logging
Four Leaf
Knee High
Tasseling Stage
Waterlogging Absent
Mean Root Length
0
10
20
30
40
Hybrid
Rampur Composite
Water Maize
Variety
Error Bars: +/- 1 SE


WaterLogging
Four Leaf
Knee High
Tasseling Stage
Waterlogging Absent
Mean Root Volume
0
20
40
60
80
Hybrid
Rampur Composite
Water Maize
Variety
Error Bars: +/- 1 SE


Water Logging
Four Leaf
Knee High
Tasseling Stage
Waterlogging Absent
Mean Root Dry Weight
0
2
4
6
8
10
Hybrid
Rampur Compsite
Water Maize
Variety
Error Bars: +/- 1 SE

Discussion

Morphological basis of water-logging tolerance in maize roots

The morphological basis of water-logging tolerance in maize roots was found to be emergence of brace roots in earlier growth stages and development of adventitious roots that rises to the water-logged surfaces. Water-logging significantly decreased root length, root volume and root dry matter of the maize. Previous research studies showed that seminal root elongation either ceased or slowed significantly and there was also significant root senescence due to the water-logging (Wenkert *et al.*, 1981; Przywara and Stepniewski, 1999). The growth of new adventitious root was found to be promoted by the water-logging (Trought and Drew, 1980; Wenkert *et al.*, 1981; Erdmann and Wiedenroth, 1986; Lizaso *et al.*, 2001; Malik *et al.*, 2001; Abiko *et al.*, 2012). The growth and development of such adventitious roots is governed by the presence of ethylene as stated by the studies done by the Voesenek *et al.*, 1993, Mergemann and Sauter 2000, Steffens *et al.*, 2000. Such roots can be thicker and shorter than those earlier roots (Malik *et al.*, 2001; Abiko *et al.*, 2012). These roots influences the root system of maize. The root dry matter or weight of maize was decreased as the decaying or senescence of the roots was pre-dominant in the prolonged water-logging conditions. The longer roots were replaced by shorter adventitious roots may also cause the loss in root volume during the water-logging conditions. Similarly the disintegration of the root cortex due to water-logging plays important role in root volume and dry weight. The presence of the functional parenchyma even after disintegration of the root cortex during the aerenchyma formation avoids the shrinkage of the root volume and dry weight. This phenomena was commonly observed in the landrace used in the experiment. They demonstrated the presence of the functional parenchyma in the root cortex whereas other two varieties failed to do so.

Anatomical basis of water-logging tolerance in maize roots

The figure of different TS of maize root under controlled condition shows that there is no disintegration of cortical parenchyma. This is the normal condition of maize root when water-logging is not imposed to maize. There is no stimulus for the production of higher amount of ethylene. The absence or lower amount of ethylene in rhizosphere fails to disintegrate the parenchyma, thus no pores are formed in internal region of roots. The figures A, B and C represent such phenomena under controlled conditions.

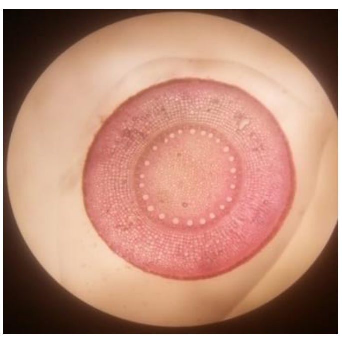


Figure- A

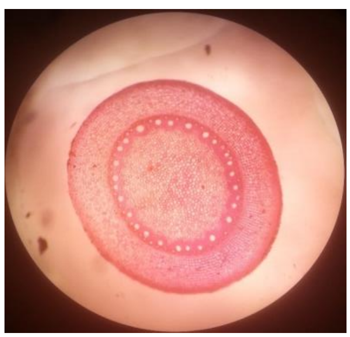


Figure- B


Figure- C

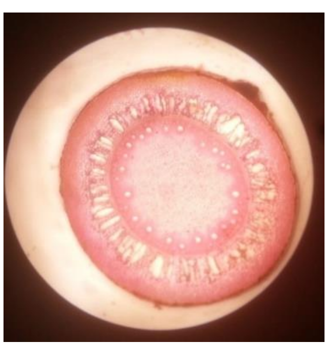


Figure- D


Figure- E


Figure- F

Figure- effects of water-logging at knee high stage of maize of different varieties on the root anatomy. Fig-A, B and C represent the TS of maize root of Water Maize, Hybrid and Rampur Composite respectively under controlled or water-logging absent condition whereas Fig.- D, E and F represents the TS of the maize root of Water Maize, Hybrid and Rampur Composite respectively under water-logging condition.

But in the case of water-logged condition, there is biosynthesis and accumulation of the ethylene in rhizosphere. The presence of higher amount of ethylene affects the cortical parenchyma. The parenchymatic cells undergo the lysis and death. This results in the formation of the porous space in the cortical region of the roots. Such porous space are the aerenchyma. The energy liberated during the cell lysis or death is used by the adjacent living cells for their survival (Kono, 1972). As earlier discussed studies of Laan et al. 1989; Visser et al. 1996 & Huber et al. 2009, this aerenchyma in maize roots help the plant to cope with the water-logging stress. Aerenchyma stores and mobilizes the oxygen in the roots of water-logged maize and such oxygen are also important with the view point of detoxifying the toxins present in the rhizosphere. This phenomenon was observed in the maize root whereas other varieties failed to do so. The roots of Hybrid and Rampur composite maize were disintegrated vastly with no presence of functional parenchyma which would have avoided the shrinkage of root volume and dry weight of the maize root. Their cortical region has disrupted structures which cannot provide the function of the aerenchyma.

4. CONCLUSION

The reduction in the maize root length, volume and dry weight induced by the water-logging is due to the disintegration of the maize root cortical parenchyma. The disintegration of cortical parenchyma helps in the formation of the aerenchyma. That aerenchyma helps in the water-logging tolerance mechanism of maize. Similarly the development of adventitious roots and brace roots in earlier stages of water-logging helps to adapt in changed rhizosphere condition in terms of excessive soil moisture. Also the study concludes that earlier the water-logging stress to maize, higher will be the detrimental effects of the root morphology and anatomy of maize. In this study, water-logging tolerant landrace was found to be superior to other used varieties, which was able to develop both the morphological and anatomical tolerance mechanism during water-logging.

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Conflict of Interest: The authors declare that there are no conflicts of interests.

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Data and materials availability: All data associated with this study are present in the paper.

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