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Effect of Waterlogging on Carbon Exchange Rate, Stomatal Conductance and Mineral Nutrient Status in Maize and Pigeonpea

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ABSTRACT

An investigation was carried out on maize (*Zea mays*) ('V-32' and 'CML-49') and pigeonpea (*Cajanus cajan*) ('ICPL-84023' and 'MAL-18') genotypes to study the effect of waterlogging on physiological parameters. Waterlogging stress was imposed after 20 days of sowing (DOS) in maize and 40 DOS in pigeonpea by placing pots in water-filled containers in such a way that the water level remained 2.5 to 3.0 cm above the soil surface in pots. Plants were kept at optimal supply of soil moisture, and labelled as "normal". Changes in photosynthetic parameters and mineral nutrient status were observed in the first fully expanded leaf from top in normal and waterlogged plants after 9 days of imposing waterlogging stress in maize and 12 days in pigeonpea, at these stages visible symptoms of waterlogging stress were evident in both the crops. Waterlogging caused significant reduction in carbon exchange rate in pigeonpea, but the reduction was not significant in maize genotypes. Under waterlogged condition stomatal conductance decreased significantly in maize genotypes, but in pigeonpea it followed a variable trend. Variations in the contents of leaf N, Mg, Ca, Fe, Cu, Mn and Al were observed under the influence of waterlogging stress. Maize plants experienced N, Ca, Mg, Fe, Mn, Zn and Cu deficiency, while pigeonpea genotypes faced deficiencies of N, Mg and Mn under waterlogged condition. Al toxicity was observed in a waterlogging-susceptible maize genotype, but no such effect was evident in pigeonpea. Genotypic differences in both maize as well as pigeonpea were evident and correlated with the relative performance of the genotypes under waterlogged condition.

Keywords: flooding, ion accumulation, nutritional imbalance, photosynthesis

Abbreviations: CER, carbon exchange rate; **Ci**, intercellular CO_2 concentration; **gs**, stomatal conductance; **PAR**, photosynthetically active radiation; **CRD**, completely randomized design; **CD**, critical difference

INTRODUCTION

Maize (*Zea mays*) is primarily cultivated during *kharif* (rainy season, July to October) in India, a period during which the crop experiences significant damage due to excess soil moisture in the root zone (Shah 2007). In South East Asia alone, more then 15% of the total maize farming area is affected by waterlogging and flooding (Rathore *et al.* 1998). In India excess soil moisture is the second most serious abiotic stress after drought, limiting maize productivity. There are reports that excess soil moisture causes an average of 25-30% losses in maize production each year (DMR 2001).

Pigeonpea [*Cajanus cajan* (L.) Millsp.], commonly known as *arhar*, *redgram*, *toovar*, *toor*, or *Gungopea* is a member of the Fabaceae family. It is an important legume crop of rainfed agriculture, mostly produced in Asia, Africa, Latin America and the Caribbean region. Globally pigeonpea is cultivated in 4.92 million ha with an annual production of 3.65 metric tons and productivity of 898 kg ha^{-1}. According to FAO (FAOSTT 2007), India is a major pigeonpea producer, having 711 kg ha^{-1} yield and 2.51 million tonnes production. Pigeonpea ranks second after chickpea among important pulse crops in India. Productivity of pigeonpea in India is low due to various biotic and abiotic stresses. Waterlogging results in reduced biomass and yield or total crop loss (Saxena 2008). In India, pigeonpea is sown in June-July (rainy season). Annual and late cultivars flower in January and harvested in March-April. Being a summer rainy crop, it is frequently exposed to the waterlogging conditions resulting in considerable loss in crop vigour and plant stand (Chauhan *et al.* 1987). The risk of crop failure or yield reduction is more in short duration genotypes when exposed to short-term waterlogging, as the recovery period is less than medium- and long-duration genotypes (Matsunaga *et al.* 1991).

Reduced plant growth and poor crop productivity under waterlogged condition is attributed to reduced oxygen concentration in the root zone, which results in switching of plant metabolism from aerobic to anaerobic (Srivastava *et al.* 2007b). Decreased photosynthesis and transpiration are among the initial important changes under waterlogging condition. Waterlogging in fact has been shown to decrease photosynthetic efficiency and biological yield in maize (Yan *et al.* 1996; Dhillon *et al.* 1998; Scholowing and Teching 1997; Ashraf and Rehman 1999; Zaidi *et al.* 2003), tomato (Else *et al.* 2009), soybean (Cho *et al.* 2006) and barley (Yordanova and Popova 2001). The closure of stomata and reduced stomatal conductance have been reported to cause a decrease in intercellular CO_2 concentration (Ci) and the carboxylation efficiency in maize plants under waterlogged condition (Zhang and Zhang 1994). Intercellular CO_2 concentration of leaf increases linearly with the duration of flooding despite reduction in stomatal conductance (Liao and Lin 1994). Waterlogging results in the reduction in transpiration rate and stomatal conductance in maize (Baranwal and Singh 2002) and lucerne (Smethurst *et al.* 2005) genotypes. It is reported that under waterlogged condition transpiration decreases in tolerant maize lines, while in susceptible lines it follows an opposite trend (Zaidi and Singh 2002). It is not known whether the decreased photosynthetic activity is due to the effect of stomatal clo-

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sure. Nevertheless, Pezeshki (1994) reported that decreased photosynthetic rate is due to decreased activity of ribulose bis-phosphate carboxylase oxygenase (RuBISCO), the enzyme responsible for CO_2 fixation.

Waterlogging causes derangement in availability and uptake of nutrients (Pezeshki 2001). It is reported that under excess soil moisture stress plants experience nitrogen deficiency on account of increased denitrification and leaching of nitrate, and this is attributed as the major cause of yellowing of older leaves. Selection of excess soil moisture-resistant genotypes of maize on the basis of lesser reduction in plant nitrogen content under excess soil moisture stress has been proposed (Thomson *et al.* 1989; Shah 2007). Under waterlogged conditions the concentration of calcium, magnesium, copper, zinc and aluminium declines in wheat and barley plants (Steffens *et al.* 2005), while toxicity of iron (Fe) and manganese (Mn) appears under waterlogged condition in plants that do not tolerate flooding (Horst 1988; De Datta *et al*. 1990).

Following the screening of a large number of available maize and pigeonpea genotypes at the Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, genotypes 'V-32' of maize and 'ICPL-84023' of pigeonpea have been found to be waterlogging resistant.

In Northern India maize and pigeonpea are sown in the beginning of rainy season (June-July). Maize is harvested in nearly three months, where as pigeonpea is harvested in March-April. Therefore, maize may be frequently exposed to waterlogging during the entire life cycle. Waterlogging stress occurs during the early growth phase in pigeonpea, and later growth phases are generally exposed to drought and low temperature stresses. Keeping this in view, the present investigation was undertaken to study the changes in photosynthetic rate, stomatal parameters and mineral nutrient status of waterlogging-resistant and susceptible maize and pigeonpea genotypes subjected to root zone waterlogging during early stages of growth.

MATERIALS AND METHODS

Maize genotypes 'V-32' (waterlogging resistant) and 'CML-49' (relatively susceptible) were sown on July 26, 2007 (wet season) in plastic pots containing 2 kg sandy loam garden soil (ECe 0.25 dSm^{-1}; pH 7.30) in the net house of the Institute of Agricultural Sciences, Banaras Hindu University, Varanasi. After germination, 5 plants of uniform vigour were maintained in each pot. When seedlings were 7 to 8 cm long, 20 ml Hoagland's solution was given to each pot (Arnon 1938). Seedlings were maintained at normal supply of moisture while waterlogging stress was imposed at 20 days after sowing by placing 10 set of pots (both genotypes) in water filled container in such a way that the pots were completely submerged and level of water in the container was 2.5 to 3.0 cm above the soil surface in the pots. The water level was maintained daily early in the morning and in the evening by adding tap water. This treatment is referred to as "waterlogged". The remaining 10 pots of each genotype were maintained at optimal supply of soil moisture and are termed as "normal".

Pigeonpea genotypes 'ICPL-84023' (waterlogging resistant) and 'MAL-18' (susceptible) were selected. Seeds were sown in plastic pots containing 5 kg soil on July 4, 2007. Waterlogging stress was imposed after 40 days of sowing by putting pots in cement containers (55 × 55 × 55 cm). The rest of the practices were as described for maize.

In maize, carbon exchange rate (CER), leaf conductance (gs), Ci were measured after 9 days of treatment in waterlogged and normal plants with the help of infra red gas analyzer (IRGA) (LiCOR 200, USA). Data was recorded between 9:00 to 11:00 h on the upper most fully expanded leaf from top. In pigeonpea, it was recorded after 12 days of imposing waterlogging stress (52 DOS). After 9 and 12 days of waterlogging, visible symptoms of stress were evident in maize and pigeonpea, respectively.

In maize and pigeonpea, contents of N, Ca, Cu, Mg, Mn, Fe, Zn, and Al were determined in first fully expanded leaf from top and leaves were removed, surface cleaned with tap water followed by distilled water, oven dried at 65°C and used for elemental analysis. Total N content was determined by nitrogen analyzer (Pelican, KEL 20L, India) adopting Kjeldahl methods. Contents of Ca, Cu, Mg, Mn, Fe, Zn, and Al were determined by atomic absorption spectrophotometer (Elico, SL-194, India) after digestion of the oven-dried samples in tri acid mixture [HNO_3: H_2SO_4: $HClO_4$ (60%) in a ratio of 75:30:15].

Data pertaining to CER, gs and Ci are mean values of five independent observations, while the data of mineral nutrients are the means of three replicates. Data were subjected to statistical analysis adopting CRD (completely randomized design) factorial with two factor analysis of variance. CD (critical difference) was calculated at 1% by the method of Gomez and Gomez (1984).

RESULTS

Carbon exchange rate

Effect of waterlogging on carbon exchange rate (CER) in maize and pigeonpea genotypes is depicted in **Table 1**. Under normal condition maize registered nearly four times higher CER than pigeonpea. Waterlogging reduced CER in both the crops.

In maize, though CER decreased under the influence of

Table 1 Effect of waterlogging on photosynthetic and transpirational parameters in maize (V-32 and CML-49) and pigeonpea (ICPL-84023 and MAL-18) genotypes.

Parameter		**Maize**			**Pigeonpea**	
		Normal	**Waterlogged**		**Normal**	**Waterlogged**
Carbon exchange rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	V-32	38.69	33.23	ICPL-84023	9.85	3.43
	CML-49	40.27	37.41	MAL-18	7.79	5.33
				CD at 1%		
	Genotype	4.93		2.59		
	Treatment	4.93		2.59		
	Genotype x Treatment	6.97		3.67		
Stomatal conductance ($mol\ m^{-2}\ s^{-1}$)	V-32	1.50	0.21	ICPL-84023	0.21	0.03
	CML-49	1.90	0.09	MAL-18	0.16	0.31
				CD at 1%		
	Genotype	1.32		0.13		
	Treatment	1.32		0.13		
	Genotype x Treatment	1.86		0.19		
Intercellular CO_2 concentration (vpm)	V-32	256.10	175.80	ICPL-84023	243.00	304.33
	CML-49	218.30	184.30	MAL-18	294.00	217.66
				CD at 1%		
	Genotype	36.60		25.98		
	Treatment	36.60		25.98		
	Genotype x Treatment	51.17		36.74		

Mean light intensities were 1230.00 and 1074.85 $\mu mol\ m^{-2}\ s^{-1}$, respectively in maize and pigeonpea.
Data were recorded after 9 and 12 days of imposing stress in maize and pigeonpea, respectively.

waterlogging, but the differences with respect to genotype were not significant. Under waterlogged conditions 'CML-49' maintained marginally higher CER than 'V-32'.

In pigeonpea, CER reduced significantly under waterlogged condition. 'ICPL-84023' maintained higher CER under normal condition, but under waterlogged condition 'MAL-18' registered marginally higher CER.

Stomatal conductance

Table 1 shows the effect of waterlogging on stomatal conductance in both maize and pigeonpea. It followed a variable trend under waterlogged condition in maize and pigeonpea genotypes and the genotypic differences were significant. In maize gs was much higher than pigeonpea while it decreased in maize under waterlogged conditions, whereas in pigeonpea it followed variable trend.

In maize under normal condition gs was marginally lower in 'V-32' than in 'CML- 49'. Under the influence of waterlogging it decreased significantly, and the reduction was more in 'CML-49' than 'V-32'.

In pigeonpea, 'ICPL-84023' registered higher gs than 'MAL-18' under normal condition. Waterlogging resulted in significant reduction in gs in 'ICPL-84023', whereas in 'MAL-18' it increased significantly.

Intercellular CO_2 concentration

As a response to waterlogging, alterations in intercellular CO_2 concentration (Ci) took place, as shown in Table 1. Under normal condition the level of Ci were comparable in maize and pigeonpea.

In maize, 'V-32', registered higher Ci than 'CML-49' under normal condition. In genotype 'V-32', Ci decreased significantly under the influence of waterlogging. It also decreased in 'CML-49' under similar condition, but the values between normal and waterlogged plants did not differ significantly.

Waterlogged pigeonpea plants registered a variable trend in intercellular CO_2 concentration than the normal plants, where it increased in 'ICPL-84023' and reduced in 'MAL-18'.

Mineral nutrient status

Nitrogen

Nitrogen content in first fully expanded leaf of normal and waterlogged plants was determined. Data are presented in **Table 2**. Pigeonpea, being a leguminous crop contained more N per unit dry matter of leaf than maize. Waterlogging caused significant reduction in leaf N content in maize and pigeonpea genotypes.

In maize, 'CML-49' contained more N than'V-32', but under waterlogged condition the later genotype contained marginally higher N in leaves.

In pigeonpea, 'ICPL-84023' registered relatively higher N content in leaves than 'MAL-18'. Under waterlogged condition though the level declined, but the former genotype maintained marginally higher level of this element in leaves.

Calcium

Amount of Ca in first fully expanded leaf from top was determined and values are depicted in **Table 2**. As compared to pigeonpea, maize contained very high level of Ca in leaf tissues.

In maize this element was present in marginally higher amount in 'CML-49' than in 'V-32'. Under waterlogging stress, calcium content in maize leaves decreased significantly. Though the genotypic differences were not significant, but 'CML-49' contained more calcium than 'V-32'.

In pigeonpea, under normal condition, 'MAL-18' contained more Ca than 'ICPL-84023'. Under the influence of waterlogging both the genotypes exhibited variable trend. In 'ICPL-84023' it significantly increased, whereas in 'MAL-18' it declined.

Magnesium

Pigeonpea leaves contained much higher level of Mg than maize (**Table 2**). In both the crops this element decreased under the influence of waterlogging.

In maize genotypic differences were not significant. The decline in leaf Mg content was not significant with respect to treatment in 'V-32' while, it was significant in 'CML-49'.

In pigeonpea differences with respect to genotype were significant but waterlogging did not cause significant reduction in the level of this element. 'ICPL-84023' contained marginally more Mg than 'MAL-18' under both the treatments.

Iron

Changes in the level of leaf Fe content under waterlogging as compared to normal in maize and pigeonpea genotypes are presented in **Table 2**. Leaf Fe contents in both the crops under normal condition were comparable.

In maize, 'V-32' contained higher content of Fe in leaves than 'CML-49' under normal condition. It decreased significantly in both the genotypes under the influence of waterlogging. Leaves of waterlogged plants of both the genotypes contained almost comparable amount of Fe.

In pigeonpea, 'ICPL-84023' contained significantly higher amount of Fe than 'MAL-18' in leaves. In 'ICPL-84023' level of this element increased significantly, while in 'MAL-18' it remained almost unaffected under the influence of waterlogging.

Manganese

Leaf Mn contents in normal and waterlogged maize and pigeonpea genotypes are expressed in **Table 2**. Maize genotypes contained higher amount of Mn in leaves than pigeonpea. Waterlogging resulted in significant reduction in the level of this element in maize, while it was marginal in pigeonpea.

In maize, 'CML-49' contained significantly higher content of Mn than 'V-32' in leaves. In both the genotypes it decreased significantly under the influence of waterlogging.

In pigeonpea, 'MAL-18' contained marginally higher amount of Mn in leaves than 'ICPL-84023' under normal condition. It decreased marginally under waterlogging, whereas 'MAL-18' maintained higher level.

Zinc

Effect of waterlogging on leaf Zn contents of maize and pigeonpea genotypes are illustrated in **Table 2**. Maize genotypes contained relatively higher amount of Zn in leaves than pigeonpea. While in maize this element decreased marginally under the influence of waterlogging, but in pigeonpea it did decrease marginally.

In maize, 'CML-49' contained marginally higher level of Zn in leaves than 'V-32'. In 'V-32' it decreased marginally, but in 'CML-49' it remained almost unchanged under the influence of waterlogging.

In pigeonpea, 'MAL-18' contained higher level of Zn than 'ICPL-84023' under normal condition. It decreased under the influence of waterlogging, but the genotypic differences were not significant.

Copper

Effects of waterlogging on leaf Cu content is presented in **Table 2**. Maize contained higher amount of Cu in leaves than pigeonpea. Both the crops exhibited variable pattern of change in the level of this element under the influence of waterlogging stress.

Table 2 Mineral nutrient status (mg g^{-1} dry weight) in first fully expanded leaf of maize (V-32 and CML-49) and pigeonpea (ICPL-84023 and MAL-18) genotypes under normal and waterlogged condition.

Element		**Maize**			**Pigeonpea**	
		Normal	**Waterlogged**		**Normal**	**Waterlogged**
N	V-32	26.15	21.70	ICPL-84023	42.43	31.26
	CML-49	30.48	18.53	MAL-18	35.50	21.00
				CD at 1%		
	Genotype	3.80		10.26		
	Treatment	3.80		10.26		
	Genotype x Treatment	5.30		14.51		
Ca	V-32	52.30	23.54	ICPL-84023	4.20	5.90
	CML-49	70.26	44.60	MAL-18	5.07	4.40
				CD at 1%		
	Genotype	13.00		0.59		
	Treatment	13.00		0.59		
	Genotype x Treatment	18.42		0.84		
Mg	V-32	0.59	0.42	ICPL-84023	8.63	7.30
	CML-49	0.62	0.41	MAL-18	3.37	2.27
				CD at 1%		
	Genotype	0.14		1.49		
	Treatment	0.14		1.49		
	Genotype x Treatment	0.20		2.10		
Fe	V-32	1.16	0.50	ICPL-84023	1.14	1.41
	CML-49	0.88	0.50	MAL-18	0.72	0.73
				CD at 1%		
	Genotype	0.10		0.22		
	Treatment	0.10		0.22		
	Genotype x Treatment	0.15		0.31		
Mn	V-32	0.39	0.27	ICPL-84023	0.17	0.06
	CML-49	0.92	0.64	MAL-18	0.19	0.15
				CD at 1%		
	Genotype	0.10		0.08		
	Treatment	0.10		0.08		
	Genotype x Treatment	0.15		0.11		
Zn	V-32	0.31	0.27	ICPL-84023	0.22	0.12
	CML-49	0.38	0.38	MAL-18	0.25	0.14
				CD at 1%		
	Genotype	0.09		0.11		
	Treatment	0.09		0.11		
	Genotype x Treatment	0.13		0.16		
Cu	V-32	0.67	0.42	ICPL-84023	0.26	0.23
	CML-49	1.18	0.80	MAL-18	0.25	0.25
				CD at 1%		
	Genotype	0.10	0.03			
	Treatment	0.10	0.03			
	Genotype x Treatment	0.14	0.04			
Al	V-32	46.70	50.40	ICPL-84023	B.D.L.*	B.D.L.*
	CML-49	46.61	86.50	MAL-18	B.D.L.*	B.D.L.*
				CD at 1%		
	Genotype	10.00				
	Treatment	10.00				
	Genotype x Treatment	14.50				

B.D.L.*: Below detection limit

In maize, the level of this element declined significantly under the influence of waterlogging. Under waterlogged and normal conditions 'CML-49' maintained higher level of leaf Cu content than 'V-32'.

In pigeonpea, Cu content in leaves declined marginally in 'ICPL-84023', whereas in 'MAL-18' it remained unchanged under waterlogged condition. The values did not differ significantly with respect to genotype and treatment in this crop.

Aluminium

Change in the Al content under the influence of waterlogging was studied in maize and pigeonpea. In case of pigeonpea, presence of Al was below the detection limit of the instrument, however, it was detected in maize and is presented in **Table 2**.

Under normal condition both the genotypes of maize contained appreciable amount of Al in leaves. The genotypic differences were significant. Under waterlogged condition Al content increased. The increment was highly significant in 'CML-49', but not in 'V-32'.

DISCUSSION

In the present investigation, CER in maize was found to be almost four folds higher than pigeonpea genotypes under normal condition. It is expected as maize is a C_4 plant, while pigeonpea belongs to C_3 category. Under waterlogged condition, in both the crops, carbon exchange rate declined (**Table 1**), but the reduction was not significant in maize, while in pigeonpea it was significant. The reduction in carbon exchange rate was more in waterlogging resistant genotypes of maize ('V-32') and pigeonpea ('ICPL-84023'). In maize, extent of reduction in gs was more than carbon exchange rate (**Table 1**), indicating that gs is more sensitive to waterlogging stress than carbon exchange rate. Significant reduction in gs, but not in the carbon exchange rate in maize indicates that carbon exchange rate is not limited by the stomatal component in this crop, even when the gs declined to a considerable extent. In pigeonpea, under waterlogging, both the genotypes exhibited significant reduction in carbon exchange rate. Stomatal conductance decreased in waterlogging resistant genotype, while in susceptible it increased under the influence of waterlogging. This indicates that in pigeonpea, carbon exchange rate is limited by non stomatal as well as stomatal components. Ahmed *et al.* (2002) reported that in mungbean leaf diffusion resistance (reciprocal of leaf conductance) is increased to a greater extent than CO_2 assimilation efficiency under the influence of waterlogging, while in alfalfa CO_2 assimilation efficiency decreased under waterlogged condition was attributed partly due to nutrient deficiency and associated inhibition of photo system II (Smethurst *et al.* 2005).

In maize, as a consequence of reduced gs, decreased intercellular CO_2 concentration and carboxylation efficiency has been reported (Zhang and Zhang 1994). Nevertheless, opposite trend has also been observed (Liao and Lin 1994). In the present study, Ci decreased under the waterlogged condition in maize genotypes, while in pigeonpea genotypes it followed variable trend (**Table 1**). It is attributed that in maize, carboxylating enzymes are not much affected, as reduction in carbon exchange rate is not significant under waterlogged conditions. In maize, PEP-carboxylase being the primary carboxylating enzyme has very high affinity for CO_2, and hence, when stomata are closed under the influence of waterlogging, intercellular CO_2 is utilized for carboxylation and Ci levels decline. This might be one of the reasons for less reduction in carbon exchange rate than gs in maize under waterlogged condition.

In pigeonpea, increased Ci was associated with decreased gs in 'ICPL-84023' while in 'MAL-18' gs increased and Ci decreased. It is inferred that in pigeonpea under waterlogging there is reduction in nonstomatal component of photosynthesis as well, and even at elevated Ci (300 volumes per million), under waterlogged condition, plants are not able to maintain carboxylation rate to the normal rate, resulting in significant reduction in carbon exchange rate even when gs increases in waterlogged 'MAL-18'. It is reported that activation level of RuBISCO generally declines as Ci increases (Von Caemmerer and Edmondson 1986; Sage *et al.* 1988; Sage 1990) and this might be one of the reasons for decreased carbon exchange rate even at elevated Ci in pigeonpea. It is also evident that genotypic differences of maize and pigeonpea to waterlogging can not be attributed in terms of their CER. However, it appears that waterlogging resistant pigeonpea genotypes exert better stomatal control under waterlogged condition. Though better regulation of gs has been reported to be associated with waterlogging resistance in maize (Zaidi and Singh 2002), but in this investigation we could not get such differences in studied maize genotypes.

Under waterlogging of root zone, metabolism shifts from aerobic to anaerobic metabolism in roots and ATP production decreases. It results in derangement in active absorption of ions, transport of water from root to shoot and carbohydrates from shoot to root (Vartapetian and Jackson 1997). In waterlogged soil, redox potential decline (Burdick Mendelessohn 1990) which causes depletion in soil nitrate level and increased availability of elements like P, Fe and Mn (Kozlowski and Pallardy 1984; Sposito 1989). Accumulation of some of the ions in toxic amounts, while others in suboptimal concentrations also takes place. Decline in N, P, K and Ca levels in barley and P, K, Ca, Mg, Cu and Zn levels in lucerne have been reported under waterlogged condition (Trought and Drew 1980; Smethurst *et al.* 2005). In the present investigation, as compared to normal plants, tissue N, Mg and Mn levels decreased in waterlogged maize and pigeonpea genotypes (**Table 2**). Amounts of Ca, Fe, and Cu also declined in waterlogged maize leaves (**Table 2**), while in pigeonpea genotypes, content of these elements followed variable trend (**Table 2**). Zn content also decreased in waterlogged maize and pigeonpea genotypes (**Table 2**). Earlier findings in our laboratory, regarding large number of maize genotypes in consideration, have clearly indicated that waterlogging reduces plant N content. Less N requiring maize genotypes perform better under waterlogged condition, and during waterlogging such genotypes register lesser reduction in N content (Gangey 2005; Shah 2007; Srivastava *et al.* 2007a). Present investigation further supports the view. Since under waterlogged condition, symbiotic nitrogen fixation is hampered (Mague and Burris 1972), therefore, leaf N content declines significantly in waterlogged pigeonpea. Waterlogging resistant genotype 'ICPL-84023', maintained higher N level than the susceptible genotype 'MAL-18'. Our observations further confirm that less reduction in leaf N content under waterlogged condition may be taken as a parameter to screen out waterlogging resistant genotypes. It appears that maize plants experience deficiency of N, Ca, Mg, Fe, Mn, Zn and Cu and pigeonpea face deficiency of N, Mg and Mn under waterlogged condition. Toxicity of Al was observed in waterlogging susceptible maize genotype. The present investigation was conducted taking almost neutral soil, but it is expected that CO_2 evolved by root respiration under flooding decreased soil pH, and increased solubility of Al. 'CML-49' probably could not restrict Al uptake and experienced Al toxicity. Such effects could not be seen in 'V-32' and pigeonpea genotypes, indicating that perhaps they have efficient Al exclusion mechanism. Accumulation of Al in wheat genotypes grown in waterlogged acidic soil have been reported (Khabaz-Saberi *et al.* 2006).

It is concluded that under waterlogged conditions, carbon exchange rate declined more in pigeonpea; a C_3 crop, than in maize; a C_4 crop along with significant reduction in stomatal conductance in all the studied genotypes except MAL-18. Study of mineral nutrient analysis indicated that under waterlogging nitrogen content decreased significantly in both the crops. Deficiency of some other essential elements like Mg, Mn, Zn and Cu was also evident in studied maize and pigeonpea genotypes. Susceptible genotype of maize also suffered from Al toxicity under waterlogged condition. It is suggested that further investigation is required to elucidate the changes in non stomatal components of photosynthesis, uptake pattern of mineral nutrients and partitioning of absorbed ions at organ, cellular and organelle level under waterlogged condition.

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