

Physio-Agronomic Response of Mungbean [(*Vigna radiata* (L.) Wilczek] Genotypes to Waterlogging

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ABSTRACT

The extent of damage from waterlogging may vary with its timing and the type of genotype exposed. Effects of week-long waterlogging during three phenological phases on physiological, growth and yield parameters of two mungbean genotypes was examined in a greenhouse experiment. Average losses in photosynthesis rate from waterlogging amounted to 42, 87 and 73% for the vegetative, flowering and seed filling phases, respectively. The corresponding drops for transpiration rate were 36, 84 and 64%. Effects on photosynthesis and transpiration rates closely followed impacts of waterlogging on stomatal conductance. Genotype MH-97-6 had shown consistently greater rates for the physiological parameters during the terminal phase. Shoot dry matter decreased by 68% due to waterlogging at flowering while falls of 39 and 45% occurred under early and terminal waterlogging, respectively. Root growth was resilient to early waterlogging while it suffered 59 and 44% losses due to flowering and terminal waterlogging, respectively. Early waterlogging increased root-shoot ratio by 104% at the end of the stress period. The highest seed yield drop of 85% appeared due to waterlogging at flowering. The remaining two phases were less affected with falls amounting to half of that observed under mid waterlogging. In spite of its better root system and greater dry matter allocation to the root, genotype Sunaina has not shown superior tolerance to waterlogging. The significant yield penalty from early waterlogging indicated the crop's sensitivity to short term waterlogging. It would be worthwhile to screen more genotypes against waterlogging with incorporation of additional factors such as nutrient management and soil type.

Key words: *genotype, photosynthesis, stomatal conductance, waterlogging, yield*

INTRODUCTION

Mungbean is a nutritious food stuff, which is very popular because of its high digestibility and relative freedom from flatulence, a problem commonly associated with most grain legumes (Fery, 2002). Another advantage of this crop is that being a legume, it does not require nitrogen fertilizer application and has short (75-90 days) growth duration which means that it requires less water than many other crops and could be easily fitted in a rotation (Imrie, 2004). Currently, the crop is mainly grown in the central lowlands such as *Kewot* and northern lowlands like *Kobbo* areas with the former as the current belt of production in Ethiopia. For instance, in *Kewot* district it was the number one crop during the 2006/07 *belg* season covering 10,985 hectares, occupying 72% of the cultivated land (Personal communication). The farmers in the area use it as a cash crop and for consumption and the straw is also a valuable feed. Mungbean performs well and gives promising results under hot irrigated and rainfed conditions of the Central Rift Valley and northern Ethiopia (Nigatu *et al.*, 1995). It has been also shown to adapt and perform well around Hawassa area in southern Ethiopia (Worku, 2008; Laekemariam and Worku, 2013). The crop commands a high market price with 46 ETB kg⁻¹ against 32 ETB kg⁻¹ for common

bean in Addis Ababa supermarket, in April 2011. In spite of its huge market demand and its recent placement as the sixth commodity by the Ethiopian Commodity Exchange, production is still lagging behind demand.

In order to exploit the existing potential of the crop in the country there is a need to identify adapted high yielding cultivars, develop appropriate agronomic packages and popularize the crop (Laekemariam and Worku, 2013). More recently, there has been a resurgence of research interest on the crop at the Ethiopian Institute of Agricultural Research and Hawassa University. These efforts resulted in release of few varieties and a number of studies on agronomic management and physiology of the crop. This trend should continue in order to understand the crop's adaptation better and to come up with efficient agronomic management alternatives.

The current trend of rainfall distribution has become increasingly unpredictable and at times unsuitable, which is considered as one of the manifestations of climate change. Some of the impacts of climate change include changes on distribution and intensity of rainfall, which increases the likelihood of waterlogging. According to IPCC (2001) precipitation extremes including their frequency and intensity are projected to increase more than

the mean. Global climate change is likely to cause substantial increases in the severity with which salinity, waterlogging and inundation affect crop production in many of the world's agricultural regions (Mullan and Barrett-Lennard, 2010).

Waterlogging is a stress due to excess water that corresponds to the full saturation of the soil pores with water and with a very thin or without a layer of water above the soil surface (Striker, 2012). It is a major abiotic stress adversely affecting crop productivity worldwide (Shimono *et al.*, 2012). Among the abiotic stresses, excess moisture or soil flooding stands prominent in limiting productivity of mungbean (Kumar *et al.*, 2013). The magnitude of adverse effect from waterlogging in a species varies depending on the phase of exposure, nature of the genotype and duration of the stress.

Waterlogging leads to several effects on plants including restricted root growth (Thomson *et al.*, 1990), reductions in stomatal conductance and assimilation rate (Oosterhuis *et al.*, 1990) and reduced nutrient uptake leading to low productivity (Robertson *et al.*, 2009). Kumar *et al.* (2013) observed losses in assimilation rate, total dry matter production, grain yield and an increase in

flower and pod abortion with relatively greater damage in sensitive genotypes of mungbean in response to waterlogging at the vegetative phase. Ullah (2006) exposed mungbean plants to one to four days of waterlogging just after sowing and observed delayed flowering, shortened reproductive duration and reduced productivity with the highest loss at the four days waterlogging. Reductions in photosynthesis, transpiration, stomatal conductance and productivity resulted from vegetative and flowering phase waterlogging in mungbean with a certain ability of recovery from the damage and varying genotypic responses (Ahmed *et al.*, 2002). Mungbean is a sensitive crop to waterlogged conditions. However, the response of mungbean to waterlogging is not adequately addressed to the extent seen in other pulses (Kumar *et al.*, 2013). Moreover, none of the studies addressed relative sensitivity of the three developmental phases to waterlogging. Thus, this research was carried out to investigate the physiological and agronomic response of two mungbean genotypes exposed to waterlogging at three developmental phases and to identify the sensitive phase (s) that limit productivity most.

MATERIALS AND METHODS

An experiment was conducted between 04 March and 20 May 2014 in a greenhouse at Hawssa University, Hawssa, Ethiopia. Hawassa is located in southern Ethiopia at an elevation of 1660 meters a.s.l. and coordinates of 7°5'N and 38°30'E. The greenhouse had a clear polyethylene roof with wire mesh walls for good aeration. Temperature and relative humidity were measured (VAISALA, Finland) at 6:00, 12:00 and 18:00 hrs and the average of these has shown that relative humidity inside was higher by 2.7% while temperature was lower by 0.38 °C, compared to the ambient conditions outside. Fraction of photosynthetically active radiation transmitted through the greenhouse was estimated by using the SunScan Canopy Analysis System (Delta T Devices Ltd. Cambridge, UK) and was found to be 41% with R/FR ratio of 1.01. The potting soil was brought from a farm in *Meskan* district, which is considered a potential mungbean growing area. The soil analysis before planting has indicated that it contained 28% silt, 35% sand and 37% clay with a clay loam texture and with a slightly acidic pH of 6.3 (Fikadu, 2014). Soil moisture holding capacity (vol/vol) was determined using a multiple regression equation (Pidgeon, 1972) and was found to be 29.5% at 0.03 MPa and 19.7% at 1.5 MPa. The experiment consisted of two factors:

moisture regimes and genotypes. The moisture regimes were the following:

1. Optimum throughout = OOO
2. Waterlogging during the vegetative phase and optimum there after (early waterlogging) = WOO
3. Waterlogging during the flowering phase and optimum at the other phases (mid waterlogging) = OWO
4. Waterlogging during the seed filling phase and optimum at the other phases (terminal waterlogging) = OOW

Where, O, optimum and W, waterlogged; positions of the letters represent phenological phases, i.e. vegetative (from sowing to 41 days after sowing), flowering (42 days from sowing to 53 days after sowing) and seed filling (54 days after sowing to 74 days after sowing) in that order. The genotypes included one released (MH-97-6) and one potential (Sunaina) variety.

A completely randomized design with three replications was used. Mungbean plants were raised in plastic pots of 6.3 liter capacity (20 cm diameter and 20 cm height). Perforations at the bottom of the pots allowed for drainage of excess water. Prior to planting diammonium phosphate (18:46:0) was added to each pot at the rate of 3 g pot⁻¹. Five seeds were hand sown

on each pot and thinned to allow three plants, a week after emergence. Plants were waterlogged according to the treatments by immersing the pots in water filled pots of 13 liter (28 cm diameter and 21 cm height) capacity for seven days. The vegetative phase waterlogging commenced 16 days after sowing when MH-97-6 is about 6 cm tall and Sunaina 7 cm tall. Waterlogging episodes at flowering and seed filling were commenced 42 and 54 days after sowing, respectively. Waterlogged plants were maintained with about 2 cm of excess water above the soil line. Physiological parameters including photosynthesis rate, transpiration rate and stomatal conductance were measured with a portable open gas exchange measurement system (Model LCi-SD Analyzer, Hoddesdon, England). The physiological parameters were measured on a fully expanded and unshaded youngest leaf from the top (Shao *et al.*, 2013) between 10:00 and 11:00 hrs local time.

Two samplings were made during the entire study. The first batch samples were taken immediately after the end of the vegetative phase waterlogging. The second sampling, which was the final was made at harvest maturity. Three pots were harvested per treatment at each sampling. Plant height, leaf area, dry weights of leaf, stem and root were collected during the first sampling. Roots

from all sample plants were carefully removed from a moist pot soil. The roots were then washed under running tap water on a sieve to remove dirt before drying. Yield and yield components were included in the final sampling. Leaf area was determined by LI-3100 area meter (LI-COR, Inc, Lincoln, USA) after all the leaves were stripped from the sample plants. All dry weights were determined after drying in a forced air ventilated drying oven at 70 °C for 48 hrs. Data were analyzed using the GLM procedure of the SAS statistical software (SAS, 2002 V. 9.00) appropriate for the design. Means were separated using Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$ whenever effects were significant.

RESULTS AND DISCUSSION

Physiological parameters

Photosynthesis rate

Photosynthesis rate declined significantly starting from the second day of exposure to early waterlogging (Fig. 1-A₁). However, during the remaining consecutive phases large reductions occurred by the time the first measurement was made after a day of exposure (Fig. 1-A₂, A₃). Mean net photosynthesis rate declined by 42, 87 and 73% due to waterlogging at the vegetative, flowering and seed filling phases averaged over genotypes, respectively. In terms of the actual assimilation rates the lowest values under waterlogging were 4.58, 0.08 and 1.50 μ

mol CO₂ m⁻² s⁻¹ for the corresponding phases. Consistent differences between the two genotypes in photosynthesis rate under optimum and waterlogged conditions. Accordingly, genotype MH-97-6 had shown better photosynthesis rate than Sunaina. As a result, photosynthesis rate of MH-97-6 was greater by 35% under optimum moisture and by 167% under waterlogged conditions, averaged over the entire treatment period. Decline in photosynthesis rate is one of the physiological parameters affected by waterlogging (Ahmed *et al.*, 2002; Islam *et al.*, 2010; Kumar *et al.*, 2013). Kumar *et al.* (2013) observed a loss of assimilation rate by as much as 80% in sensitive mungbean genotypes at the end of a 9 day early waterlogging. The decline in assimilation rate could be attributed to increased stomatal resistance (Takele and McDavid, 1994; Ahmed *et al.*, 2002; Kumar *et al.*, 2013), drop in leaf water potential (Takele and McDavid, 1994; Islam *et al.*, 2010) and reduction in leaf chlorophyll content (Kumar *et al.*, 2013). In this experiment, the increased diffusive resistance could be the major contributing factor for loss of assimilation rate due to waterlogging. Moreover, the chlorosis observed under waterlogging at each of the waterlogging episodes during the three phases could be an additional contributing factor. A significant drop in leaf chlorophyll concentration is observed in mungbean due to waterlogging

appeared only during the seed filling phase, both

(Kumar *et al.*, 2013), which could be manifested as leaf chlorosis. Chlorosis is possibly a symptom to lack of adequate available nitrogen in waterlogged plants. This may be the result of nitrogen deficiency because of leaching (Nathanson *et al.*, 1984), dilution and volatilization and also uptake restriction due to hampered root respiration (Lövenstein *et al.*, 1995). Drop in leaf water potential due to waterlogging was observed in mungbean after exposure to waterlogging at vegetative and flowering phases (Islam *et al.*, 2010). Wilting was apparent only during the flowering and seed filling stresses in this experiment and, thus, it was more likely to affect assimilation rate during these phases.

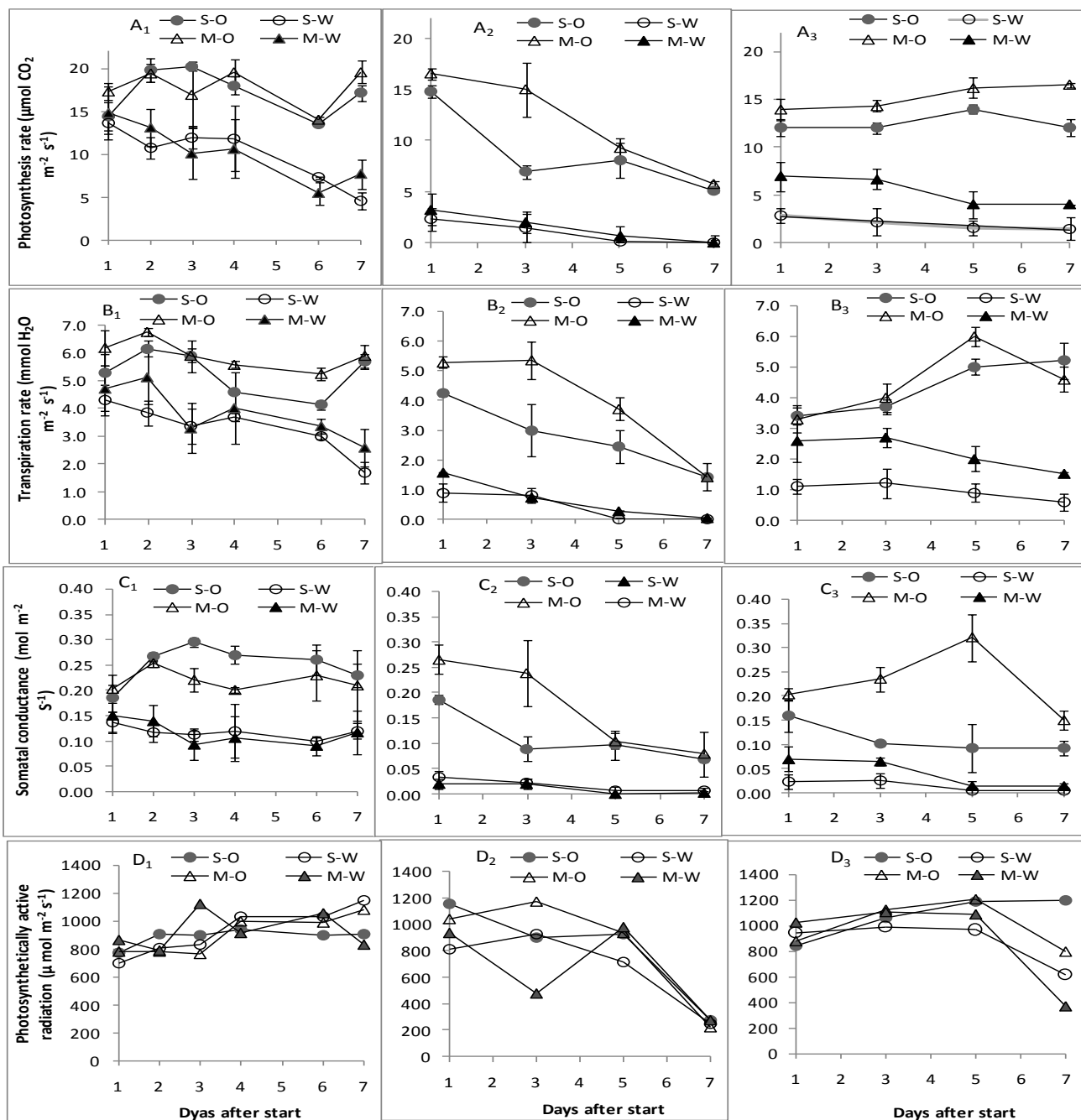


Figure: 1 Waterlogging effects on photosynthesis rate (A₁, A₂, A₃), transpiration rate (B₁, B₂, B₃) and stomatal conductance (C₁, C₂, C₃); Photosynthetically active radiation incident on the leaf during measurement is shown at D₁, D₂, D₃; S-O, Sunaina with optimum moisture; S-W, Sunaina waterlogged; M-O, MH-97-6 with optimum moisture; M-W, MH-97-6 waterlogged; The figure label subscripts 1, 2, 3 designate vegetative, flowering and seed filling phases, respectively.

Photosynthesis declined most from waterlogging at flowering closely

followed by terminal waterlogging. Most leaves have attained full size by the time the plants flowered and any stress markedly accelerates senescence limiting the photosynthetic capacity of the leaves. This also matched the visual observation on the leaves where wilting and senescence were severe under waterlogging at flowering. Similar to our results, photosynthesis was reduced more

from an 8 day waterlogging at flowering compared to that at the vegetative phase (Ahmed *et al.*, 2002). Photosynthesis rate was recovered to pre-stress levels only after exposure to early waterlogging (Table 1). This may be because at later stages senescence could have prevented complete recovery because of aging leaves.

Table 1: Rates of photosynthesis under optimum moisture and after mungbean plants were relieved from waterlogging during vegetative, flowering and seed filling phases*.

Genotype	Rates of photosynthesis ($\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)					
	Vegetative		Flowering		Seed filling	
	Optimum	After terminat ion	Optimum	After terminati on	Optimum	After terminatio n
Sunaina	14.86 \pm 0.62	14.87 \pm 1.01	13.07 \pm 0.66	5.68 \pm 0.67	11.45 \pm 0.90	4.57 \pm 0.73
MH-97-6	16.61 \pm 0.55	16.77 \pm 1.12	16.82 \pm 0.72	7.95 \pm 0.71	15.32 \pm 0.56	6.23 \pm 0.61

*, Measurements were taken two weeks after termination of waterlogging during vegetative and flowering phases and one week after termination at seed filling phase.

Consistent genotypic differences in assimilation rate in response to waterlogging occurred during the terminal phase only (Fig. 1, A₃). The trends of stomatal conductance also support the enhanced assimilation rate of MH-97-6 genotype. The better performance of this genotype in terms of assimilation rate may be due to differences in the onset and rate of leaf senescence, which has a bearing on

assimilation rate. In spite of its greater assimilation rate, MH-97-6 did not exceed Sunaina either in the amount of total biomass or grain yield. This may be primarily attributed to the relatively smaller assimilatory area of MH-97-6, which ultimately influences amount of dry matter accumulated over a period of time.

Secondly, the remaining duration after seed filling was too short to cause a substantial difference in total biomass. Genotypic differences in physiological responses under waterlogging have been reported in mungbean cultivars (Ahmed *et al.*, 2002; Islam *et al.*, 2010; Kumar *et al.*, 2013). These differences translated in to significant yield variation in Kumar *et al.* (2013) but not in Ahmed *et al.* (2002) while no grain yield data was included in Islam *et al.* (2010). The variation in the results could be due to differences in the other attributes of the genotypes that affect dry matter accumulation over a given period of time. For instance, mungbean genotypes, which produced greater grain yield also maintained significantly larger leaf area (Kumar *et al.*, 2013).

Transpiration rate

Impact of waterlogging on transpiration rate was greatest at flowering followed by the seed filling and vegetative phases, respectively (Fig. 1, B₁-B₃). Accordingly, mean losses during the treatment periods were 36, 84 and 64% for the vegetative, flowering and seed filling phases averaged over genotypes, respectively. Clear differences for transpiration rate were apparent under waterlogged conditions of the terminal phase where genotype MH-97-6 had shown

consistently greater rates under waterlogged conditions. Transpiration rate declined in response to waterlogging at any of the growth phases. Similar results have been reported in mungbean (Ahmed *et al.*, 2002), in cowpea (Takele and McDavid, 1994) and in pigeonpea (Takele and McDavid, 1995; Bansal and Srivastava, 2015). Curtailment of transpiration rate could be primarily attributed to loss of stomatal conductance as observed in this study in response to waterlogging at all growth stages. The reduction in transpiration resulting from flooding appeared to be due to a reduction in stomatal conductance and not to a hydraulic change (Gill *et al.*, 2007) nor is not due to a transient water deficit, as leaf water potential is unchanged, even though root conductance is decreased by the stress (Bradford and Hsiao, 1982). Reduced transpiration during stressful conditions may be considered as defense/avoidance mechanism against the stress (Zaidi *et al.*, 2003). Stomatal closure appears to prevent a decrease in leaf water potential, rather than being the result of a leaf water deficit and together with epinasty it may act to restrict transpiration soon after waterlogging, when root conductance has decreased (Bradford and Hsiao, 1982).

Stomatal conductance

Stomatal conductance declined more or less similarly under waterlogging stress at flowering (90%) and seed filling (83%) while the impact of early stress was relatively moderate (50%) (Fig. 1, C₁-C₃). Significant and consistent differences in stomatal conductance between the two genotypes was apparent during the seed filling phase where MH-97-6 had shown greater conductance under optimum moisture while differences narrowed under increasing stress.

Stomatal conductance declined under waterlogging stress irrespective of the growth phase the stress was applied. However, the impact had become more pronounced at later growth phases owing to the natural aging of the leaves. On the other hand, approximately similar sensitivities of stomatal conductance were recorded to waterlogging at vegetative and flowering phases in mungbean (Ahmed, 2002). The rapid increase in stomatal resistance and subsequent reduction in transpiration and net photosynthesis rates of waterlogged plants may be an adaptive response to water stress caused either by water deficit or excesses (Takele and McDavid, 1995). High stomatal resistance under waterlogging could be related to lack of oxygen availability, which affects normal root functions. Moreover, accelerated leaf senescence that decreases density of functional stomata after exposure to

waterlogging especially at mid and terminal phases is another contributing factor. On the other hand, no significant decline on root growth was observed under early waterlogging due to compensatory adventitious root production, in this study. This may show that additional factors could be contributing in initiating the stomatal closure mechanism in waterlogged plants. Flooding may induce stomatal closure apparently without detectable changes in leaf water potential because oxygen shortage in roots can stimulate abscisic acid production which ultimately causes stomatal closure (Taiz and Zeiger, 2002). Moreover, partial closure of stomata during waterlogging may have beneficial role in avoiding the upward movement of toxic elements (Zaidi *et al.*, 2003).

Shoot growth

Leaf area was significantly reduced by 31% just after termination of early stress and this was accompanied by 38% loss in its dry weight (Table 2). At final harvest the reduction in leaf dry weight has become more severe (46%) for the same waterlogging period (Table 3). Waterlogging at flowering decreased leaf dry matter by half while the terminal one reduced it by about two third (Table 3). Plant height and its dry weight were not affected at the end of the early waterlogging treatment (Table 2). However, it was moderately suppressed due to early waterlogging when observed

at final harvest while its dry weight was not affected (Table 3). Waterlogged plants at flowering and seed filling had slightly shorter heights though this was accompanied by dry matter loss only for the former (Table 3). Shoot dry weight declined nearly by one third due to early waterlogging at the end of the treatment period (Table 2) and this had slightly

increased at final harvest for the same treatment (Table 3). The increased drop from early stress at final harvest was due to additional fall in reproductive growth. Waterlogging during the flowering and the seed filling phases decreased shoot dry matter by 68% and 45% at maturity, respectively.

Table 2: Effects of waterlogging at the vegetative phase on shoot and root growth parameters of mungbean genotypes, immediately after termination*.

Treatment	Plant height (cm)	Leaf area (cm ²)	Leaf dry wt (g)	Stem dry wt (g)	Shoot dry wt (g)	Root dry wt (g)	Root-shoot ratio
Moisture							
Optimum	9.8a	45a	0.180a	0.058a	0.239a	0.018a	0.079b
Waterlogged	8.4a	31b	0.112b	0.055a	0.167b	0.026a	0.161a
Genotypes							
Sunaina	9.7a	45a	0.166a	0.063a	0.230a	0.025a	0.117a
MH-97-6	8.5a	31b	0.126b	0.050a	0.176b	0.019a	0.122a
LSD _{5%}	1.36	8.7	0.028	0.018	0.041	0.008	0.051

*, data are given on per plant basis; column means with the same letter are not significantly different at $P \leq 0.05$.

Leaf growth was the most sensitive above ground vegetative growth parameter and was affected by waterlogging at all phases. Both leaf dry matter and leaf area suffered a loss immediately after the seven day waterlogging episode. The damage on leaf dry matter did not recover at maturity either. The impact from the stress on leaf growth increased with the advancing age of the plant because of the additional impact due to

accelerated senescence. Similarly, decrement of leaf area was observed in mungbean due to eight days waterlogging event during the vegetative and flowering phases (Ahmed *et al.*, 2002). The reduced canopy size due to early waterlogging could be attributed to reduced leaf growth rate because of inadequate assimilate supply since neither senescence nor leaf abscission was observed at this phase. Restriction of

canopy size from waterlogging during flowering and seed filling phases was due to combined contributions from reduced growth rate, senescence and abscission. Leaf area reduction could be an adaptive mechanism against restricted water uptake as observed from reduced transpiration rate. Reduction of water loss through decreased leaf area and enhanced adventitious root growth could be adaptive mechanisms against waterlogging (Bacanamwo and Purcell, 1999). It could also be partly attributed to a shift in allocation of dry matter in

favour of the root as observed in this experiment immediately after early stress. Kumar *et al.* (2013) reported higher dry matter accumulation in root and lower in stem and leaf under waterlogging in tolerant genotypes while the reverse happened in sensitive ones. As a site of light interception and assimilation leaf area reduction has far reaching consequences by affecting productivity. As a result it has shown a strong and significant relationship with total dry matter ($r = 0.83^{***}$) and seed yield ($r = 65^{**}$).

Table 3: Effects of waterlogging at three growth phases on shoot and root growth parameters of mungbean genotypes, at maturity*.

Treatment	Plant height (cm)	Leaf dry wt (g)	Stem dry wt (g)	Root dry wt (g)	Shoot dry wt (g)	Root-shoot ratio
Moisture**						
OOO	25.8a	1.93a	0.873a	0.125a	6.56a	0.054a
WOO	20.5b	1.05b	0.688ab	0.093a	3.99b	0.059a
OWO	21.5b	0.95b	0.563b	0.051c	2.09c	0.073a
OOW	22.5b	0.72b	0.706ab	0.070bc	3.59b	0.057a
LSD _{5%}	3.05	0.35	0.189	0.040	0.81	0.018
Genotypes						
Sunaina	23.7a	1.33a	0.810a	0.109a	4.41a	0.076a
MH-97-6	21.5b	0.99b	0.605b	0.060b	3.70b	0.045b
LSD _{5%}	2.15	0.24	0.134	0.028	0.572	0.025

*, data are given on per plant basis; **, O, optimum, W, waterlogged and positions of the letters represent vegetative, flowering and seed filling phases in that order; column means with the same letter are not significantly different at $P \leq 0.05$.

The stem was found to be resilient and did suffer only a moderate reduction from mid waterlogging. Similarly, Henshaw *et al.* (2007) did not find a significant drop on stem dry matter after a two week waterlogging treatment on soybean. On the other hand, an eight day early waterlogging caused a considerable effect on mungbean stem height while the impact was slight due to waterlogging at flowering (Ahmed *et al.*, 2002). Greater stem dry matter accumulation under waterlogging may be associated with a genotype's susceptibility to the stress as observed in mungbean (Kumar *et al.*, 2013) and in cowpea (Takele and McDavid, 1994). Lodging and plant mortality were the other problems observed during the experiment. Plants lodged markedly under waterlogging especially at mid and terminal phases because the roots lacked firm anchorage and became loose. It could be a problem under field conditions affecting both amount and quality of produce since it would be difficult to get every plant supported, unlike pot grown plants. On the other hand, 20% plant mortality occurred only due to early waterlogging. Under field conditions this will impact productivity by causing permanent reduction in population density.

Root growth and root-shoot ratio

No change was observed on root growth due to vegetative waterlogging either at the end of the stress (Table 2) or at physiological maturity (Table 3).

On the other hand, early waterlogging increased root-shoot ratio by 104% at the end of the stress period (Table 2) while differences were not significant at physiological maturity (Table 3). Mid and terminal waterlogging caused a 59 and 44% drop in root dry matter, respectively and their root-shoot ratios were not significantly different from the control. Root growth was most sensitive to terminal waterlogging followed by mid waterlogging while it was resilient to early waterlogging. This was mainly due to disintegration and decay of the existing root biomass under mid and terminal waterlogging. Similarly, root growth was found to be more tolerant to waterlogging during the vegetative phase compared to the reproductive phase in mungbean (Islam *et al.*, 2010) and in cowpea (Umaharan *et al.*, 1997). On the other hand, both vegetative and reproductive phases were found to be similarly susceptible to waterlogging for root growth in mungbean (Ahmed *et al.*, 2002). The disparity in the results could be attributed to genotype variation and differences in commencement of the waterlogging episode. A greater root-shoot ratio for waterlogged plants under early waterlogging indicated a

preferential investment on the root contributing to growth of adventitious roots. Absence of differences in root-shoot ratio after the vegetative phase could be because the root is no longer a priority for assimilate distribution as the plant ages. Moreover, root growth subsides after the end of the vegetative growth period in determinate types. Formation of adventitious roots could be responsible for maintenance of root dry matter under vegetative waterlogging, which is one of the adaptation mechanisms. Waterlogging greatly accelerated the development of new adventitious roots in mungbean (Ahmed *et al.*, 2002; Kumar *et al.*, 2013). In spite of a tolerant root system to early waterlogging shoot dry matter production declined. This could be mainly attributed to the lower assimilation rate and smaller assimilatory area observed under waterlogging. Moreover, adventitious roots might not be as effective as the main root system in absorption of minerals and water and were also operating under hypoxia.

Genotype differences

Genotype Sunaina produced 31% more shoot dry matter than MH-97-6 at the end of early waterlogging (Table 2). This was attributed to its greater dry matter production in its leaf, which was maintained to the final harvest, though narrowed (Table 3). Additionally, Sunaina exceeded in root and stem dry

matter at final harvest contributing further to its superiority in shoot biomass. Sunaina had also increased dry matter partitioning in favor of the root by 69% compared to MH-97-6. However, no genotype by moisture interaction was observed for vegetative growth parameters showing that the two genotypes responded to the stress in a similar way.

Sunaina has shown a clear superiority over MH-97-6 in all vegetative growth components including stem, leaf and root. However, in spite of its better root system and greater dry matter allocation to the root it has not shown better tolerance to waterlogging. It has been shown that better root growth and adventitious root production could be contributors to waterlogging tolerance. For instance, in faba bean, Solaiman *et al.* (2007) indicated that waterlogging tolerance might be related to formation of adventitious roots with modest amounts of aerenchyma. Similar to our results, Palta *et al.* (2010) observed that greater early vigor and better root growth did not make a kabuli chickpea genotype tolerant to waterlogging compared to the desi type. On the other hand, physiological parameters such as assimilation and transpiration rates were better especially during the terminal phase in MH-97-6 genotype though this does not contribute to improved performance under stress.

These events may indicate the fact that tolerance is better conferred on a genotype through coordinated contributions of various traits rather than from an expression of a trait or two.

Yield, yield components and harvest index

The highest loss of 85% in seed yield occurred due to waterlogging at flowering (Table 4). The stresses at seed filling and vegetative phases affected yield to a lesser degree and were equally sensitive to waterlogging with reductions of 43 and 44 % , respectively. Number of

Pods per plant reflected changes observed in seed yield in that it suffered its greatest drop at mid stress while equally and moderately affected under the other two stresses (Table 4). Seed number per pod was equally sensitive to waterlogging administered at each of the three phases. On the other hand, seed weight was reduced by a third due to the stress at flowering only, contrary to the expectation. Harvest index dropped by 54% due to flowering stress while not affected by stress at the other two phases (Table 4). Statistically significant genotype by moisture interactions was not observed for productivity parameters.

Table 4: Effects of waterlogging at three phenological phases on seed yield, yield components and harvest index of mungbean genotypes at maturity*.

Treatment	Seed yield plant ⁻¹ *	Pod no. plant ⁻¹	Seed no. pod ⁻¹	Hundred seed wt* (g)	Harvest index
Moisture**					
OOO	2.81a	8.6a	6.9a	4.6a	0.424a
WOO	1.60b	6.5b	5.5b	4.4a	0.395a
OWO	0.43c	2.3c	5.7b	3.0b	0.196b
OOW	1.56b	5.9b	5.6b	4.6a	0.418a
LSD _{5%}	0.44	1.24	1.1	0.6	0.085
Genotypes					
Sunaina	1.69a	6.05a	5.7a	4.47a	0.351a
MH-97-6	1.51a	5.75a	6.1a	3.89b	0.366a
LSD _{5%}	0.31	0.87	0.77	0.42	0.060

*, Given as dry matter; **, O, optimum, W, waterlogged and positions of the letters represent vegetative, flowering and seed filling phases in that order; column means with the same letter are not significantly different at $P \leq 0.05$.

The flowering phase was most sensitive to grain yield under waterlogging. The greatest root damage, maximum diffusive resistance, highest senescence, largest flower drop and the utmost pod abortion that occurred under waterlogging at this phase may have contributed for its susceptibility. The terminal waterlogging effect had been relatively milder on these parameters making seed yield to fare better under this stress. Comparable average losses from vegetative waterlogging were observed in mungbean though with more severe impacts on sensitive genotypes (Kumar *et al.*, 2013). On the other hand, Ahmed *et al.* (2002) observed much smaller yield reduction at vegetative and flowering stress compared to ours to a comparable duration of waterlogging. This may be because, the plants were grown in sand culture where waterlogging could be stopped immediately after treatments were taken off immersion pots while in our case complete drainage required more time. Also, plants were grown under a continuous supply of nutrient solutions, thus, preventing stress from poor nutrition due to leaching of key elements like nitrogen unlike our soil grown plants. Differential sensitivity of growth phases to waterlogging have been reported in various pulses. Accordingly, Cowie *et al.* (1996) observed that the seed filling phase is most sensitive to a 10 day waterlogging followed by flowering and

vegetative phases, respectively, in chickpea. In soybean, Linkemer *et al.* (1998) identified that the podding period was the most sensitive with some yield reductions observed at flowering, seed filling and early vegetative phase from a seven day waterlogging. The number of pods per plants was found to be the most sensitive among the yield components. The most dominant yield component, number of pods per plant, reflected the changes observed in seed yield and it was strongly correlated with grain yield ($r = 0.95^{***}$). Similarly, Ahmed *et al.* (2002) and Ullah (2006) reported a severe reduction of pod number per plant in mungbean following waterlogging during the vegetative and the vegetative and reproductive phases, respectively. As a result, waterlogging at vegetative and flowering stages reduced seed yield primarily by reducing the number of pods per plant. The two genotypes had statistically similar yield though Sunaina gave 12% more yield (Table 4). Also, they did not vary either for harvest index or for yield components except for seed size where Sunaina had heavier seed weight. In spite of differences in total dry matter production no significant variation was observed on seed yield between the two genotypes. In another study Worku (2008) reported a significant yield advantage for Sunaina over MH-97-6. In the presence of significant variation in total dry matter and seed weight and

absence of difference in harvest index the greater performance of Sunaina should not be ignored and needs to be watched in future tests. On the other hand, given the use of mungbean straw as a valuable feed Sunaina could be a potentially useful genotype owing to its superior biomass production.

CONCLUSION

The experiment has shown that developmental phases varied in sensitivity to waterlogging with the flowering phase being most susceptible both for seed yield and total biomass. The stress at flowering also affected seed quality by decreasing seed size. The two remaining phases were similarly influenced in terms of yield and yield components. The crop did not show growth recovery after exposure to short term early waterlogging. Rather, the high yield penalty noticed under early waterlogging is an indicator of the crop's

high sensitivity to the stress. Moreover, the two tested genotypes did not vary for tolerance to waterlogging. Thus, the best guarantee against waterlogging would be to grow the crop in soils not prone to waterlogging and sow it in the short rainy season where the risk for waterlogging is relatively low. Moreover, adjusting planting time to avoid coincidence of flowering with intense rainfall spell is an additional measure. It would be worthwhile to screen more genotypes against waterlogging with incorporation of additional factors such as nutrient management and soil type.

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