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WATERLOGGING EFFECTS ON GROWTH, NODULATION AND PRODUCTIVITY OF DESI AND KABULI CHICKPEA (*CICER ARIETINUM* L.)

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ABSTRACT: Early planting against terminal drought and increase in precipitation extremes due to climate change may expose chickpea production to transient waterlogging. Desi and kabuli type chickpea were subjected to 10 days waterlogging during three phases to assess relative sensitivity among phases and between genotypes and to identify traits that may contribute for performance under the stress. Waterlogging increased stomatal resistance with full conductance recovery made only after relief from early waterlogging. The desi type maintained consistently greater stomatal resistance against waterlogging. Root growth and nodulation were most resilient to early stress while irreversibly destroyed by mid and terminal waterlogging. On the other hand, aboveground vegetative growth suffered most from early and mid waterlogging while it was not affected by terminal stress. A moisture by genotype interaction showed that the desi type suffered a 21% loss in seed yield while the kabuli lost almost twice as much, 39%. The flowering phase was most susceptible to waterlogging followed by seed-filling irrespective of chickpea type with mean reductions of 97% and 56%, respectively. Susceptibility of the flowering phase was due to large flower abortion, severe root and nodule degradation, shortened seed filling duration, detrimental leaf senescence and persistently high stomatal resistance. Relative tolerance of desi type against vegetative waterlogging for yield performance may be associated with fast recovery from chlorosis, increased pod production on the main stem and better nodulation capacity. It seems that the desi genotype, Naatolii, can be a better choice when risk of early waterlogging is anticipated from early planting or weather variability.

Key words/phrases: Chickpea, Growth, Nodulation, Seed yield, Waterlogging.

INTRODUCTION

Globally, chickpea is the third important pulse crop next to soybean (*Glycine max*) and dry beans (*Phaseolus vulgaris*) (FAO, 2013). In Ethiopia, chickpea also ranks third among staple pulses (CSA, 2013) and is considered as one of the strategic crops to improve food and nutrition security and to boost foreign exchange earnings. Ethiopia is the largest producer of chickpea in Africa contributing nearly half of the production in the continent, estimated at 682,384 tonnes (FAO, 2013). Chickpea cropping

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system is largely rainfed and terminal drought of varied intensities is a major constraint to its productivity worldwide (Krishnamurthy *et al*., 2010). In Ethiopia, the crop is predominantly grown on conserved soil moisture as a rainfed crop on Vertisols beginning from September to October (Million Eshete, 1994) with a high probability of facing drought (Geletu Bejiga and Yadeta Anbessa, 1994). Given the current practices, chickpea productivity on Vertisols is constrained by severe waterlogging when sown early and by drought when sown late (Getachew Agegnehu and Woldeyesus Sinebo, 2012). There is a possibility of reducing the impact of terminal drought, which mostly coincides with the reproductive phase by planting earlier. However, this at times coincides with heavy rainfall, which creates a waterlogging problem. The situation could be aggravated because chickpea is mostly grown on Vertisols, which are prone to poor drainage. Early planting on a Vertisol in mid-August using a conventional flat seed bed reduced grain yield by 74% due to waterlogging while the loss was 60% for early September planting compared to plots drained with improved technology (Regassa Ayana, 2011). In another study, grain yield dropped by 42 and 13% due to poor drainage on a Vertisol from early and late August plantings, respectively, in central Ethiopia (Getachew Agegnehu and Woldeyesus Sinebo, 2012). Moreover, 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 major abiotic stress adversely affecting crop productivity worldwide (Solaiman *et al*., 2007; Shimono *et al*., 2012; Bansal and Srivastava, 2012). Impacts of waterlogging on various agronomic and physiological parameters have been studied in many pulses. Loss of productivity in grain yield and pod number per plant from waterlogging has been reported in chickpea (Cowie *et al*., 1996; Palta *et al*., 2010) and in soybean (Linkemer *et al*., 1998). Reductions in stomatal conductance and rate of assimilation due to waterlogging has been observed in mungbean (*Vigna radiata*) (Kumar *et al*., 2013), pigeonpea (*Cajanu cajan*) (Abuhay Takele and McDavid, 1995), snap bean (*Phaseolus vulgaris*) (Singh *et al*., 1991) and soybean (Oosterhuis *et al*., 1990) while losses in leaf area and transpiration rate were reported in cowpea (*Vigna unguiculata*) (Abuhay Takele and McDavid, 1994) and in snap bean (Singh *et al*., 1991).

Root growth, nodulation and nitrogen fixation are known to be affected by waterlogging. For instance, reduced root growth was observed in chickpea (Solaiman *et al*., 2007; Palta *et al*., 2010), in cowpea (Umaharan *et al*.,

1997) and in soybean (Henshaw *et al*., 2007a) while Jung *et al*. (2008) and Maekawa *et al*. (2011) reported a decline in both nodulation and nitrogen fixation activity in soybean. On the other hand, Guafa *et al*. (1993) and Nathanson *et al*. (1984) observed enhanced nodulation and nitrogen fixation under a saturated soil culture where saturated irrigation is maintained a few centimetres below the soil line, in soybean.

The tolerance of grain legumes to waterlogging may vary between and within species (Solamain *et al*., 2007). Genetic variation for waterlogging tolerance has been shown in chickpea (Palta *et al*., 2010), in pigeonpea (Bansal and Srivastava, 2012), in faba bean (*Vicia faba*) (Solaiman *et al*., 2007), in cowpea (Abuhay Takele and McDavid, 1994), in soybean (Hartley *et al*., 1993, Henshaw *et al*., 2007a) and in lentil (*Lens culinaris*) (Ashraf and Chishti, 1993). The traits identified to be responsible to confer tolerance are variable. In cowpea, Abuhay Takele and McDavid (1994) have suggested that cultivar differences in the number of secondary roots maintained and in the extent and distribution of aerenchyma may contribute to the relative tolerance of the cultivars to waterlogging. Similarly, Solaiman *et al*. (2007) indicated that waterlogging tolerance in faba bean might be related to formation of adventitious roots with modest amounts of aerenchyma. On the other hand, Palta *et al*. (2010) observed that in spite of greater early vigour and better root growth the kabuli genotype suffered greater yield loss than the desi type and suggested fast growth of new roots and rapid recovery of root growth to be useful traits for waterlogging tolerance. However, Henshaw *et al*. (2007a) did not get evidence to support linkage between grain yield and early season morphological response advocating the need for full season trials that go to final yield to screen potentially tolerant genotypes.

From an agronomic point of view, plant tolerance to waterlogging involves the maintenance of a relatively high grain yield under these conditions (San Celedonio *et al*., 2014). There are limited studies made to compare sensitivities of chickpea types to waterlogging. Palta *et al*. (2010) evaluated the response of desi and kabuli cultivars to severe subsurface waterlogging (12 days) during the vegetative growth phase. They observed that the transient waterlogging reduced seed yield by 54% in the kabuli genotype and by 44% in the desi type showing the relative sensitivity of the former. Cowie *et al*. (1996) exposed a desi genotype to 10 days waterlogging at various growth phases and observed that waterlogging at any stage reduced yield with losses amounting to 35, 53 and 67% for vegetative, flowering and pod filling phases, respectively. So far, limited information is available on the comparison of the response of both desi and kabuli chickpea types to waterlogging at different phenological phases.

This research was, therefore, initiated to: (1) investigate the response of desi and kabuli chickpea genotypes exposed to waterlogging at different phases, (2) identify the sensitive phase(s) that limit productivity most and (3) observe whether the two chickpea types differ in their response or not and identify the contributing factors if there are differences.

MATERIALS AND METHODS

Experiment set-up

Two greenhouse experiments were carried out; the first between December 2011 and March 2012 and the second between October 2013 and January 2014 at Hawassa University, Hawassa, southern Ethiopia. Hawassa is located 7°5' N and 38°30' E at 1660 metres a.s.l. The greenhouse had a clear polyethylene roof and the sides were covered with wire mesh for better aeration. Based on averaged temperature and relative humidity measurements (VAISALA, Finland) the relative humidity inside was higher by 2.7% while temperature was lower by 0.38°C, compared to the ambient conditions outside. The average photosynthetically active radiation transmission was 41% with R/FR ratio of 1.01. The potting soil was brought from Jole Andegna site of Meskan district in southern Ethiopia from a farmer’s field where chickpea production is practiced. The soil analysis before planting has indicated that it contained 28% silt, 35% sand and 37% clay with a clay loam texture (Askalech Fikadu, 2014). The soil has also 0.042% total nitrogen, 2.6% organic matter, 17 mg kg^{-1} available phosphorus and 18 cmol kg^{-1} cation exchange capacity. The pH of the soil was slightly acidic (6.5) and the water holding capacity (v/v) was 29.5% at 0.03 MPa and 19.7% at 1.5 MPa. The physico-chemical characteristics of the soil were generally within the range considered suitable for chickpea production.

Treatments, design and procedures

The treatments were made from a factorial combination of two chickpea types (desi and kabuli) and four moisture regimes (optimum throughout, waterlogging during either of the three growth phases and waterlogging during each of the growth phases). The genotypes used in the experiment were Naatolii and Habru representing the desi and kabuli types, respectively. Both are released improved varieties for commercial production in Ethiopia. Moreover, these varieties were selected through participatory variety selection to expand chickpea production in southern Ethiopia.

The following were the moisture levels used:

1. Optimum throughout = OOO
2. Waterlogging during the vegetative phase and optimum thereafter = WOO
3. Waterlogging during the flowering phase and optimum at the other phases = OWO
4. Waterlogging during the seed filling phase and optimum at the other phases = OOW
5. Waterlogging during each of the three growth phases = WWW

A completely randomized design was used with three replications.

Similar establishment and maintenance procedures were followed for both experiments. Five pre-germinated seeds were planted in six litre capacity (20 cm diameter and 19 cm height) plastic pots perforated at the bottom for drainage. Seeds were kept in a petridish with moistened paper towel for four days to initiate germination. A commercial *Bradyrhizobium* inoculant was applied in each planting hole just before transplanting. The fertilizer diammonium phosphate (18:46:0) was applied at a rate of 3 g pot^{-1}, 8 days after planting. The seedlings were thinned to three plants per pot 10 days after transplanting.

Waterlogging was administered by immersing the experimental pots in a pot of 13 litre capacity (28 cm diameter and 21 cm height) for 10 days. About 2 cm of water layer was maintained above the soil line of the experiment pots during the waterlogging period. At the end of the waterlogging period, the pots were taken out of the immersion pots and were allowed to drain. The vegetative period waterlogging was started ten days after transplanting. The flowering and seed filling phase waterlogging events were carried out at the respective dates the genotypes attained these phases. Commencement of seed filling phase was taken as the date where all plants in a pot had their first full pod.

Data measurement

Stomatal resistance was measured with a leaf porometer (Decagon Devices, Inc, Pullman, USA) on a fully expanded and unshaded youngest leaf from the top between 10:00 and 11:00 hrs local time, in the first experiment. It was measured during each of the three waterlogging events that were administered at the vegetative, flowering and seed filling phases. Measurement started one day after the commencement of the waterlogging episodes at each of the three phases and continued mostly at daily or at every other day interval. For the vegetative and flowering phase stresses, the measurements continued after the 10 day stress period until measurements become stable on plants relieved from waterlogging. However, measurement under seed filling stress was stopped eight days after commencement of waterlogging due to severe leaf senescence. All of the stomatal resistance measurements were made on both waterlogged and non waterlogged plants involving the three replications per treatment.

The initial samples from the first experiment were taken at about mid-flowering: 23 and 30 days after kabuli and desi types were relieved from vegetative waterlogging, respectively. From the second experiment, first sampling was made immediately after the vegetative phase waterlogging was terminated. Three pots were harvested for each of the four treatments at each sampling under both experiments. Data recorded from first sampling of each experiment included branch number, leaf area, leaf dry weight, stem dry weight, branch dry weight, root dry weight, nodule number, nodule dry weight, total dry weight, branch weight ratio, stem weight ratio and root-shoot ratio. Days to flowering and nodule-shoot ratio were additionally recorded from the first experiment. For leaf area measurement, all the leaves were stripped from sample plants and their area was determined by a LI-3100 area metre (LI-COR, Inc, Lincoln, USA). Branch and stem weight ratios were determined as a ratio of branch dry weight and stem dry weight to total dry weight, respectively. Root-shoot ratio and nodule-shoot ratio were calculated as a ratio of root dry weight and nodule dry weight to above ground dry weight, respectively. All dry weight measurements were made after drying samples in a forced air ventilated oven at 70°C for 48 hrs.

The three sample plants in each pot were carefully uprooted from a moistened pot soil for determination of nodulation. The soil adhering to the roots was washed carefully over a metal sieve under a running tap water. The nodules were then carefully detached from the root and were counted and weighed after oven drying.

The second samplings from both experiments were made from a final harvest that was made at physiological maturity. Harvests were made on treatment basis, not on experiment basis, due to the variation among treatments to reach maturity. As in the first sampling, three pots were harvested per treatment. The data collected included days to maturity, number of basal and upper branches, nodule number, leaf dry weight, stem dry weight, branch dry weight, nodule dry weight, root dry weight, total dry weight, straw dry weight, number of pods per plant and branches, 100 seed weight, seed yield and harvest index. Seed weight was reported as dry matter after oven drying at 70°C for 48 hrs. Harvest index was determined as a ratio of dry seed yield to total dry matter.

Data analyses

Data were analyzed using the GLM procedure of the SAS statistical software (SAS, 2000) appropriate for the design. A combined analysis of variance was made for data collected from the two experiments at maturity based on Gomez and Gomez (1984), except phenology. Means were separated using Fisher's Least Significant Difference (LSD) test at $P<0.05$.

RESULTS

Stomatal resistance

Stomatal resistance increased following waterlogging during any of the developmental phases with maximum values attained in the reproductive phases (Fig. 1). While full recovery of stomatal conductance was made three days after relief from vegetative waterlogging, no recovery was possible during either of the two remaining phases. The desi and kabuli genotypes differed consistently in the magnitude of their response with the desi type maintaining relatively greater stomatal resistance during the waterlogging periods.

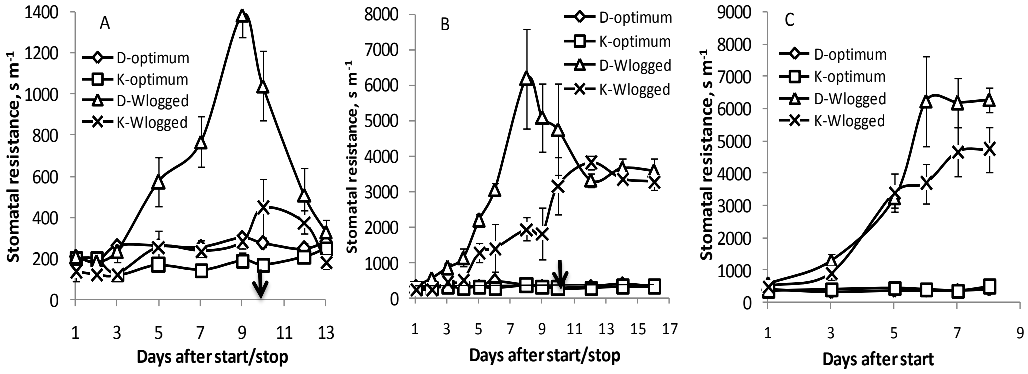

Fig. 1. Effects of waterlogging on stomatal resistance in desi and kabuli chickpea during (A) vegetative (B) flowering and (C) seed filling phase. D, desi; K, kabuli; wlogged, waterlogged; arrow indicates date treatment stopped.

Immediately after termination of vegetative waterlogging

Shoot growth: Vegetative waterlogging severely retarded shoot growth parameters: branch number, leaf area, dry weights of branch and leaf (Table 1). The reductions amounted to 83% in branch dry weight, 73% in leaf area and 71% in leaf dry weight. As a result, waterlogged plants had total dry matter less by 72% compared to plants under optimum moisture.

The kabuli type maintained better growth rates for all observed parameters (Table 1). Notable differences were observed for stem and branch dry weights where the kabuli had 49% more dry matter.

Table 1. Effects of waterlogging during the vegetative phase on various parameters of desi and kabuli chickpea immediately after termination[a].

Treatment	**Branch no.**	**Leaf area (cm^2)**	**Stem dry wt (g)**	**Branch dry wt (g)**	**Leaf dry wt (g)**	**Total dry wt (g)**	**Branch wt ratio**
Moisture							
Optimum	3.6a	130a	0.143a	0.188a	0.667a	1.23a	0.145a
Waterlogged	2.1b	35b	0.0 91b	0.031b	0.193b	0.36b	0.084b
Chickpea type							
Desi (Naatolii)	2.5b	73b	0.094b	0.088b	0.385b	0.76b	0.098b
Kabuli (Habru)	3.1a	92a	0.140a	0.132a	0.474a	0.90a	0.129a
$LSD_{5\%}$	**0.419**	**11**	**0.020**	**0.026**	**0.064**	**0.12**	**0.0128**

[a] data are given on per plant basis except the ratio; column means with the same letter are not significantly different at P<0.05.

Root growth, nodulation and partitioning: Genotype by moisture interaction influenced root dry weight, nodule number, root-shoot ratio and stem weight ratio (Fig. 2). Root dry weight, nodule number and root-shoot ratio were greater for the desi under optimum moisture while no differences were observed under waterlogging. On the other hand, the kabuli had greater stem weight ratio under optimum moisture with no differences between the two types under stress. Both types raised their stem weight ratio under waterlogging; the desi by 176% and the kabuli by 97%. Conversely, waterlogging reduced amount of assimilates allocated to branches by 42% (Table 1).

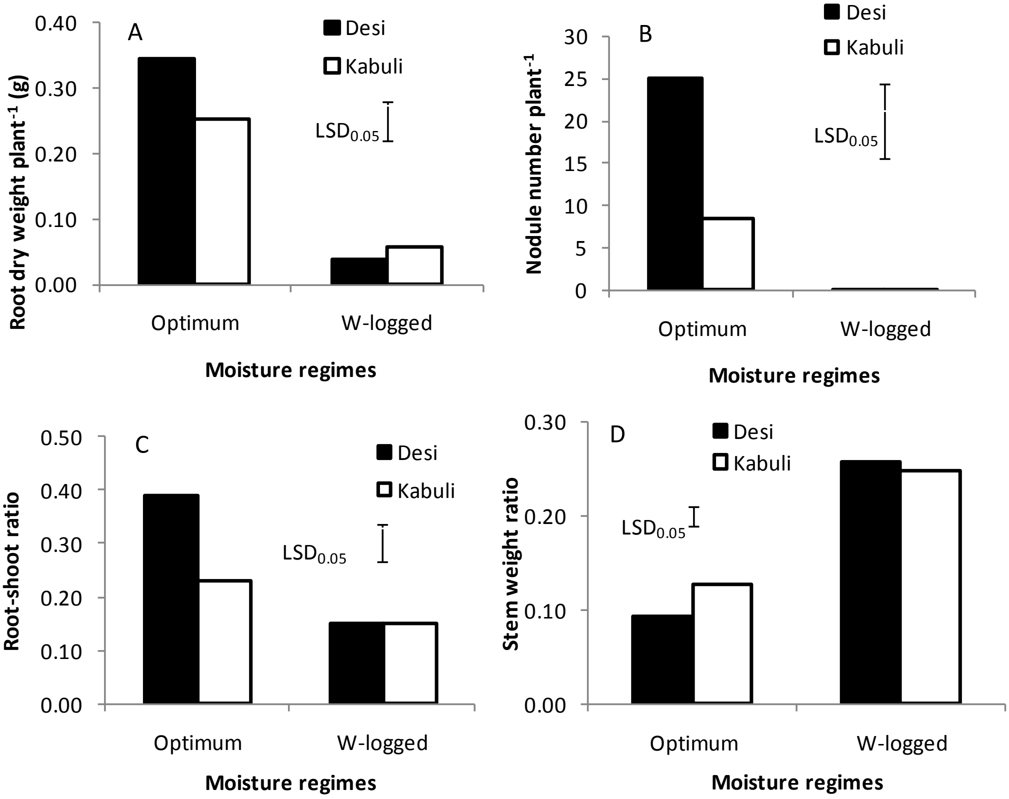

Fig. 2. Effects of moisture x genotype interaction on (A) root dry weight (B) nodule number (C) root-shoot ratio and (D) stem weight ratio in kabuli and desi chickpea immediately after termination of vegetative waterlogging.

At mid flowering after a recovery period

Phenology and shoot growth: Early waterlogged plants required six more days to attain flowering (Table 2). On the other hand, these plants had fewer branch number, smaller leaf area, lower leaf dry matter and lesser total biomass. Reductions were 37% for branch number, 27% for leaf area, 34% for leaf dry matter and 35% for total biomass. Also, moisture x genotype interaction affected stem and branch dry weights (Fig. 3). Accordingly, the desi type had larger branch dry matter compared to stem under optimum moisture while the reverse was true for the kabuli type. However, the two genotypes did not differ in their stem and branch dry weights under waterlogging.

Table 2. Effects of waterlogging during the vegetative phase on various parameters of desi and kabuli chickpea, at mid flowering[ab].

Treatment	**Days to flower**	**Branch no.**	**Leaf area (cm^2)**	**Leaf dry wt (g)**	**Root dry wt (g)**	**Nodule no.**	**Total dry wt (g)**	**Root-shoot ratio**	**Nodule-shoot ratio**
Moisture									
Optimum	33.0b	2.7a	450a	1.45a	0.20a	81a	3.36a	0.066a	0.059b
Waterlogged	39.0a	1.7b	330b	0.96b	0.16a	74a	2.20b	0.085a	0.088a
Chickpea types									
Desi (Naatolii)	40.0a	2.2a	411a	1.25a	0.17a	96a	3.03a	0.067a	0.097a
Kabuli (Habru)	32.0b	2.2a	369a	1.16a	0.19a	59b	2.53b	0.085a	0.050b
$LSD_{5\%}$	**1.3**	**0.4**	**49**	**0.12**	**0.05**	**22**	**0.27**	**0.021**	**0.028**

[a] data are given on per plant basis except for days to flower and the ratios; [b] data were taken about 23 and 30 days after plants were relieved from vegetative waterlogging for kabuli and desi types, respectively; column means with the same letter are not significantly different at P<0.05.

Root growth, nodulation and partitioning: Unlike the shoot, root growth has recovered from the vegetative phase stress (Table 2). Differences were not observed in number of nodules between the two moisture regimes, either. While both types recovered for nodule dry weight the desi type was superior at both moisture levels with a larger difference under optimum moisture (data not shown). Root-shoot ratio showed a tendency to increase under waterlogging (P=0.07), which was a reverse trend from the result at the end of the early stress. Similarly, nodule-shoot ratio increased due to waterlogging by 49%. The interaction on the stem weight ratio and branch weight ratio reflected opposite trends on the investment of dry matter to the stem and branches (Fig. 3).

At mid flowering, the desi type took eight more days to flower, had more nodules and nodule mass and produced greater total biomass, while at par with the kabuli for the remaining parameters (Table 2). The desi type had 63% more nodules which were two and half times heavier than the nodule mass from kabuli. The nodule-shoot ratio of the desi types was twice as much as that in the kabuli type.

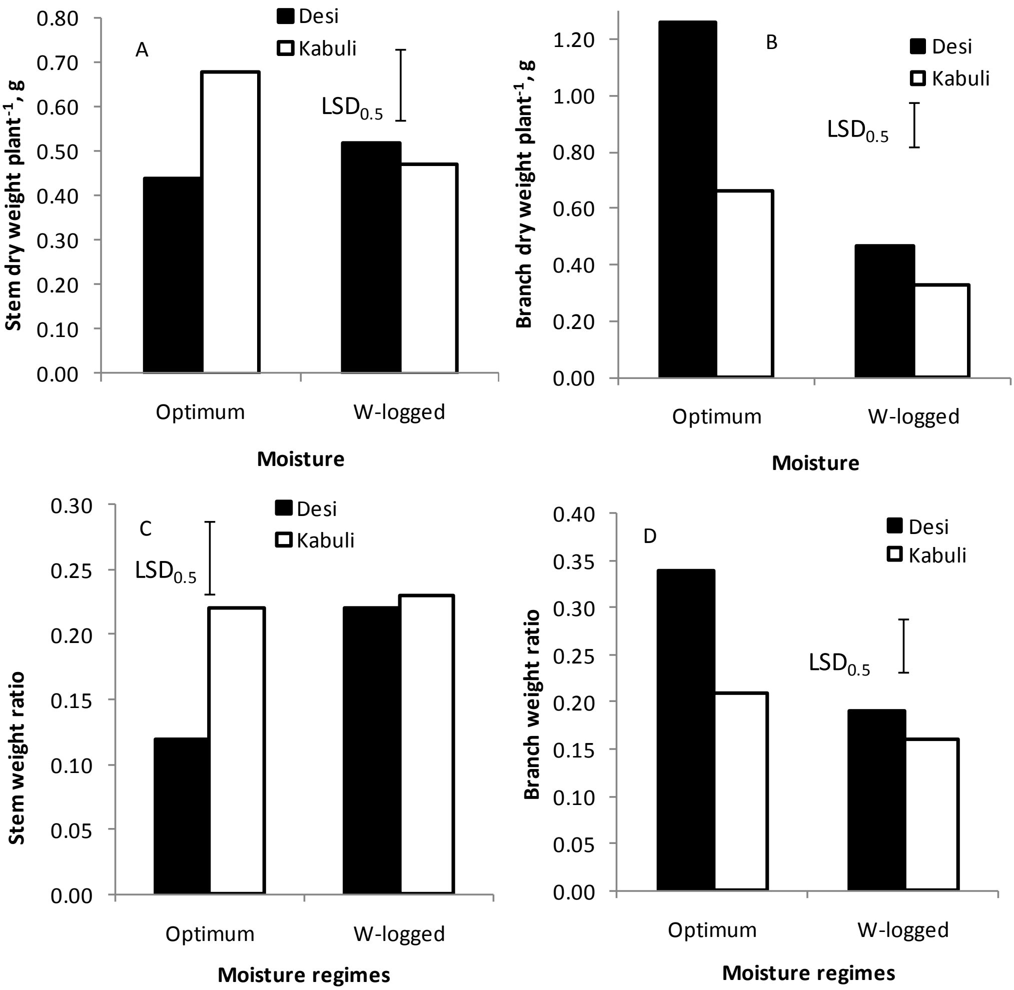

Fig. 3. Effects of moisture x genotype interaction on (A) stem dry weight, (B) branch dry weight, (C) stem weight ratio and (D) branch weight ratio in kabuli and desi chickpea at mid-flowering.

At maturity

Phenology and shoot growth: Early waterlogging extended commencement of physiological maturity by five days (Table 3). On the other hand, waterlogging during the flowering and the seed filling phases accelerated days to maturity by up to a week.

Basal branch number suffered most from vegetative waterlogging and the impact was more pronounced on the desi type confirming observations from the two previous samplings (Fig. 4). On the other hand, flowering stress restricted upper branch number more than other phases. The desi type had fewest basal branches due to vegetative waterlogging but initiated more upper branches under the same stress.

The greatest loss in total dry matter occurred from mid waterlogging (70%) followed by terminal (33%) and early stresses (19%) (Table 3). Loss of total dry matter from flowering stress was contributed from all shoot and underground growth parameters while the loss from terminal stress was limited to reproductive and underground components.

The two genotypes had similar total dry matter in spite of a modest difference in growth duration (Table 3). The shortfall in vegetative growth in the desi type was compensated by a greater reproductive growth as evidenced by a higher harvest index (Table 4).

Table 3. Effects of waterlogging during three phenological phases on various parameters of desi and kabuli chickpea at maturity[a].

Treatment	**Days to mature**	**Branch dry wt (g)**	**Stem dry wt (g)**	**Leaf dry wt (g)**	**Straw dry wt (g)**	**Nodule no.**	**Nodule dry wt (g)**	**Root dry wt (g)**	**Total dry wt (g)**
Moisture									
OOO	76.0b	2.24a	0.763a	1.41a	5.26a	116a	0.24a	0.512a	10.35a
WOO	81.1a	1.67bc	0.848a	0.98bc	4.21b	113a	0.29a	0.591a	8.42b
OWO	70.5dc	1.43dc	0.574b	0.79c	2.84c	2b	0.00b	0.100b	3.08d
OOW	68.5d	2.0ab	0.702ab	1.3ab	4.67ab	0b	0.00b	0.195b	6.90c
WWW	72.0c	1.17d	0.765a	0.57c	2.54c	0b	0.00b	0.127b	2.86d
$LSD_{5\%}$	**2.7**	**0.37**	**0.161**	**0.41**	**0.89**	**16**	**0.05**	**0.095**	**1.23**
Chickpea types									
Desi (Naatolii)	75.6a	1.57b	0.522b	0.82b	3.43b	55a	0.108a	0.293a	6.14a
Kabuli (Habru)	71.6b	1.83a	0.939a	1.41a	4.38a	37b	0.104a	0.316a	6.50a
$LSD_{5\%}$	**1.75**	**0.23**	**0.102**	**0.26**	**0.56**	**10**	**0.031**	**0.060**	**0.76**

[a] data are given on per plant basis except days to mature; column means with the same letter are not significantly different at $P<0.05$; O, optimum, W, waterlogged; the three letters represent the vegetative, flowering and seed filling phases, respectively.

Root growth and nodulation: Nodule number, nodule mass and root dry matter fully recovered from early stress with a tendency for an increase in nodule mass under stress (Table 3). This was consistent to the data from mid-flower sampling. Waterlogging at flowering and seed filling extremely damaged both nodulation and root mass.

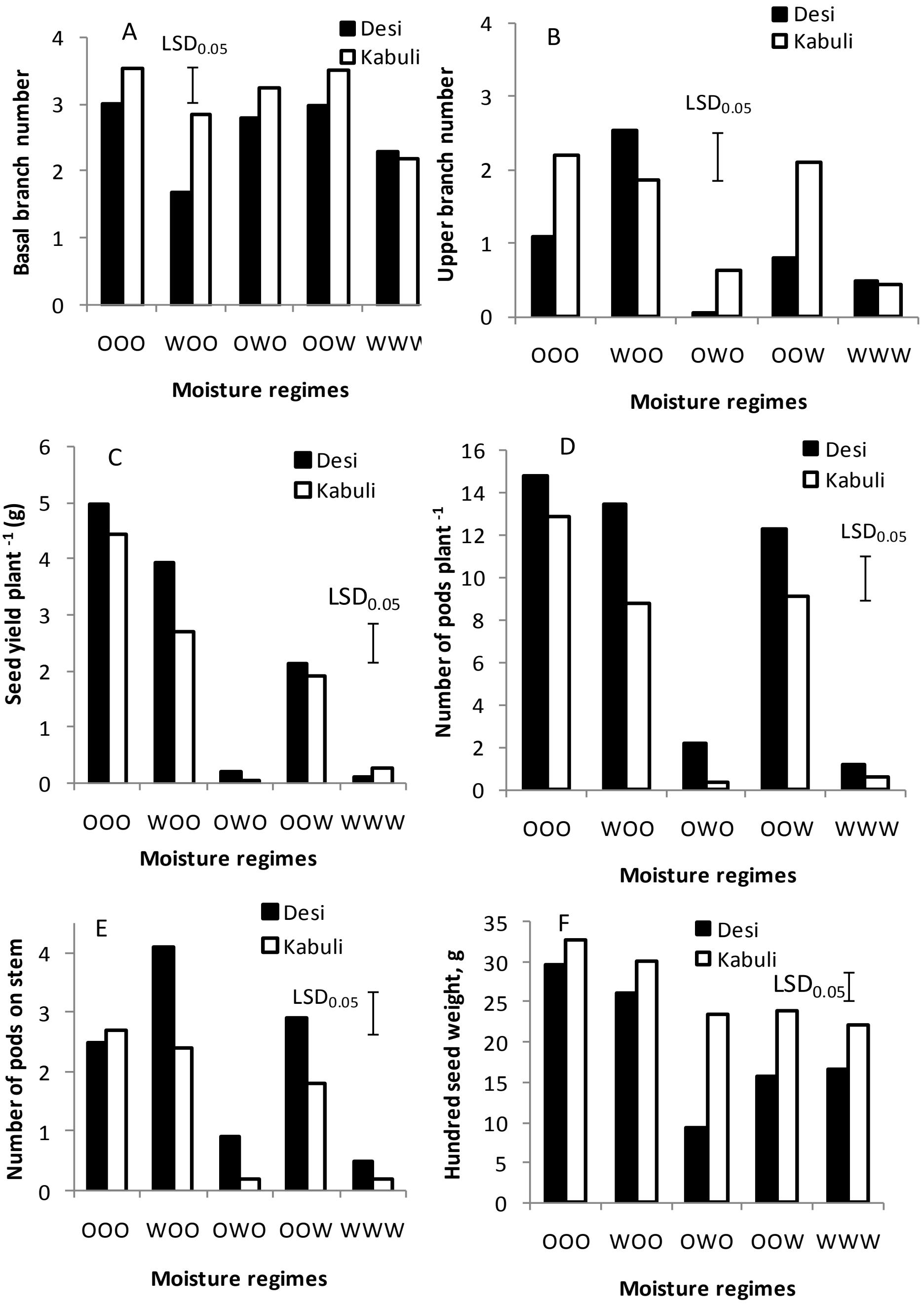

Fig. 4. Effects of moisture x genotype interaction on (A) basal branch number, (B) upper branch number, (C) seed yield per plant, (D) number of pods per plant, (E) number of pods on stem and (F) hundred seed weight, at maturity. O, optimum, W, waterlogged; the three letters represent the vegetative, flowering and seed filling phases, respectively.

Yield, yield components and harvest index: Genotype by moisture interaction influenced seed yield, pod number per plant, pod number on the main stem and seed weight (Fig. 4). Flowering stress affected grain yield of both types most adversely; losses amounted to 95% for the desi and 99% for the kabuli. The seed filling period was the second sensitive phase with a more or less similar loss of about 56%. The two genotypes varied significantly only in their response to early waterlogging. Accordingly, the desi type lost 21% while the kabuli suffered almost twice as much, 39%.

The interaction trend on number of pods per plant reflected that of seed yield, generally (Fig. 4). The desi type increased pods on the main stem by 64% in response to early stress as opposed to the kabuli. Yield losses following stresses at flowering and seed filling were attributed to losses in pod number and seed weight, on both chickpea types.

Harvest index dropped most due to stress at flowering (88%) followed by the stress at seed filling (31%), as expected (Table 4). Early waterlogging did not change harvest index significantly.

Table 4. Effects of waterlogging during three phenological phases on number of pods and seeds and harvest index of desi and kabuli chickpea.

Treatment	**Pods on basal branches plant^{-1}**	**Seed no. pod^{-1}**	**Harvest index**
Moisture			
OOO	9.68a	1.02a	0.42 1a
WOO	6.70b	1.05a	0.383a
OWO	0.56c	0.85b	0.050c
OOW	7.73b	0.97ab	0.298b
WWW	0.41c	0.54c	0.050c
LSD$_{5\%}$	**1.13**	**0.16**	**0.039**
Chickpea types			
Desi (Naatolii)	6.22a	0.97a	0.276a
Kabuli (Habru)	3.816	0.80b	0.206b
LSD$_{5\%}$	**0.71**	**0.10**	**0.024**

Column means with the same letter are not significantly different at $P<0.05$; O, optimum, W, waterlogged; the three letters represent the vegetative, flowering and seed filling phases, respectively.

DISCUSSION

Stomatal resistance

High stomatal resistance under waterlogging could be related to poor aeration conditions that limit oxygen availability for normal root functions. Loss of stomatal conductance from waterlogging could also be attributed to the severe leaf senescence that restricted density of functional stomata especially at later growth phases. Thus, the greatest loss in stomatal conductance occurred from waterlogging during the seed filling phase followed by the flowering phase. Senescence was so severe due to terminal waterlogging, measurement for stomatal resistance was abandoned eight days after commencement. Therefore, impact of reduced stomatal conductance on growth could be negligible after relief from exposure to early waterlogging while it could be significant following mitigation of stress at later stages.

The rapid increase in stomatal resistance and subsequent reduction in transpiration and net photosynthesis of waterlogged plants as a result of stomatal closure may be an adaptive response to water stress caused either by water deficit or excesses (Abuhay Takele and McDavid, 1995). Increase in stomatal resistance in response to waterlogging is observed in soybean (Oosterhuis *et al*., 1990), in navy bean (Singh *et al*., 1991), in cowpea (Abuhay Takele and McDavid, 1994), in pigeonpea (Abuhay Takele and McDavid, 1995) and in lentil (Ashraf and Chishti, 1993). Differences among genotypes for the response were also observed whereby tolerant genotypes had shown lower stomatal resistance (Ashraf and Chishti, 1993; Abuhay Takele and McDavid, 1994). Maintaining lower stomatal resistance under waterlogging could be attributed to maintenance of favourable root characteristics (Solaiman *et al*., 2007) and to an antioxidant defense system scavenging against reactive oxygen species (Bansal and Srivastava, 2012). However, the genotype that has shown consistently lower stomatal resistance under waterlogging did not perform better in this experiment. Rather, the desi type, which maintained greater stomatal resistance has shown superior yield performance under early waterlogging. Perhaps, it might be possible that the increased stomatal resistance may have contributed to enhance tolerance against waterlogging especially when its occurrence was not associated with leaf senescence. Similar observations were reported by others where reduced stomatal conductance contributed for adaptation against waterlogging stress (Zaidi *et al*., 2003).

Shoot growth

The ten days vegetative waterlogging caused growth retardation on both above and below ground components, at the end of the treatment period. This could primarily be attributed to loss of assimilation because of increased stomatal resistance and reduced canopy size. Moreover, the damage on the root system would have an additional negative influence on acquisition of moisture and nutrients. The reduced canopy size was attributed to reduced leaf growth rate because of inadequate assimilate supply since neither senescence nor leaf abscission was observed. Only slight chlorosis was observed towards the end of the treatment period. On the other hand, Cowie *et al*. (1996) observed leaflet abscission and anthocyanin pigmentation in addition to chlorosis symptoms due to early waterlogging for 10 days on a desi chickpea. Abuhay Takele and McDavid (1995) also reported wilting, chlorosis, senescence and abscission of lower leaves from as little as two days early waterlogging, in pigeonpea. Solaiman *et al*. (2007) did not observe reductions in shoot dry weight at the end of a seven day waterlogging period during the vegetative phase in desi chickpea. Such differences in reported results could partly be attributed to variation in sensitivity among species and genotypes and disparity in stress duration.

None of the above ground growth parameters except stem weight showed full recovery from early stress either at mid flowering or at maturity in spite of an extended growth duration. This could be mainly attributed to the reduced leaf area that restricted assimilation. Loss of leaf area was detrimental as indicated by a significant positive relationship (r = 0.92***) with total dry matter production. The other parameters such as stomatal conductance, root growth and nodulation have shown full recovery indicating their smaller impact on restricting later growth after stress mitigation. Palta *et al*. (2010) observed that compared with the well-drained plants, subsurface waterlogging for 12 days during vegetative growth reduced leaf area and shoot growth on desi and kabuli chickpea. Similarly, early waterlogging of 10 days reduced branch number and shoot yield by 30-35% in comparison with the controls on desi chickpea (Cowie *et al*., 1996).

Timing of waterlogging and genotype affected number of basal and upper branches variably. Early waterlogging restricted basal branch number while flowering stress curtailed upper branch growth. The response was related to the time of appearance and active growth periods for these structures. Basal branches develop starting from emergence during the vegetative phase while upper branches develop later towards flower initiation. Restriction of basal branch number may be more important than that of upper branches because the former carries more pods. For instance, basal branches carried 73% of the pods under optimum moisture compared to 7% carried by upper branches. However, upper branches could still contribute to productivity as a source of assimilates since they carry more active leaves during the seed filling period. The desi type had a drastic reduction in basal branch number from vegetative waterlogging. However, it produced significantly more seed than the kabuli. This could be because the desi type increased pod production on the main stem under early stress and developed more upper branches to ensure assimilate supply to these pods.

The flowering phase stress affected vegetative growth most because it restricted upper branch development while the existing leaves were lost to senescence and abscission leading to reduced assimilation. Moreover, the roots and nodules were irrecoverably damaged limiting their function of absorption and nitrogen fixation. Furthermore, stomatal resistance remained substantially high after relief causing additional impact on assimilation rate. On the other hand, above ground vegetative growth parameters seemed not sensitive to terminal waterlogging because most growth for branches, stem and leaves was completed by the time the stress was imposed at seed filling.

Root growth and nodulation

Root growth recovered fully from vegetative waterlogging as observed both at mid flowering and at maturity. The extended vegetative growth and the preferential investment on the root after the stress could have contributed to its quick recovery. Umaharan *et al*. (1997) observed recovery of root growth from an early cyclic waterlogging during the vegetative phase, in cowpea. On the other hand, subsurface waterlogging reduced the root dry matter of both types of chickpea by 67% two weeks after the cessation of a 12 day early waterlogging and also failed to recover at maturity (Palta *et al*., 2010) probably owing to the longer stress duration.

Early waterlogging curtailed nodulation in both genotypes as observed immediately after relief. Because waterlogging prevents the development of root hair and sites of nodulation and interferes with normal diffusion of oxygen in the root system of plants (Mulongoy, 1992). However, plants under vegetative waterlogging recovered their nodulation capacity both in terms of mass and number similar to root growth. Given nodulation was absent in waterlogged plants immediately after relief, only an enhanced nodulation activity could have made these plants to be at par with optimum plants. More nodulation during recovery from waterlogged plants could have occurred due to lower N levels because of leaching (Nathanson *et al*., 1984). Absence of significant reduction in root dry matter and nodulation indicate the resilience of the root system and Rhizobia to early waterlogging provided that growth conditions are improved afterwards. As a result, early waterlogging may not have detrimental effect on nitrogen fixation at later stages as indicated by the number and mass of nodules. Nitrogen fixation activity reflects the patterns of nodulation (Guafa *et al*., 1993). After relief from early waterlogging, the desi type regained green colour while the kabuli remained light yellowish especially on lower leaves. This could partly be attributed to the superior nodulation ability of the desi type under both moisture levels. The rate of recovery is probably more important in making a given genotype tolerant than its performance during the actual waterlogging period. Umaharan (1990) reported genetic variability for tolerance to waterlogging during the vegetative phase and suggested that selection for early recovery from chlorosis could be used as a selection criterion in breeding varieties for environments prone to waterlogging.

Maximum losses on roots and nodules occurred from the stresses at flowering and seed filling. The losses in nodule number and nodule dry weight were almost complete while that on root dry matter was 61% at each phase. These losses were mainly attributed to the disintegration and decay of existing root and nodule mass. Similarly, Umaharan *et al*. (1997) observed that all tested varieties showed a significant degeneration in root dry matter in response to waterlogging during the reproductive phase, except one.

Dry matter partitioning

Changes on the pattern of dry matter partitioning in response to waterlogging have been observed in terms of root-shoot ratio, nodule-weight ratio, branch weight ratio and stem weight ratio. Root-shoot ratio dropped remarkably immediately after treatment showing the damaging impact of early waterlogging on underground growth. A reverse trend was observed during the recovery period where waterlogged plants have shown a tendency for greater root-shoot ratio. Similarly, an increase in nodule-shoot ratio was observed after recovery period from early waterlogging. The increased investment in root and nodulation during the recovery period could be a useful recuperating mechanism that enabled these structures to regain their growth after early waterlogging.

Both genotypes had shown increased partitioning to the stem at the expense of branches immediately after termination of early stress. However, after the recovery period only the desi type maintained this trend. Accordingly, the desi type made preferential allocation to the stem in response to early waterlogging at the expense of branches while the kabuli type maintained comparable allocation on both traits. However, yield performance has shown a negative correlation with stem weight ratio ($r = -0.72^*$) while the relationship was positive with branch weight ratio ($r = 0.83^*$). It could probably be suggested that an increase in stem weight ratio under waterlogging may be partly an after effect of a significant drop on branch dry weight as indicated by a strong negative correlation between the two parameters (r = -0.98*). Henshaw *et al*. (2007b) and Abuhay Takele and McDavid (1994) reported that early waterlogging has increased partitioning of dry matter to the stem but was negatively related with tolerance to waterlogging in soybean and cowpea, respectively.

Seed yield and its components

Early waterlogging had a moderate impact on seed yield compared to the other phases. This could be attributed to the ability of the plants to recover fully for some of the growth parameters unlike the other phases. Accordingly, root growth, nodulation, stem growth and stomatal conductance were fully recovered after vegetative waterlogging was terminated. The moisture by genotype interaction indicated that the desi type suffered lesser seed yield loss compared to the kabuli type. Drop in seed yield due to vegetative waterlogging seems to be caused by source limitation as a result of reduced leaf area and a reduction in basal branch number, which normally carry most of the pods. However, the desi type partially compensated for this loss by increasing the number of pods on the main stem. A positive correlation existed between seed yield and number of pods on the main stem (r = 0.79*). The relative tolerance of the desi type to early waterlogging to yield performance was reported by Palta *et al*. (2010) who observed greater yield reduction (55%) for the kabuli compared to the desi type (42%) due to a 12 days early subsurface waterlogging. They suggested that it appears that kabuli chickpeas are more sensitive to water shortage and water excess, than desi chickpea and this is not associated with root growth characteristics.

Both genotypes were equally sensitive to waterlogging at flowering, which was most damaging. The yield loss during this phase was due to restriction of reproductive growth as evidenced by low harvest index and reduction of the yield components. This was the result of enormous flower abortion leading to extremely small number of pods on both genotypes. Further recovery growth was curtailed after relief probably because of severe root and nodule degradation and detrimental leaf senescence causing low and unrecoverable stomatal conductance. Moreover, the shortened growth duration had its impact on seed dry matter accumulation. According to Cowie *et al*. (1996), waterlogging of desi chickpea for 10 days during the flowering phase was accompanied by 53% yield reduction making it the second most sensitive next to the terminal phase.

Seed filling stress caused the second largest yield loss in both chickpea types. The reasons contributing to this loss were quite similar to those mentioned for the stress at flowering except flower abortion. The loss in productivity from terminal stress may have been moderated because the already developing seeds may have had a better chance to be filled from remobilized assimilates as observed from the severe leaf senescence. Remobilization of reserves compensates partly for the decline in photosynthesis during grain filling in stressed plants (Kramer and Boyer, 1995). On the other hand, lodging could be an additional problem from terminal waterlogging that may further affect productivity and quality (data not shown).

Waterlogging during each of the three phenological phases (WWW) did not cause impact more than that observed for the most sensitive phase. For instance, impact in terms of yield and yield components of waterlogging exposed at each of the growth phases was more or less similar to effects observed for a single waterlogging episode during the most sensitive phases. This seems to show that the impact of waterlogging was not expressed in an additive manner. On the other hand, exposure to stress during previous stages did not improve tolerance against waterlogging. Similarly, Cowie *et al*. (1996) observed that tolerance to waterlogging was not enhanced by prior exposure to waterlogging in desi chickpea.

CONCLUSION

This study indicated that none of the genotypes and growth phases were immune from the impacts of waterlogging. However, sensitivity among the three phases varied significantly. Moreover, moisture by genotype interaction indicated differences in relative sensitivity between the two chickpea types. Susceptibility differences between the two chickpea types was observed in response to early waterlogging only. The ability to adapt to waterlogged conditions during the vegetative phase may be independent of the plant's ability to adapt during the reproductive phase (Umaharan *et al*., 1997). The better performance of the desi type under vegetative waterlogging could be attributed to the combined effects of faster recovery from chlorosis, increased pod production on the main stem and greater nodulation capacity, which could be used as a criteria for screening tolerant genotypes against early waterlogging. It seems that nodulation under waterlogging was more influenced by the ability of the host to withstand the stress and its capacity for recovery rather than the characteristics of the bacteria itself. It may be possible to use the desi type, Naatolii, for early planting to minimize the risk of early waterlogging, after field verification. However, the decision to change to an earlier sowing date needs to weigh the probability and extent of losses associated with waterlogging versus terminal drought. If early planting is adopted it is necessary to ensure that sowing and germination until emergence take place under non-saturated soil. The flowering phase was the most sensitive to waterlogging irrespective of chickpea type causing a near complete loss in seed yield and a drop in quality. Thus, maximum care should be taken in avoiding excess moisture either from precipitation or irrigation during this phase. A comparative study that would examine the possible influences of different soil types on the impacts of early waterlogging would be worthwhile.

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