

## Components of genetic variation in short-duration pigeonpea crosses under waterlogged conditions

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### ABSTRACT

Waterlogging inflicts considerable stress and yield-loss on short-duration pigeonpea and the present study investigates the genetical control of phenotypic variation expressed in the basic generations of some elite crosses under waterlogged conditions. Comparisons of the parental and F<sub>1</sub> families for the 22 traits representing various facets of morphological variability revealed that the additive and dominance effects were present for a large number of these traits. Better parent heterosis was present in one or more crosses for all except two traits (ILN40 and NTR40) and a maximum of five (out of six) crosses showed heterosis for plant height (PH40) and days to lenticel formation (DYL). Analyses of the P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub>, Bc<sub>1.1</sub> and Bc<sub>1.2</sub> generations further indicated that the genetical control of various traits was rather complex. Epistasis was detected for 86 (out of 126) cross/trait combinations and there was no trait for which epistasis was non-significant in all the crosses. Presence of predominantly duplicate epistasis also pointed to a transient advantage for the hybrid varieties and better prospects of extracting superior recombinant inbred lines. In general, crosses between the tolerant and susceptible lines showed more variation compared to those involving only the tolerant lines and therefore possessed better potential for further breeding. Lack of apparent association between plant vigour and tolerance to waterlogging also indicated that plant vigour does not play a direct role in determining the tolerance to waterlogging in short-duration pigeonpea.

*Key words:* Basic generations, Gene action, Pigeonpea crosses, Waterlogging tolerance

### INTRODUCTION

Pigeonpea is a crop of marginal lands. It is grown in India as a rain-fed crop whose seed is consumed as a curry and stems are used for basket making, roof thatching and fire wood. Young pigeonpea plants are also used as a green fodder (NENE and SHEILA, 1990) and the crop can be ratooned successfully for two or more seasons. The major benefit of pigeonpea to the farmer, however, lies in its low financial and labour inputs; it requires minimal fertilisation and manpower resources for hoeing or weeding etc., except at sowing and harvesting.

Until recently, pigeonpea was grown as a long duration crop that matured 6-8 months after sowing and its main growing season spanned from June till November. But now, short duration varieties have been released that mature within 120 days of sowing (SINGH *et al.*, 1990).

These varieties have a faster growth rate but they stay short and flower early. Consequently, they are highly affected by the storm floods that occur regularly during the monsoon season (REDDY and VIRMANI, 1981; MATSUNAGA *et al.*, 1991; KUMAR RAO *et al.*, 1996). In some seasons, the whole crop has been lost or at least severely damaged by floods that cause transient waterlogging in the low lying areas (CHAUHAN, 1987; NAM *et al.*, 1993).

Since the release of short duration varieties in the early nineties and the subsequent revelation of their potential susceptibility to waterlogging, scientists at ICRISAT have identified several accessions that show tolerance to waterlogging (CHAUHAN, 1987; KUMAR RAO *et al.*, 1996). Most importantly, they have perfected a technique that simulates flooding in the glasshouse (see CHAUHAN *et al.*, 1997) and allows large populations to be screened under artificial water-

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logging. In the present study, we have used this technique to determine the genetical control of morphological variation expressed under waterlogged conditions in the early generations of elite pigeonpea crosses that have been produced by crossing known waterlogging tolerant/susceptible accessions.

## MATERIALS AND METHODS

The material consisted of the P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub>, BC<sub>1.1</sub> and BC<sub>1.2</sub> generations derived from each of the following crosses of pigeonpea that are known to display varying degrees of tolerance to waterlogging.

Cross C-1	ICPL84023 × ICPL86012	(tolerant × susceptible)
Cross C-2	ICPL90004-1 × ICPL86012	(tolerant × susceptible)
Cross C-3	ICPL88034-3 × ICPL86012	(tolerant × susceptible)
Cross C-4	ICPL84023 × ICPL88009	(tolerant × tolerant)
Cross C-5	ICPL90004-1 × ICPL88009	(tolerant × tolerant)
Cross C-6	ICPL88034-3 × ICPL88009	(tolerant × tolerant)

Parents of these crosses were the elite inbreds ICPL84023, ICPL88009, ICPL88034-3, ICPL90004-1 and ICPL86012, all of them except the last show tolerance to waterlogging (PERERA, 1998). The crosses were made during October 1996, the F<sub>2</sub> and backcross generations produced in winter 1996-7 and 30 randomly chosen F<sub>2</sub> plants from each cross selfed in July 1997 to get the F<sub>3</sub> seed. All seeds were produced either in the glasshouse or in the field in insect proof cages and the experiment was conducted in the glasshouse where waterlogging was induced using the procedures of CHAUHAN *et al.* (1977). Materials of each cross were assessed separately in a single randomised block and 10 pots were allocated to each of the parental and F<sub>1</sub> generations, 20 to the F<sub>2</sub>, 16 to each of the backcross generations and two to each of 30 F<sub>3</sub> families. Pots (18 × 18 cm in size) were filled with soil from a local field and five sibs of the same family/generation (eg P<sub>1</sub> or F<sub>2</sub> etc) were raised in each pot. The experiment was grown under normal watering conditions for the first 40 days and plastic trays (52 × 22 × 17 cm) containing pots were then filled with water to commence waterlogging. Water level was maintained in the trays by adding water regularly and care was taken to keep the water undisturbed so that it would remain stagnant. All plants were exposed to continuous waterlogging (ie., pots were kept submerged in water) for a total of 21 days.

Altogether 22 morphological traits were scored on each plant; three before the imposition of waterlogging, ten during the waterlogged period and nine after waterlogging for 21 days (see Table 1). Data for traits NAD, LAD, DYL, DAD and AWT, and LAR were transformed to square root and log scales respectively, to fulfil the normality and homogeneity of variance requirements. All data were analysed fol-

lowing CAVALLI (1952) and MATHER and JINKS (1982). Further details of the analytical procedures, the criteria for the best model and the definitions of the parameters can be found in KEARSEY and POONI (1996).

**TABLE 1**  
**Morphological traits scored on the material**

Symbol	Description
<i>Measurements recorded before waterlogging</i>	
PH40	Plant height at 40 days after sowing.
NTR40	Number of trifoliolate leaves at 40 days after sowing.
ILN40	Average length of the first 4 internodes at 40 days after sowing
<i>Measurements recorded during waterlogging</i>	
PH47, PH54 & PH61	Plant height at 47, 54 and 61 days after sowing.
LAG43	Leaf angle (°) of the 4 <sup>th</sup> fully expanded leaf measured at 43 days after sowing.
CC45	Chlorophyll content, measured on day 45, on the 4 <sup>th</sup> fully expanded leaf using a chlorophyll meter that determined the absorption of the leaf in two wave lengths. From the average of these readings (X values), CC was calculated following Adu-Gyamfi, J.J. (GOJ Project, ICRISAT Asia Centre) as: CC=0.0156753 X -0.052616
NTR47	Measured as NTR40 at 47 days after sowing
DYL	Days to lenticel formation, recorded as the number of days taken from the date of waterlogging (=day 1) to the initiation of the lenticels.
DAD	Days to adventitious root formation recorded as DYL.
DFL	Days to flowering, taken from the sowing to the opening of the first flower on each plant.
DYW	Days to wilting from sowing time.
<i>Post-waterlogging measurements, recorded on day 61</i>	
NFL	Number of fresh green leaves present on each plant.
DM	Stem diameter (mm), measured nearer to the base of the plant using Vernier Calipers.
NAD	Number of adventitious roots, counted after carefully uprooting the plants and washing the roots.
LAD	Length of adventitious roots (cm), recorded by measuring each root individually in cm and then obtaining the total length for each plant.
LAR	Length of lenticel area (cm), measured along the length of the stem after removing the adventitious roots.
RWT, SWT & AWT	Root, shoot and adventitious root weights (g), recorded after dividing the plant into roots, shoots and adventitious roots and drying the material in an oven at 70°C for 48 hrs.
S/R	Shoot to root ratio (S/R), calculated by dividing the dry weight of shoots by that of the roots, for each plant.

## RESULTS

*Parental difference and heterosis*

The presence of genetic variation in a cross, initially detected by comparing the means of its parental generations using Student's *t* test, showed that the genetic variation was significant in crosses C-1, C-2 and C-3 for 20, 19 and 19 traits respectively (Table 2). As one of the parents is common to these crosses, this further suggested that ICPL86012 is distinctly different from the other parents. Differences between the same three lines (ICPL84023, ICPL90004 and ICPL88034-3) and another common parent, ICPL88009, on the other hand,

were not that clear because only four traits showed significant variation between the parental scores for these crosses.

All crosses also displayed some heterosis. Positive heterosis was present in crosses C-1, C-2 and C-3 for 2, 4 and 4 traits respectively, but it was significant for only DYL in cross C-2, which incidentally also showed negative (but non-significant) heterosis for DYW and LAR. Crosses C-4, C-5 and C-6 displayed more heterosis than crosses C-1, C-2 and C-3, largely because their parents had very similar means. Heterosis was present in these crosses for 10 (4 cases +ve and 6 cases -ve), 10 (7 cases +ve and 3 cases -ve) and 14 (12 cases +ve and 2 cases -ve) traits respectively, but it was significant on on-

TABLE 2  
Difference ( $\bar{P}_1 - \bar{P}_2$ ) between the parental scores and the magnitude of heterosis displayed by each cross (C-1 to C-6) for various traits

Trait	Differences between the parents of cross:						Heterosis in cross					
	C-1	C-2	C-3	C-4	C-5	C-6	C-1	C-2	C-3	C-4	C-5	C-6
<i>Traits measured before waterlogging</i>												
PH40#	*	*	*	ns	ns	ns	-	0.82	0.08	0.46	2.26	1.34
NTR40	*	*	*	ns	*	*	-	-	-	-	-	-
ILN	*	*	*	*	ns	ns	-	-	-	-	-	-
<i>Traits measured during waterlogging</i>												
PH47	*	*	*	*	ns	ns	-	-	-	-	4.46	2.38
PH54	*	*	*	ns	ns	ns	-	-	-	-	4.72	4.98*
PH61	*	*	*	ns	ns	ns	-	-	-	-	4.74	4.64*
LAG43	*	ns	*	ns	ns	*	-	2.00	-	-2.00	0.50	-
CC45	*	*	ns	*	*	*	0.02	-	0.03	-	-	-
NTR47	ns	ns	ns	ns	ns	ns	-	-	-	-	0.10	-
DYL	*	*	*	ns	ns	ns	-	0.14*	0.01	0.04*	0.01	-0.03
DAD	*	*	*	ns	ns	-	-	-	-	-	-0.01	-0.04
DFL	-	-	-	-	ns	ns	-	-	-	-0.03	-0.03	-
DYW	*	*	*	*	-	-	-	-0.04	-	-	-	-
<i>Traits measured after waterlogging</i>												
NFL	*	*	*	ns	ns	ns	-	1.48	-	-0.36	-	1.46*
DM	*	*	*	ns	ns	ns	-	-	-	-	-	0.71
NAD	*	*	*	ns	*	ns	-	-	-	-0.21	-	0.61
LAD	*	*	*	ns	*	ns	-	-	-	-0.50	-	0.85
LAR	*	*	*	ns	ns	ns	-	-0.12	-	-	-	0.17
RWT	*	*	*	-	ns	ns	-	-	0.01	0.03	-	-
SWT	*	*	*	-	ns	*	-	-	-	0.08	0.11	0.10
AWT	*	*	*	ns	ns	-	0.01	-	-	-	-	0.01
S/R	ns	ns	ns	ns	ns	ns	-	-	-	-2.82	-1.22	0.78

- = no heterosis.

# See text for abbreviations.

\*  $p < 0.05$ .

ly four occasions (for DYL in cross C-5 and for PH3, PH4 and NFL in cross C-6).

None of the crosses however seems to show any genetic variability for S/R, indicating that either this trait is not segregating, or the genes controlling it are in complete dispersion and are showing ambidirectional dominance.

Traits NTR40 and ILN, on the other hand, show little dominance or non-additive effects while additive effects are detected in four and five crosses respectively. For the remaining traits, some differences were detected, indicating that genetic variation was present, at least in some crosses. None of the traits, however, showed genetic differences in all six crosses (Table 2).

#### Gene action/interaction

Models with more than one parameter were needed in all but nine trait/cross combinations (Table 3). Component m (mid-parental value) alone fitted in all these (nine) cases, most of which belonged to crosses C-4 (LAG3, NFL, SWT and RWT) and C-5 (LAG3 and NFL) and remainder to crosses C-2, C-3 and C-6 (for NTR2, NTR2 and ILN respectively). In general, more crosses showed epistasis for PHO, PH2, PH3, PH4, DYL, DAD, NAD, LAD, LAR and S/R, indicating that these traits were controlled by complex gene action/interaction. On the other hand, NTR2, NFL and SWT subscribed to simple inheritance because epistasis was detected for these traits in only one or two crosses.

Among the crosses, cross C-6 showed the additive/dominance gene action for the highest number (11) of traits (Table 4). Next came C-4 that showed simple inheritance for eight traits. Epistasis was significant for a minimum of 15 traits in each of the remaining crosses. Parameter-wise, additive ([a]) and dominance ([d]) components were significant with equal frequency (86 and 84) and the same applied to the three epistatic components except that their frequencies (42-52) were much lower than those of [a] or [d] (see Table 5). On the other hand, significantly more [d] and [a] (additive x additive interaction) components took positive sign ( $\chi^2_{(1)}=6.90^{**}$  and  $6.80^*$  respectively) while the opposite was true for [ad] parameter (additive x dominance interaction component,  $\chi^2_{(1)}=6.23^{**}$ ). Parameter [dd] (dominance x dominance inter-

action) displayed a similar trend as [ad], but the frequencies of the +ve and -ve [dd] values did not differ significantly ( $\chi^2_{(1)}=1.52^{ns}$ ).

TABLE 3

The number of crosses (out of 6) that required the additive/dominance or epistatic models to explain the genetic variability among their generation means for each trait

Trait	Types of model			
	m parameter	Additive/dominance	Epistatic	Perfect fit
<i>Traits measured before waterlogging</i>				
PH40#			6	
NTR40		2	4	
ILN	1	2	3	
<i>Traits measured during waterlogging</i>				
PH47		1	4	1
PH54			6	
PH61			6	
LAG43	2	1	3	
CC45		3	3	
NTR47	2	2	2	
DYL			6	
DAD		1	5	
DFL			2	1
DYW		1	2	
<i>Traits measured after waterlogging</i>				
NFL	2	3	1	
DM		2	4	
NAD		1	5	
LAD		1	5	
LAR		1	5	
RWT	1	1	4	
SWT	1	3	2	
AWT		3	3	
S/R		1	5	

# See Table 1 for abbreviations.

TABLE 4

The numbers of traits (out of 22) for each cross for which the additive/dominance or epistatic models were observed adequate

Cross	Types of model		
	m alone	Additive/dominance	Epistatic
Cross C-1	—	4	17
Cross C-2	1	5	15
Cross C-3	1	4	16
Cross C-4	4	4	13
Cross C-5	2	2	17
Cross C-6	1	10	10

TABLE 5

The number of traits (out of 22) for which various components were detected significant in each cross

Cross	Significant components and their signs											
	[a]#	[d]		[aa]		[ad]		[dd]		[c]		
		+ve	-ve	+ve	-ve	+ve	-ve	+ve	-ve	+ve	-ve	
Cross C-1	21	9	3	9	5	5	1	1	8	1	0	
Cross C-2	19	10	7	2	3	2	7	3	5	1	1	
Cross C-3	19	8	8	5	3	0	9	6	6	1	0	
Cross C-4	12	2	3	3	1	3	8	2	2	9	2	
Cross C-5	8	13	3	11	2	6	5	3	1	0	0	
Cross C-6	7	13	5	4	2	1	5	2	3	1	1	
Sub total		55	29	34	16	17	35	17	25	13	4	
Total	86		84		50		52		42		17	

# See text for symbols.

While all components were estimated as regression coefficients and therefore were orthogonal to each other, it was however worthwhile to investigate if their presence/absence was associated with each other. The contingency  $\chi^2$  showed that strong positive associations existed between [d], [aa] and [dd] (see below).

Components	$\chi^2$ (1)	Association
[a] and [d]	0.07 <sup>ns</sup>	-
[a] and [aa]	1.26 <sup>ns</sup>	-
[a] and [ad]	0.22 <sup>ns</sup>	-
[a] and [dd]	2.54 <sup>ns</sup>	-
[d] and [aa]	10.43 <sup>***</sup>	positive
[d] and [ad]	0.59 <sup>ns</sup>	-
[d] and [dd]	20.39 <sup>***</sup>	positive
[aa] and [ad]	2.89 <sup>ns</sup>	-
[aa] and [dd]	4.83 <sup>*</sup>	positive
[ad] and [dd]	0.02 <sup>ns</sup>	-

#### Type of epistasis

As gene dispersion influences all but two ([d] and [dd]) components, it is not possible to use the significance and signs of [a], [aa] and [ad] for interpreting the type of epistasis which may be prevailing in a cross. Furthermore, it is not possible to determine if gene effects are equal across the loci that may be segregating for a particular trait. Consequently, epistasis can only be classified as predominantly duplicate or predominantly complimentary, depending on the signs of [d] and [dd] (see KEARSEY AND POONI, 1996 for more details).

Table 6 shows that [d] and [dd] always take opposing signs, whenever they are significant for a trait simultaneously. Therefore, genes segregating in these crosses show duplicate epistasis and there is no hint of complimentary gene interaction anywhere. It is however possible that some genes may be showing complimentary epistasis but they are clearly in a tiny minority and their effects are being cancelled out by those showing duplicate epistasis.

TABLE 6

The number of traits (out of 22) for which dominance ([d]) and dominance x dominance interaction ([dd]) components were detected significant and these components took opposite signs. There were no cases where [d] and [dd] took the same sign

Crosses	+ve [d] and -ve [dd]	-ve [d] and +ve [dd]
Cross C-1	7	1
Cross C-2	5	3
Cross C-3	6	6
Cross C-4	2	2
Cross C-5	1	2
Cross C-6	3	2

#### Less affected vs. badly affected plants

While the above analyses were carried out using the data from all plants, it was also possible to assign plants into two arbitrary groups, i.e., those which showed severe effects of water-logging (badly affected) and the remainder that displayed little damage (less affected) and could be classed as tolerant. Table 7 shows that the in-

TABLE 7  
Frequency of the *less affected* and *badly affected* plants in the basic generations of each cross

Generation	Condition of the plants from different crosses											
	Cross C-1		Cross C-2		Cross C-3		Cross C-4		Cross C-5		Cross C-6	
	less	bad	less	bad	less	bad	less	bad	less	bad	less	bad
P <sub>1</sub>	49	1	48	2	43	7	49	1	48	1	45	5
P <sub>2</sub>	2	48	2	48	2	48	47	3	47	3	47	3
F <sub>1</sub>	37	13	9	41	19	31	44	6	50	0	50	0
F <sub>2</sub>	69	31	42	58	34	66	87	8	94	6	98	2
Bc <sub>1,1</sub>	75	5	45	35	34	46	80	0	73	5	77	3
Bc <sub>1,2</sub>	32	48	8	72	13	67	79	1	80	0	77	3

TABLE 8  
Comparison between the *less affected* and *badly affected* plants of generations derived from crosses C-1, C-2 and C-3 for the two traits (PH40 and NTR40) that were scored before the commencement of waterlogging

Cross	Generation	Mean plant height (PH40)			Mean trifoliolate leaves (NTR40)		
		<i>Less affected</i>	<i>Badly affected</i>	Difference	<i>Less affected</i>	<i>Badly affected</i>	Difference
Cross C-1	F <sub>1</sub>	38.16	38.23	ns	7.27	7.77	ns
	F <sub>2</sub>	36.70	38.26	ns	7.16	7.55	*
	BC <sub>1,1</sub>	41.83	38.80	ns	6.87	6.00	ns
	BC <sub>1,2</sub>	35.59	35.63	ns	7.31	7.35	ns
Cross C-2	F <sub>1</sub>	38.22	36.71	ns	7.11	7.15	ns
	F <sub>2</sub>	36.38	36.48	ns	7.26	7.22	ns
	BC <sub>1,1</sub>	37.56	37.43	ns	6.80	6.71	ns
	BC <sub>1,2</sub>	36.00	35.93	ns	7.25	7.21	ns
Cross C-3	F <sub>1</sub>	36.11	37.39	ns	7.42	7.61	ns
	F <sub>2</sub>	34.53	34.85	ns	7.24	7.40	ns
	BC <sub>1,1</sub>	38.24	37.80	ns	7.82	7.35	*
	BC <sub>1,2</sub>	35.69	34.78	ns	7.62	7.52	ns

dividuals of many generations suffered severe damage due to waterlogging. In general, plants of the susceptible parent showed higher damage compared to those of the tolerant lines. F<sub>1</sub>s of crosses 1-3 also showed a high degree of susceptibility indicating clearly that waterlogging tolerance may only be partially dominant to susceptibility. These results were also supported by the F<sub>2</sub> and BC<sub>1,2</sub> populations from the tolerant x susceptible crosses as they showed high levels of susceptibility too. Backcrosses to the tolerant parents, on the other hand, provided mixed results because many more plants were badly affected in two of these populations (crosses C-2 and C-3) while a large number of plants showed high tolerance to waterlogging in other populations.

Among the tolerant lines, ICPL88034-3 was significantly less tolerant than others. It had sig-

nificantly more plants that fell under the badly affected category ( $\chi^2_{(1)} = 11.15^{***}$ ), suggesting that it possessed different allele(s) for tolerance. Further, counts in Table 7 do not subscribe to any simple segregation ratios, indicating that tolerance to waterlogging may have multi-genic control. Comparisons of the average scores of the less affected and badly affected plants for PH40 and NTR40, the traits scored before exposing the material to waterlogging, on the other hand, indicated that waterlogging tolerance/susceptibility was not critically associated with these traits (Table 8).

#### Components of variance

Model fitting detected genetic differences at variance level (significant V<sub>A</sub>, V<sub>D</sub> and V<sub>AD</sub> etc, see

KEARSEY and POONI, 1996 for definitions) for 67 (out of 126) trait/cross combinations. Analyses of the  $F_3$  families further revealed that segregation was occurring for most of the remaining trait/cross combinations too (results not shown). Thus, the failure to detect variation in the basic generations was largely due to smaller experimental size and not due to lack of segregation. Further, due to the complications caused by epistasis and genotype  $\times$  micro-environmental interactions, no variance models could be fitted in 31 cases.

As most of the genetic variation at the variance level is caused by the additive effects of genes and proportionally little is attributed to dominance or epistasis, the above analysis indicated clearly that it would be possible to extract better performing inbred lines from these crosses.

## DISCUSSION

Several important conclusions can be drawn from the present study. As little was known about the behaviour of accessions/lines under waterlogged conditions prior to the present investigation, it is very satisfying to observe that the genotypes previously labelled tolerant or susceptible by KUMAR RAO *et al.*, (1996) have been confirmed to be so by the present study as well. At the same time, the study has also revealed that all tolerant genotypes do not show the same level of tolerance to waterlogging. For example, line ICPL88034-3 shows lower level of tolerance and consequently more of its plants are badly affected by waterlogging compared to other genotypes (see Table 7). Therefore, it is more appropriate to classify it as partially tolerant while the remaining lines can be called tolerant because >98% of their plants showed tolerance to prolonged waterlogging.

The  $F_1$  response to waterlogging is also interesting, particularly of those crosses that involved tolerant and susceptible lines as parents (Tables 7 and 8). Normally, being better buffered, the  $F_1$ s should be better able to withstand waterlogging, at least in the early stages of development. However, more  $F_1$  plants are badly affected compared to any of their tolerant parents (Table 8) and this can happen only when susceptibility is partially dominant to tolerance. Most of the  $F_1$  plants are

also, on average, taller than their parental lines and heterosis is present for PH40 in all crosses except cross 1 (Table 2). Plant vigour, therefore does not seem to play any significant role in helping the  $F_1$  plants cope with waterlogged conditions.

All crosses, however, show ample variability when raised under waterlogged conditions and a large proportion of this variability is inherited (Table 4). The parental and  $F_1$  generations show marked differences in their mean performance (Table 2) and such differences are also observed among the  $F_2$  and backcross generations (data not shown). Model-fitting has indicated that these differences are caused by both the additive and dominance effects of genes as well as their interactions (Tables 4 and 5). As most of the intragene effects and gene interactions can be manipulated through recombination and selection, there are therefore high chances of producing new genotypes from these crosses that would be markedly less susceptible to waterlogging and perhaps will be able to withstand other abiotic stresses too. The type of epistasis prevailing in the material also indicated that only the recombinant inbred lines would be better than the present set of parents and their crosses (second cycle hybrids) are not likely to show better adaptability to waterlogging (Table 7), unless they involve tolerant parents.

Finally, any conclusions that we have drawn from the present study are also expected to hold under field conditions because every effort was made to simulate natural flooding, eg., using soil from local fields and water from the local lake, and making the water stagnant. However, how far we have been successful in creating true waterlogged conditions remains to be seen and it is essential that the present study is repeated in the field to confirm if we have truly identified tolerant and susceptible lines and if the results of the study apply in practice.

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