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Inheritance of salt tolerance in wild mungbean (*Vigna radiata* var. *sublobata*)

Artitaya Deeroum, Khwanruedee Thepphomwong, Kularb Laosatit, Prakit Somta*

Department of Agronomy, Faculty of Agriculture at Kamphaeng Saen, Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom 73140, Thailand

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Abstract

Importance of the work: Soil salinity is a major stress causing yield loss in crops. Wild progenitors and relatives of crops are reservoirs of genes conferring salt tolerance. The results from this investigation of the genetics of the salinity tolerance in a wild mungbean (*Vigna radiata* var. *sublobata*) should be useful in the breeding of salt tolerance in mungbean.

Objectives: To investigate the genetic control of salt tolerance in the wild mungbean accession CPI 100834.

Materials & Methods: Cultivated mungbean (var. *radiata*) accession V2278AG (P_1: salt-susceptible) and wild mungbean (var. *sublobata*) accession CPI 100834 (P_2: salt-resistant) were used to develop F_1 ($P_1 \times P_2$), F_2 ($P_1 \times P_2$), BC_1P_1 [$P_1 \times (P_1 \times P_2)$] and BC_1P_2 [$P_2 \times (P_1 \times P_2)$] populations/generations. The six basic generations, (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) were grown and evaluated for salinity tolerance at 75 mM NaCl using a hydroponic system. Segregation analysis, generation mean analysis and estimation of the number of effective factors (genes) were carried out.

Results: The segregation analysis showed that salt tolerance was controlled by either one recessive gene or two genes with an inhibitory gene effect. The generation mean analysis and estimation of the number of effective factors consistently demonstrated that the tolerance was controlled by a single gene. Broad-sense heritability calculated for the salt tolerance was moderate (47–49%). Altogether, these results indicated that the salinity tolerance of the wild mungbean CPI 100834 was controlled by a single gene.

Main finding: The salt tolerance in the wild mungbean CPI 100834 appeared to be a quantitative trait controlled by a single gene.

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* Corresponding author.
E-mail address: agrpks@ku.ac.th (P. Somta)

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Introduction

Soil salinity is the presence of sodium (Na^+), potassium (K^+), chloride ($Cl^–$) and sulphate (SO_4^{2-}) in the soil and is one of principal abiotic stressors of plants and the most important constraint in crop production because the salinity negatively affects the growth and development of plants (Stavi et al., 2021). A soil is considered saline when it generates electrical conductivity of the saturation extract in the root zone that exceeds 4 dS/m (equivalent to 40 mM NaCl) at 25°C and exchangeable sodium of 15% (Munns, 2005; Jamil et al., 2011). Approximately, 20% (45 million ha) of cultivated land globally is affected by salinity, causing major crop losses and food security challenges (Shrivastava and Kumar, 2015). Soil salinity causes stresses to plants by creating: 1) ion toxicity, especially Na^+ and $Cl^–$, in plant tissues; 2) osmotic pressure that opposes the water uptake pressure of the plant roots; and 3) a nutrient imbalance in the soil that makes it difficult for plants to obtain the nutrients they need (Munns, 2005; Jamil et al., 2011; Shrivastava and Kumar, 2015; Machado and Serralheiro, 2017). Consequently, alleviating salt stress is a major target in crop production.

Mungbean is an important tropical legume crop of Asia and is now gaining popularity in other regions of the world. The total production area of mungbean is more than 7.0 million ha, of which 90% or more is in Asia (Somta et al., 2022). Mungbean is a very short-duration crop that can be harvested at about 60–75 days after planting (Fernandez and Shanmugasundaram, 1988); it is relatively drought tolerant and requires low amounts of water or moisture for growth and development. With these characteristics, mungbean can be grown in several cropping systems, albeit it is popularly grown in rotation with cereal crops such as rice, maize and wheat (Somta et al. 2022. Dry seeds of mungbean contain 20–25% proteins and 60–75% carbohydrates (Somta and Srinives, 2007). The seeds are used to prepare several kinds of foods, such as soups, cakes, snacks, sweets and milk products and are processed into several food products including sprouts, noodles, starch, protein concentrates, plant-based meats and egg substitutes (Somta et al., 2022). Like most legume crops, mungbean is sensitive to salinity. Previous studies on the effect of salinity on the germination or vegetative growth or seed yield of mungbean cultivars revealed that this crop is susceptible to salinity (Sharma et al. 1971; Ashraf and Rasul, 1988; Salim, 1989; Huq and Larher, 2006). However, accessions of some wild mungbean (*Vigna radiata* var. *sublobata*) from Australia have tolerance to soil salinity as they have been collected from saline soils and performed better than cultivated mungbeans under saline growth conditions (Lawn et al., 1988).

Plant breeders have long been interested in developing new mungbean cultivars with tolerance to salinity. However, there have been only a few published studies on mungbean germplasm showing resistance to salinity. In addition, up to the present, there has been no report on the genetics of salt tolerance in mungbean. Therefore, the current study investigated genetic control of resistance to salinity in the wild mungbean accession CPI 100834.

Materials and Methods

Plant materials

Two mungbean accessions V2278AG (designated P_1) and CPI 100834 (designated P_2) were used in this study. P_1 is a landrace mungbean (*V. radiata* var. *radiata*) from India and susceptible to salinity, whereas P_2 is a wild mungbean (*V. radiata* var. *sublobata*) from Papua New Guinea and tolerant to salinity (Fig. 1). P_1, as the female parent, was crossed with P_2, as the male parent, to obtain F_1 ($P_1 \times P_2$) seeds. P_1, P_2 and F_1 plants were grown in a crossing block, and an F_1 plant was self-pollinated to produce the F_2 population, while the other F_1 plants, as the male parent, were backcrossed with P_1 and P_2 plants, as the female parents, to produce BC_1P_1 ($P_1 \times (P_1 \times P_2)$) and BC_1P_2 ($P_2 \times (P_1 \times P_2)$), respectively.

Fig. 1 Leaf wilt and injury of V2278AG (left) and CPI 100834 (right) at 16 d after salt stress (growing in hydroponic solution with 75 mM NaCl)

Salinity tolerance evaluation

The six basic generations/populations—P_1 (60 plants), P_2 (60 plants), F_1 (70 plants), F_2 (220 plants), BC_1P_1 (170 plants) and BC_1P_2 (170 plants)—were used for salt tolerance evaluation in a floating hydroponic system. The seeds of these populations were sown in a non-replicated trial in germination trays for 4 days using peat moss as the growing medium. Then, the plants were washed off the peat moss and transplanted to a hydroponic culture box. The box contained a diluted nutrient solution of a 1:1 ratio of Otsuka house 1-to-Otsuka house 2 (Otsuka Chemical Co.; Osaka, Japan). Otsuka house 1 contained 11 % total N, 8% P_2O_5, 7% K_2O, 0.1% MgO, 0.1% B_2O_3 and 0.2% F, while Otsuka house 2 contained 11% total N and 23% CaO. At 6 d after transplanting, the salt treatment was applied by adding NaCl. The NaCl concentration was 25 mM for the first 4 d and was increased by 25 mM at intervals of 3 d, until a final concentration of 75 mM was reached. After that, the NaCl concentration was maintained at 75 mM throughout the experiment. Leaf wilt and injury for each plant were evaluated based on visual scoring at 3 d, 6 d and 9 d after applying the 75 mM NaCl. The scoring scale range was 1–9, where 1 = normal healthy leaves, 3 = 1–25% of leaves wilted and injured, 5 = 26–50% of leaves wilted and injured, 7 = 51–75% of leaves wilted and injured, and 9 = 76–100% of leaves wilted and injured or the plant was completely dead (Fig. 2; Chankaew et al., 2014). The scoring was performed separately by three staff members and average score was used for data analysis. The leaf wilt scores were also calculated using the area under the salt-injury progress stairs (AUSPS) following the calculation of the area under the disease progress stairs (AUDPS) proposed by Simko and Piepho (2011). AUSPS was used as the indicator of the rate of wilting and leaf injury.

Fig. 2 Leaf wilt and injury of each plant based on visual score using scale of 1–9, where 1 = normal healthy leaves, 9 = 76–100 % of leaves wilted and injured or plant completely dead

Data analysis

The data for the leaf wilt and injury were subjected to qualitative and quantitative genetic analysis. For the qualitative genetic analysis, in each population, plants with AUSPS ≤ 50 were classified as resistant, while those with AUSPS > 50 were classified as susceptible. The numbers of resistant and susceptible plants were subjected to segregation analysis based on a chi-squared test ($\chi 2$) using the R software program 2.14.0 (R Core Team, 2013).

The quantitative genetic analysis involved generation mean analysis (Hayman, 1958) and determining the number of effective factors. Mean, variance and SE values for the leaf wilt scores of each of the six populations were calculated using the R software program 2.14.0. The mean value and SE of each generation were tested for the adequacy of the additive-dominance model using a joint scaling test (Cavalli, 1952). Genetic effects with a three-parameter model involving mean (*m*), additive (*d*) and dominance (*h*), according to Hayman (1958), were estimated using the weighted least squares method, as described by Mather and Jinks (1982). Based on the estimated parameters, the expected generation means were calculated as:

$P_1 = m - d$

$P_2 = m + d$

$F_1 = m + h$

$F_2 = m + (1/2)h$

$BC_1 = m - (1/2)d + (1/2)h$

$BC_2 = m + (1/2)d - (1/2)h$

These models were used to apply a χ^2 test for the goodness of fit of the model (Hayman, 1958; Mather and Jinks, 1982). Significance of the gene effects was determined based on a t test (Mather and Jinks, 1982.)

The variance values of the P_1 (σ^2_{P1}), P_2 (σ^2_{P2}), F_1 (σ^2_{F1}) and F_2 (σ^2_{F2}) generations were used to estimate the variation due to phenotype (P), environment (E) and genotype (G) (Warner, 1952; Wright, 1968) as:

$$\sigma^2_P = \sigma^2_{F2}$$
$$\sigma^2_E = (\sigma^2_{P1} + \sigma^2_{P2} + \sigma^2_{F1})/\,3$$
$$\sigma^2_G = \sigma^2_P - \sigma^2_E$$

Then, broad-sense heritability was calculated as $\sigma^2_G/\,\sigma^2_P$ The number of effective factors (EF; number of genes) controlling the salinity tolerance was calculated using two methods:

Method I (Wright, 1968):

$$\mathrm{EF1} = \frac{(P1 - P2)^2[1.5 - 2h\ (1 - h)]}{8[\sigma 2\ _{F2} - 0.25\,(\sigma 2\ _{P1} + \ \sigma 2\ _{P2} + 2\sigma 2\ _{F1}]}$$

where F_1, P_1 and P_2 are the generation means, while σ^2 P_1, σ^2 P_2, σ^2 $_{F1}$ and σ^2 $_{F2}$ are the variance values of the disease scores of the respective generations and $h = (F_1 - P_1) / (P_2 - P_1)$.

Methods II (Lande, 1981):

$$\mathrm{EF2} = \frac{(P1 - P2)^2}{8[\sigma 2\ _{F2} - 0.25\,(\sigma 2\ _{P1} + \sigma 2\ _{P2} + 2\sigma 2\ _{F1})]}$$

The generation means and variances in the EF2 model were the same as in EF1 above. All the above formulas are based on the assumption that genes segregating for the salinity resistance are from the resistant parent, not linked, have equal effects and there are no dominance effect and genotype × environment effect (Wright, 1968).

Results

Variation of salt tolerance in parents and segregating populations

P_1 and P_2 showed contrasting leaf injury responses to salinity at 75 mM NaCl. The P_1 plants were highly susceptible, whereas the P_2 plants were highly tolerant. The tolerance scores in the P_1 and P_2 samples at 3 d, 6 d and 9 d after being subjected to salinity were 3.95, 6.90 and 8.47, respectively, for P_1, and 1.13, 1.87 and 5.54, respectively, for P_2 (Table 1). All the F_1 population were susceptible on each day of assessment, with scores of 3.83, 5.83 and 8.19, respectively. In the F_2 population, the scores varied at 3 d (1.00–8.33, with an average of 4.57) at 6 d (1.00–9.00, with an average of 6.13) and at 9 d (2.33–9.00, with a mean of 7.87). In the BC_1 population, the scores varied at 3 d (1.00–9.00, with an average of 3.44), at 6 d (1.00–9.00, with an average of 5.45) and at 9 d (3.67–9.00, with a mean of 8.67). In the BC_2 population, the scores varied at 3 d (1.00–9.00, with an average of 3.78), at 6 d (1.00–9.00, with an average of 5.08) and at 9 d (1.67–9.00 with a mean of 7.04).

In addition, the P_2 plants showed slower progress in the leaf injury response to the salinity test than the P_1 plants, with AUSPS values of 38.17 and 102.38, respectively. The AUSPS value in the F_1 population was in the range 36.00–162.00, with an average of 97.09. The AUSPS in the F_2 population was in the range 32.00–156.00, with an average of 101.53. The AUSPS value in the BC_1P_1 population was in the range 38.00–162.00, with an average of 89.68, whereas the AUSPS in the BC_1P_2 population was in the range 20.00–156.00, with an average of 85.39. The frequency distributions of leaf wilt scores and AUSPS values for all populations are shown in Fig. 3.

Mendelian inheritance of the salt tolerance

The χ^2 analysis for the F_2 population revealed that segregation of the leaf wilt score at 3 d did not fit the 1 (resistant)-to-3 (susceptible) ratio nor the 3 (resistant)-to-13 (susceptible) ratio (Table 2). However, the segregation at 6 d in the F_2 population fitted the 13:3 ratio, while the segregation at 9 d fitted both the 1:3 and 3:13 ratios (Table 2). Nonetheless, the segregation at both 6 d and 9 d for the BC_2 population did not fit the 1:1 ratio (Table 2). Based on the results for the F_2 population, salinity resistance was controlled by either a single-recessive gene or two genes with inhibitory gene actions, respectively.

Table 1 Visual leaf wilt scores after salt stress for V2278AG (P_1) and CPI 100834 (P_2), and F_1, F_2, BC_1P_1 and BC_1P_2 populations derived from cross between P_1 and P_2

Generation (number of plants)	Time after salt stress (d)									AUSPS		
	3			6			9					
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
P_1 (71)	1.00	7.67	3.95	1.00	9.00	6.90	7.00	9.00	8.47	36.00	150.00	102.38
P_2 (59)	1.00	3.00	1.13	1.00	4.33	1.87	3.00	8.33	5.54	24.00	78.00	38.17
F_1 (46)	1.00	9.00	3.83	1.00	9.00	5.83	3.00	9.00	8.19	36.00	162.00	97.09
F_2 (225)	1.00	8.33	4.57	1.00	9.00	6.13	2.33	9.00	7.87	32.00	156.00	101.53
BC_1 (157)	1.00	9.00	3.44	1.00	9.00	5.45	3.67	9.00	8.67	38.00	162.00	89.68
BC_2 (177)	1.00	9.00	3.78	1.00	9.00	5.08	1.67	9.00	7.04	20.00	156.00	85.39

Min = minimum; Max = maximum; AUSPS = area under the salt-injury progress stairs;
Leaf wilt score (1–9) where 1 = normal healthy leaves, 9 = 76–100% of leaves wilted and injured or plant completely dead

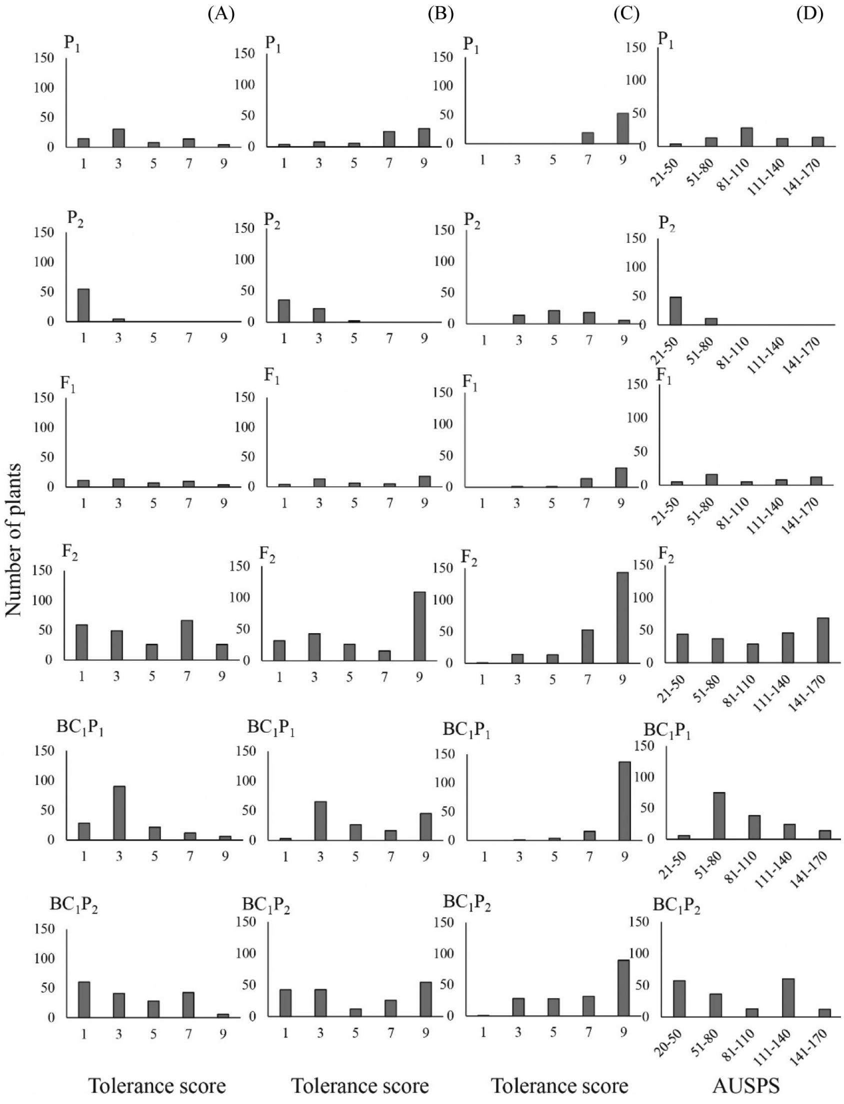

Fig. 3 Distribution of leaf wilt scores [1 (normal healthy leaves) to 9 (76–100 % of leaves wilted and injured or plant completely dead)] in six populations derived from cross between susceptible mungbean V2278AG and resistant mungbean CPI 100834: (A) at 3 d after salt stress; (B) 6 d after salt stress; (C), 9 d after salt stress; (D) area under the salt-injury progress stairs (AUSPS), where salt stress = growing in 75 mM NaCl

Table 2 Segregation analysis of salt resistance in four segregated populations derived from cross between V2278AG (P_1; susceptible) and CPI 100834 (P_2; resistant)

Generation	Ratio		Expected number		3 d After salt stress				6 d After salt stress				9 d After salt stress			
					Observed number		χ2	*p* Value	Observed number		χ2	*p* value	Observed number		χ2	*p* Value
	R	: S	R	S	R	S			R	S			R	S		
P_1	0	: 1	0	71	23	48	-	-	4	67	-	-	4	67	-	-
P_2	1	: 0	59	0	57	2	-	-	40	19	-	-	52	7	-	-
F_1	0	: 1	0	46	16	30	-	-	6	40	-	-	5	41	-	-
F_2	1	: 3	56.25	168.75	71	154	5.16	0.02*	38	187	7.89	0.01**	44	181	3.56	0.06^{ns}
	3	: 13	42.19	182.81	71	154	24.22	>0.001	38	187	0.51	0.47^{ns}	44	181	0.10	0.76^{ns}
BC_1	0	: 1	0	157	45	112	-	-	6	151	-	-	6	151	-	-
BC_2	1	: 1	89	89	68	109	9.50	>0.001	53	124	28.48	$>0.001^{**}$	57	121	23.01	>0.001

R = resistant; S = susceptible; ns = not significant;
* = $p < 0.05$, ** = $p < 0.01$

Generation mean analysis and heritability of the salt tolerance

A joint scaling test for the generation mean analysis revealed that a simple additive-dominance model was able to adequately explain the variation among the generations for leaf wilt scores and AUSPS (Table 3). This indicated that a single gene with additive and dominance gene effects controlled salinity resistance in the wild mungbean CPI 100834 and there was no nonallelic interaction effects for resistance. The additive gene effect (*d*) and dominant gene effect (*h*) estimated for the leaf wilt scores at 3 d, 6 d and 9 d are shown in Table 3. The *d* value range was 1.14–2.26, whereas the *h* value range was 1.39–2.45. The *d* and *h* values estimated for AUSPS were 27.47 and 37.92, respectively (Table 3). The potency ratios for these traits were 2.15, 0.89, 0.95 and 1.38 for 3 d, 6 d and 9 d and AUSPS, respectively. This suggested that the gene controlling salinity tolerance expresses incomplete dominance or overdominance.

Table 3 Joint scaling test and estimated gene effects for salinity resistance in six generations derived from cross between susceptible mungbean V2278AG and resistant mungbean CPI 100834

	Period after salt test (d)			AUSPS
Scale	3	6	9	
A	-1.23^{ns}	-1.83^{ns}	0.68^{ns}	-20.10^{ns}
B	2.25^{ns}	2.46^{ns}	0.35^{ns}	35.52^{ns}
C	4.86^{ns}	4.09^{ns}	1.09^{ns}	71.39^{ns}
Genetic effect				
m	2.32**	4.27**	7.08**	84.81**
d	1.14**	2.26**	1.47**	27.47**
h	2.45**	2.02**	1.39**	37.92**
chi-square	6.20^{ns}	4.60^{ns}	0.97^{ns}	0.05^{ns}
[*d*/*h*]	2.15	0.89	0.95	1.38

Leaf wilt score (1 to 9) where 1 = normal healthy leaves, 9 = 76–100 % of leaves wilted and injured or plant completely dead;
AUSPS = Area under the salt-injury progress stairs;
ns = not significant, * = $p < 0.05$, ** = $p < 0.01$

The broad-sense heritability (H^2) values calculated for leaf wilt and injury scores at 3 d, 6 d and 9 d were 46.54%, 49.03% and 49.08 %, respectively, while AUSPS was 46.84%. These values indicated that genetic factors played a moderate role in salinity tolerance in the wild accession CPI 100834.

Estimation of number of effective factors for salt tolerance

The number of effective factors calculated for leaf wilt and injury scores at 3, 6 and 9 days based on methods I and II were in the range 0.35–0.98 (Table 4), with an overall mean of average of 0.74, whereas that estimated AUSPS values were 0.76 and 1.00, respectively, with an average of 0.88 (Table 4). Based on these results, the salinity tolerance in the wild mungbean accession CPI 100834 is controlled by a single gene, which was in agreement with the results from generation mean analysis.

Discussion

In general, although salinity tolerance in crop plants is a complex trait, some landraces and wild relatives of crop plants possess high tolerance with simple genetic inheritance (Anson and Pavithan, 2014; Chankaew et al., 2014; Qi et al., 2014; Iseki et al., 2016; Guo et al., 2021). Based on the results from the current study, the frequency distribution for the segregating populations (F_2, BC_1P_1 and BC_1P_2) were continuous, suggesting that salinity tolerance in the wild mungbean CPI 100834 is a quantitative and possibly a polygenic trait; however, both qualitative and quantitative genetic analyses indicated that the tolerance was controlled by only one gene with moderate heritability (Tables 2, 3 and 4). This suggested that transfer of salt tolerance from the wild mungbean CPI 100834 to cultivated mungbeans could be achieved using simple breeding methods—for example backcross breeding. The current results were consistent with other results obtained based on genome-wide association study (GWAS) that indicated that salt tolerance in the mungbean was controlled by one (Liu et al., 2022) or two (Breria et al., 2020) regions (loci). The candidate genes for salt tolerance in the mungbean include *EVM0031157* (Liu et al., 2022), *Vradi07g01630*, *Vradi09g09510* and *Vradi09g09600* (Breria et al., 2020). It would be worthwhile to investigate whether these genes were associated with the wild mungbean accession CPI 100834. However, notably neither Liu et al. (2022) nor Breria et al. (2020) included wild mungbean in their studies. In addition, the wild accession CPI 100834 had the highest tolerance to salinity in the screening in the current study of about 500 accessions of mungbean germplasm.

Table 4 Number of effective factors/genes estimated by methods I (EF I) and II (EF II) and broad-sense heritability (H^2) for salinity resistance

Effective factor (EF)	3 d After salt stress	6 d After salt stress	9 d After salt stress	AUSPS
EF I	0.58	0.96	0.98	1.00
EF II	0.35	0.82	0.74	0.76
Average	0.46	0.89	0.86	0.88
H^2	46.54	49.03	49.08	46.84

AUSPS = Area under the salt-injury progress stairs

This wild mungbean may possess unique gene(s)/allele(s) for salinity tolerance. Gene/quantitative trait locus mapping and gene cloning for salt tolerance in CPI 100834 should be conducted in the future to identify the gene responsible for the tolerance.

In summary, the current study conducted qualitative and quantitative genetic analyses to determine genetic control of salt tolerance at 75 mM NaCl under hydroponic condition in the wild mungbean accession CPI 100834. Based on the results, it was concluded that salt tolerance in CPI 100834 was controlled by only one gene and that the heritability of the tolerance was moderate.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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