

Inheritance of Calcium Use Efficiency in Tomatoes Grown under Low-calcium Stress

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Abstract. Sixty highly homozygous tomato (*Lycopersicon esculentum* Mill.) strains, some selected from previous studies and some collected from known low-Ca regions, were screened under a low-Ca culture system (10 mg of Ca per plant). Four strains were selected to represent the extremes for Ca efficiency and used as parents to create a series of F₁, F₂, and backcross generations for inheritance studies of Ca use under low-Ca stress. Based on total plant dry weight, additive and dominance gene effects were most important for the efficiency of Ca use. Maternal control of efficiency in Ca use was not observed. Estimates of broad-sense heritability ranged from 63% to 79% for total plant dry weight. Narrow sense heritabilities, determined in only two of the families, were 47% to 49% and 68% to 75%.

The classification of plant species as calcifuge and calcicole plants by Clarkson (1965) showed clearly that plant species have evolved in different ways based on genetic changes and on the probable selection pressure associated with high and low Ca in their environments. Phenotypic differences in Ca efficiency have been reported to be associated with genotypic differences in Ca uptake, transport, and distribution (Marschner, 1986).

The systematic isolation and characterization of differences in Ca use among strains of tomato by Giordano et al. (1982), using solution culture, was the first study of naturally occurring phenotypic variance with *Lycopersicon esculentum*. Their data indicated that difference; in Ca efficiency were associated with differences in uptake, controlled by the genotype of the plant top, and in Ca use.

Subsequently, Behling (1987) demonstrated that the Mg ion concentration in Giordano's low-Ca solution interfered with Ca uptake; by lowering the Mg²⁺ from 48ppm to 24 ppm, the entire 10 mg Ca in solution was removed by the plant. Differences between strains were associated with transport and use of Ca.

The many Ca-associated disorders among agricultural crops, e.g., tipburn in cabbage and lettuce, blossom-end rot in tomato, and bitter pit in apple, are primarily in leaves and fruit with low transpiration. A recent report (Banuelos et al., 1987) indicated that the basipetal transport of IAA contributes to the acropetal transport of Ca into low-transpiring tissues, such as tomato fruit. Their latter research (Banuelos et al., 1988) also showed that, in the low-transpiring leaves of lettuce the basipetal auxin transport favors the acropetal transport of Ca. Efficient strains of tomato transported ⁴⁵Ca into the leaf lamina in the absence of any significant transpiration, while inefficient strains did not (Behling, 1987). Thus, the development of a seedling test that identifies efficiency in Ca use, particularly if it reflects movement of Ca into the leaf lamina in the absence of transpiration, could have wide application in breeding for tolerance to these many Ca-deficiency syndromes.

The purpose of our study was to investigate the efficiency of Ca use in tomato strains using Behling's low-Ca solution modified for Mg. Our primary objective was to use strains with

maximum differences in Ca use efficiency to study the inheritance of efficiency under low-Ca stress.

Materials and Methods

Sixty homozygous tomato strains, including some from known low-Ca regions previously selected by Giordano et al. (1982), were evaluated using a low-Ca nutrient solution. Seeds were germinated in disposable growth pouches (Northrup-King) with 25 ml of a half-normal concentration Hoagland solution. The growth pouch medium was maintained at the proper moisture level by addition of distilled water only. After 11 to 12 days, seedlings were transplanted singly into plastic pots containing 1.8 liter of a nutrient solution composed of 2.5 mM (KNO₃), 5.0 mM (NaNO₃), 0.5 mM (KH₂PO₄), 1.0 mM (MgSO₄·7H₂O), 25 μM (H₃BO₃), 5 μM (MnSO₄·H₂O), 2 μM (ZnSO₄·7H₂O), 0.5 μM (CUSO₄·5H₂O), and 0.015 μM (NH₄)₆Mo₇O₂₄·4H₂O. Iron was supplemented as Fe-EDTA at an initial concentration of 0.04 mM. Initial Ca concentrations were adjusted to 5 mg·kg⁻¹ with the addition of CaCl₂·2H₂O. Distilled water was added as needed throughout the experiment to maintain ≈ 1.8 liter of solution. Initially the solution was adjusted to pH 5.5 with 0.01 N NaOH. Magnesium was adjusted to 24 mg·kg⁻¹ (Behling, 1987).

Plants were grown for 28 to 30 days, at which time nearly all the available Ca had been removed from solution and growth had almost stopped. Temperatures in the growth room were maintained at ≈ 32 to 35C during the light period and 21 to 25C during the dark period. A light intensity of 200-300 μmol·s⁻¹·m⁻² at the top of the canopy was provided by cool-white fluorescent lamps for 16 hr in each 24-hr cycle. Calcium analyses were made with a Varian atomic absorption spectrophotometer model Spectra AA-20 (Mulgrave, Victoria, Australia).

Strains were characterized as Ca-efficient (E) and Ca-inefficient (I) in the screening phase based on 1) the amount of total plant dry matter produced, 2) the plant Calcium Efficiency Ratio (CaER = mg of total plant dry weight/mg of Ca in total plant), and 3) calcium deficiency symptoms—that is, reduction in plant size, distortion of leaves, and death of terminal buds.

Fifteen tomato strains were selected from preliminary trials and evaluated simultaneously in a replicated test. In addition to the low-Ca stress level (10 mg Ca/plant), plants of these strains were also grown at 400 mg Ca/plant. The adequate Ca level was included to observe if differences among tomato strains existed when Ca was not limiting. Strains that grew poorly at the adequate Ca level might be inefficient in dry matter accumulation, regardless of Ca availability, and such strains were

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not selected for further inheritance study. Seven of the 15 strains were chosen for a final evaluation using the two levels of Ca. A randomized complete block design was used with four replications of each strain in all screening experiments. Four strains were selected from the final screening experiment to represent the extremes for Ca efficiency.

A preliminary study was made to determine if maternal differences were important for Ca use efficiency. A diallel cross of four parent strains resulted in 16 entries of F_1 , reciprocal F_1 , and selfed progeny that were grown simultaneously under low-Ca conditions. A completely randomized block design was used with four replications of each entry. Analyses were made on total plant dry weight and CaER values.

A family was composed of six generations, as follows: P_1 and P_2 (parent strains), F_1 s ($P_1 \times P_2$ and $P_2 \times P_1$), F_2 (F_1 -selfed), BC_1P_1 ($P_1 \times F_1$), and BC_1P_2 ($P_2 \times F_1$). All six possible families originating from crosses among the two efficient and the two inefficient strains were grown in six separate generation means experiments. In evaluating each family, 12 plants of each parent, eight of each reciprocal F_1 , 40 of each backcross, and 40 F_2 plants from each reciprocal F_1 hybrid were grown. Because total plant dry weights were highly correlated with CaER values and Ca deficiency symptoms at the low-Ca stress level, only total plant dry weight data are presented. Generation mean analyses were calculated by using the method of Mather and Jinks (1977) and genetic effects were estimated. Environmental and genetic variances for total plant dry weight of segregating populations were determined by the methods of Voigt et al. (1966), and broad-sense heritabilities estimated in each family.

Parent-offspring regression was used to estimate narrow-sense heritability only. Two of the four families, derived from crosses between efficient and inefficient strains ($E \times I$), were used to develop the required later generation. Before harvest, 20 F_2 plants, 20 BC_1P_1 , and 20 BC_1P_2 plants in each of the two families were chosen randomly. Fresh weights were determined, and the selected plants returned to the growth medium containing a normal Hoagland's solution to permit recovery from the effects of Ca deficiency. After 7 to 10 days of recovery, the plants were transferred to the greenhouse and transplanted to 1.8-liter (9-inch) pots containing greenhouse soil. F_3 , $BC_1P_1S_1$, and $BC_1P_2S_1$ seeds were obtained and tested in separate experiments. Each experiment consisted of eight plants of each parent, P_1 and P_2 , and five plants of each derived F_3 , $BC_1P_1S_1$, and $BC_1P_2S_1$ progeny. All five members of each F_3 , $BC_1P_1S_1$, and $BC_1P_2S_1$ progenies traced back either to a single F_2 or a single backcross plant, respectively. Thus, each of the two experiments included 100 F_3 plants, 100 $BC_1P_1S_1$, and 100 $BC_1P_2S_1$ plants.

Progenies of selected plants (F_3 , $BC_1P_1S_1$, and $BC_1P_2S_1$) were regressed on their respective parents (F_2 , BC_1P_1 , and BC_1P_2). Because only fresh weights of selected plants were available, the dry weight of parental plants had to be estimated by other means. A basic linear regression, based on a procedure outlined by Fawole et al. (1982), was used. Narrow-sense heritability estimates for total plant dry weight and standard error of the heritability estimates were calculated according to the methods described by Smith and Kinman (1965), and Hallauer and Miranda (1981).

Results

A wide range in efficiency in Ca use was found among 60 selected strains tested (Li, 1989). In the final rescreening experiment, significant differences among strains were observed

for total plant dry weight. Efficient strains 113 and 99 and inefficient strains 67 and 118 were chosen to represent extremes in Ca use for inheritance studies. There were no significant differences in total plant dry weight among these four strains when grown under the adequate Ca level (Table 1). All, or nearly all, of the Ca in the low-Ca solution was taken up by the plants. Root dry weight of efficient and inefficient strains did not differ. However, differences in shoot dry weight between these strains were large and appeared to be the major reflection of differences in Ca efficiency.

In the preliminary inheritance study, four parent strains and all possible combinations of reciprocal F_1 progenies were tested under low-Ca stress. Comparisons of total plant dry weight and CaER between reciprocal F_1 s were nonsignificant in all crosses

Table 1. Mean total plant dry weight of seven tomato strains grown under low-Ca stress and at adequate Ca level in the final screening experiment.

Strain	Dry wt (g) ^{z,y}		Ca efficiency classification ^x
	Low Ca (10 mg)	High Ca (400 mg)	
113	4.46 a	6.25 b ^x	E
99	4.33 a	6.39 b	E
100	4.23 a	7.34 a	
35	4.20 a	7.01 ab	
67	3.42 b	6.47 b	I
118	3.39 b	6.20 bc	I
186	3.27 b	5.61 c	
LSD _{0.05}	0.417	0.859	

^zMean of four replications.

^yMean separation within columns by Fisher's protected LSD at the 5% level.

^xE = Ca-efficient, I = Ca-inefficient.

Table 2. Mean total plant dry weight and CaER of the four parents and their six reciprocal F_1 hybrids grown under low-Ca stress (10 mg Ca/plant) in a diallel experiment.

Entry	Criterion ^{z,y}	
	Plant dry wt (g)	CaER
Parents ^x		
99 (E) ^y	4.22 a	430 a
113 (E)	4.41 a	449 a
67 (I)	3.35 b	342 b
118 (I)	3.23 b	330 b
LSD _{0.05}	0.320	58
Crosses		
99 × 113	4.43	451
113 × 99	4.39 NS	448 NS
99 × 67	4.11	423
67 × 99	4.02 NS	414 NS
99 × 118	3.93	401
118 × 99	4.16 NS	424 NS
113 × 67	4.02	441
67 × 113	4.06 NS	445 NS
113 × 118	4.35	444
118 × 113	4.18 NS	430 NS
67 × 118	3.54	365
118 × 67	3.45 NS	359 NS

^zMean separation within columns by Fisher's protected LSD at the 5% level.

^yMean of four replications per entry. CaER = mg of total plant dry weight/mg of Ca in plant.

^xCa efficiency classification: E = Ca-efficient; I = Ca-inefficient.

^{NS}Nonsignificant.

Table 3. Generation means, phenotypic variances, and broad-sense heritability estimates of total plant dry weight for six families in generation mean experiments.

Generation	n	113(E) x 67(I)		99(E) x 118(I)		113(E) x 118(I)		99(E) x 67(I)		113(E) x 99(E)		67(I) x 118(I)	
		Mean (g)	CV	Mean (g)	CV	Mean (g)	CV	Mean (g)	CV	Mean (g)	CV	Mean (g)	CV
P ₁ ^z	12	4.11	6.8	3.53	15.0	4.41	7.1	4.48	9.7	3.82	7.0	3.15	11.5
P ₂	12	3.25	9.0	2.82	19.7	3.30	9.8	3.60	11.3	3.81	7.0	3.04	8.4
F ₁	16	3.97	6.4	3.54	13.4	4.47	7.8	4.08	8.5	3.94	3.0	3.30	6.5
(P ₁ xP ₂)	8	3.89	8.3	3.33	15.2	4.56	7.4	4.06	9.9	3.98	2.0	3.35	6.3
(P ₂ xP ₁)	8	4.04	3.6	3.96	9.4	4.39	8.5	4.11	5.8	3.90	3.9	3.25	6.8
F ₂	80	3.68	15.1	3.11	26.5	4.26	16.6	4.13	15.8	3.74	11.2	3.04	17.8
BC ₁ P ₁	40	4.01	9.3	3.41	25.4	4.58	9.7	4.41	13.7	3.82	11.9	3.21	15.6
BC ₁ P ₂	40	3.75	15.0	3.18	25.9	3.90	11.6	4.12	11.6	3.68	13.2	3.20	11.4
Phenotypic variance		0.308		0.682		0.502		0.427		0.167		0.294	
Broad-sense heritability (%)		76		66		79		63		70		72	

^zP₁ is the first parent designated for each family; P₂ is the second.

Table 4. Frequency distribution for total plant dry weight (g) of the six derived generations in the family involving 99(E) and 67(I), grown under low-Ca stress (10 mg/plant).

Generation	Number of plants per class										N	(g)	(%)
	2.0-2.3	2.4-2.7	2.8-3.1	3.2-3.5	3.6-3.9	4.0-4.3	4.4-4.7	4.8-5.1	5.2-5.5	5.6-5.9			
P ₁ (99 E)						2		9	1		12	4.48	9.7
P ₂ (67 I)		1	2	1	7	1					12	3.60	11.3
F ₁					6	9	1				16	4.08	8.5
F ₂	1		4	5	15	26	14	9	4	2	80	4.13	15.8
BCP ₁				2	4	15	10	6	2	1	40	4.41	13.7
BCP ₂			1	3	10	17	9				40	4.10	11.6

(Table 2). Based on total plant dry weight, differences between efficient and inefficient strains were fairly consistent in all separate generation means experiments. Plant dry weight cvs of the non-segregating P₁, P₂, and F₁ generations were usually smaller than cvs of the F₂, BC₁P₁, and BC₁P₂ segregating generations (Table 3). There were no differences in generation means for the progenies derived from the hybrid of strain 113(E) x 99(E) and 67(I) x 118(I). Consequently, these two families were eliminated from further genetic analysis. Since results obtained from the families of the four crosses between efficient and inefficient strains (E x I) were similar, segregation data are presented (Table 4) only for one family (99 E x 67 I). Frequency distributions and means for this family suggested additive gene effects. The F₁ was intermediate compared to the two parents, the BC₁P₁ was skewed toward the P₁, and the BC₁P₂ was skewed toward the P₂. The F₂ mean also was intermediate to the parents with individual plants distributed across and beyond the range of both parents. These results indicate the presence of transgressive segregation.

The means of six generations in each family provided estimates of various gene effects for total plant dry weight (Table 5). The resulting three-parameter model (mean, additive, and dominance) was adequate for all (E x I) families. A significant additive component was found in all (E x I) families. The dominance component was significant in three of the four families.

Broad-sense heritability estimates for plant dry weight were > 60% in all families (Table 3). Estimates of narrow-sense heritability were 47% to 49% and 68% to 75%, respectively, in two families analyzed (Table 6).

Discussion

Genetic variation in the efficiency of Ca use by tomato strains was demonstrated. The results obtained from progenies grown

Table 5. Estimates of gene effects in a three-parameter model for total plant dry weight of (E) x (I) families.

Parameter	113 x 67	99 x 118	113 x 118	99 x 67
Mean	3.663**	3.101**	3.895**	4.135**
(SE)	(0.056)	(0.087)	(0.060)	(0.072)
Additive	0.401**	0.330*	0.587**	0.382**
(SE)	(0.058)	(0.089)	(0.058)	(0.070)
Dominance	0.280*	0.314*	0.634**	0.049
(SE)	(0.093)	(0.122)	(0.119)	(0.121)
χ ^{2z}	7.293 ^{NS}	5.451 ^{NS}	2.179 ^{NS}	6.688 ^{NS}

^zχ² = value from a three-parameter model.

***Significant at P = 0.05 or 0.01, respectively.

under low-Ca stress indicated that differences in efficiency were fairly consistent over experiments—strains 99 and 113 were always Ca-efficient and strains 67 and 118 were always Ca-inefficient. The averages of total plant dry weight produced by efficient strains were ≈ 30% greater than those produced by inefficient strains. The selection for efficient and inefficient extreme types in the screening phase at low-Ca conditions provided reliable parental strains for genetic study.

The solution culture technique for evaluating the response to low-Ca stress permits response differences to be expressed in only 28 to 30 days. The seedling test for efficiency in Ca use found in tomatoes, therefore, may have wide usage in breeding for tolerance to Ca-related disorders, such as tip burn in cabbage and lettuce, and black heart in celery.

There were no maternal effects on the efficiency of Ca use, confirming the results of Giordano et al. (1982) for tomato strains studied in a somewhat different low-Ca nutrient system.

Previous studies in our laboratory revealed different genetic mechanisms for nutrient use, varying from a single gene for K

Table 6. Regression coefficients, narrow-sense heritability (H_N) estimates, and the standard errors of the estimates for the families (99 × 118) and (113 × 118).

Family	Mean dry wt of designated parents (random plants)		Mean dry wt of progenies derived from designated parents		Regression of derived progenies on their parents		Standard error of regression	Heritability estimates (%)	Standard error of H_N estimates
	Source	Dry wt (g)	Source	Dry wt (g)	Source	RC ^z			
99(E) × 118(I)	F ₂	4.068	F ₃	4.205	F ₃ ,F ₂	0.74	0.07	49	0.05
	BC ₁ P ₁	4.063	BC ₁ P ₁ S ₁	4.204	BC ₁ P ₁ S ₁ ,BCP ₁	0.72	0.26	48	0.17
	BC ₁ P ₂	3.950	BC ₁ P ₂ S ₁	4.085	BC ₁ P ₂ S ₁ ,BCP ₂	0.70	0.08	47	0.05
113(E) × 118(I)	F ₂	4.511	F ₃	4.706	F ₃ ,F ₂	1.03	0.13	69	0.09
	BC ₁ P ₁	4.524	BC ₁ P ₁ S ₁	4.685	BC ₁ P ₁ S ₁ ,BCP ₁	1.02	0.11	68	0.07
	BC ₁ P ₂	4.155	BC ₁ P ₂ S ₁	4.174	BC ₁ P ₂ S ₁ ,BCP ₂	1.13	0.15	75	0.10

^zRC = regression coefficient.

in beans (Shea et al., 1967) to multigenic differences between efficient and inefficient strains for K in tomatoes (Makmur et al., 1978; Figdore et al., 1989), N in tomatoes (O'Sullivan et al., 1974), and P in beans (Whiteaker et al., 1976). Our results suggest that relatively few major genes control the efficiency of Ca use in tomatoes. In all families from E × I parents, additive and dominance gene effects, made significant contributions to the efficiency of Ca use (Table 5). Broad-sense heritability was > 60% for total plant dry weight. Thus, efficiency of Ca use is a highly heritable trait in tomato.

In our study, narrow-sense heritability (H_N) estimates were obtained by using the parent-offspring regression, a method commonly used to estimate narrow-sense heritability of quantitative characters. Smith and Kinman (1965) reported that the regression coefficient estimates of narrow-sense heritability in a self-pollinated population will be biased upward if the inbreeding coefficient of the parent is greater than zero, as with the regression of F₃ progeny on F₂ parents. They suggested that the correct estimator for the general case is $b/(2r_{xy})$. Fawole et al. (1982) did not adjust for the previous inbreeding of parents when they regressed offspring on parents, which might explain why the estimates of narrow-sense heritability in some crosses were > 100% and higher than broad-sense heritability estimates for P use in the bean strains they studied. In our study, the regression coefficient (B) was very high in all progenies of the family 113(E) × 118(I), and was relatively high in all progenies of the family 99(E) × 118(I). To avoid an upward bias, estimates of narrow-sense heritability were calculated using the formula $H_N = b/2r_{xy}$, which provides an adjustment for the known level of inbreeding.

The high and moderately high broad- and narrow-sense heritability values found for total plant dry weight suggested that the heritable differences in Ca efficiency among the tomato strains may warrant the use of these strains, especially strain 113(E), in a tomato breeding program aimed at improved adaptation to low-Ca stress. Some F₃, BC₁P₁S₁, and BC₁P₂S₁ plants had higher dry matter than efficient parent strains 113 and 99 (Li, 1989), suggesting that selection of superior individuals in segregating populations would be successful.

Behling et al. (1989) reported that efficient strain 113 was able to continue growth and metabolism in all parts of the plant under a relatively low percentage of Ca in its tissue. They also pointed out that the efficiency of Ca use in strain 113(E) was associated with distribution and translocation of Ca even in the apparent absence of transpiration. In the present study, all crosses with strain 113(E) had high broad- and narrow-sense heritability values. The crosses with strain 99(E) had lower broad- and narrow-sense heritability values than other crosses, suggesting

that breeding tomatoes for Ca efficiency using this strain would probably be more difficult, and the gain from selection would be smaller than from using efficient strain 113. However, strain 99(E) always continued growing until harvest time in every low-Ca experiment. Behling (1987) reported that efficient strain 99 removed ions from solution at a different rate than did other strains. The slow removal of ions by strain 99(E) appeared to be correlated with its growth pattern. Thus, the character of slow growth rate under low-Ca stress in strain 99(E) also could be valuable for developing cultivars adapted to low-Ca environmental conditions.

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