BARD

FINAL REPORT

PROJECT NO. IS-2971-98

**Genes Controlling Calcium-Mediated Tolerance to
Salinity in Plants**

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Project Title: Genes controlling calcium-mediated tolerance to salinity in plants

Investigators

Institutions

Principal Investigator (PI): H. Fromm Weizmann Institute of Science, Israel

Co-Principal Investigator (Co-PI): J-K Zhu, University of Arizona, Tucson, USA

Collaborating Investigators:

A. Danon, The Weizmann Institute of Science, Israel

Keywords *not* appearing in the title and in order of importance. Avoid abbreviations.

Stress, Gene expression, Calmodulin, Arabidopsis

Abbreviations commonly used in the report, in alphabetical order:

CaM: Calmodulin

SOS: Salt Overlay Sensitive

Ca: Ca²⁺

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US: \$141,000

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Signature
Principal Investigator

Signature
Authorizing Official, Principal Institution

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Publication Summary (numbers)

	Joint IS/US authorship	US Authors only	Israeli Authors only	Total
Refereed (published, in press, accepted)	0	0	0	0
Submitted, in review, in preparation		2	1	3
Invited review papers		1		1
Book chapters				
Books				
Master theses			1	1
Ph.D. theses			1	1
Abstracts				
Not refereed (proceedings, reports, etc.)				

Postdoctoral Training: List the names and social security/identity numbers of all postdocs who received more than 50% of their funding by the grant.

Masaru Ohta SS# 764-09-3395, University of Arizona

Boaz Kaplan, The Weizmann Institute of Science (PhD student)

Cooperation Summary (numbers)

	From US to Israel	From Israel to US	Together, elsewhere	Total
Short Visits & Meetings	0	0	2	2
Longer Visits (Sabbaticals)	0	0	0	0

Description of Cooperation:

Cooperation involved exchange of information, cDNAs, and methods. A former postdoc (R. Sunkar) in the lab of H. Fromm is currently a postdoc in the lab of J-K Zhu.

Patent Summary (numbers)

	Israeli inventor (s) only	US inventor (s) only	Joint IS/US inventors	Total
Submitted				0
Issued (allowed)				0
Licensed				0

Abstract

The specific objectives of the proposed research were to identify, clone and characterize downstream cellular target(s) of SOS3 in *Arabidopsis thaliana*, to analyze the Ca^{2+} -binding characteristics of SOS3 and the *sos3-1* mutant and their interactions with SOS3 cellular targets to analyze the SOS3 cell-specific expression patterns, and its subcellular localization, and to assess the *in vivo* role of SOS3 target protein(s) in plant tolerance to salinity stress. In the course of the study, in view of recent opportunities in identifying Ca^{2+} -responsive genes using microarrays, the group at Weizmann has moved into identifying Ca^{2+} -responsive stress genes by using a combination of aequorin-based measurements of cytosolic Ca and analysis by DNA microarrays of early Ca-responsive genes at the whole genome level. Analysis of *SOS3* (University of Arizona) revealed its expression in both roots and shoots. However, the expression of this gene is not induced by stress. This is reminiscent of other stress proteins that are regulated by post-transcriptional mechanisms such as the activation by second messengers like Ca. Further analysis of the expression of the gene using promoter - GUS fusions revealed expression in lateral root primordial. Studies at the Weizmann Institute identified a large number of genes whose expression is up-regulated by a specific cytosolic Ca burst evoked by CaM antagonists. Fewer genes were found to be down-regulated by the Ca burst. Among the up-regulated genes many are associated with early stress responses. Moreover, this study revealed a large number of newly identified Ca-responsive genes. These genes could be useful to investigate yet unknown Ca-responsive gene networks involved in plant response to stress.

Achievements

- (1) We have established a system to measure in vivo Ca signals in response to salinity stress based on the luminescence of the aequorin protein in transgenic tobacco and Arabidopsis. The Ca response to NaCl is dose dependent (Fig. 1)
- (2) We have characterized a transient Ca burst activated in response to treatments with CaM antagonists (Fig 2 A-C), which blocked with Ca channel blockers (Figure 2E). This study was expanded through collaboration with M. Knight (Oxford University UK), providing the facility to perform a real-time in vivo computer-based imaging of the Ca-burst (Figure 2D).
- (3) We have identified several genes that are rapidly (within an hour) up-regulated or down-regulated by a cytosolic Ca burst (Tables 1 and 2 respectively)
- (4) Many of the genes identified to respond to Ca are associated with stress (Table 3)
- (5) We identified the salt-induced gene ZAT10 (EST number R90419) as a rapid Ca-responsive gene (Table 3).
- (6) We have used promoter-GUS fusions to study the cell-specific expression pattern of *SOS3* (Fig. 3) and RT-PCR to show that expression of *SOS3* is not induced by NaCl (Fig. 4).

Significance of the main scientific achievements or innovation:

To our knowledge, our results provide the first whole-genome-based profile of early Ca-responsive genes. The discovery of numerous genes up-regulated by Ca allows a wide-basis analysis of Ca-mediated pathways. Further analysis of promoter elements of the newly identified genes is likely to reveal novel mechanisms underlying response to stress.

Agricultural and/or economic impacts of the research findings:

Although there is no short-term impact on agriculture and economy, the discovery of numerous rapidly activated genes in response to a Ca burst provide a basis to elucidate

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novel mechanisms involved in stress responses, and these could serve as potential targets for future engineering of stress tolerance.

Details of cooperation:

The PIs met twice in international conferences, and continued exchanging ideas, information and biological material (cDNAs). In particular, the US PI has received the list of Ca-induced stress responsive genes from the Israeli PI, and has identified interesting salt-stress genes (e.g. ZAT10). This information was shared with the US PI who is currently studying mutants of this gene. This exchange of unpublished information is expected to facilitate the functional analysis of this gene.

List of publications:

Three manuscripts are in preparation.

A

Ca is in nM

B

Figure 2: A cytosolic Ca-burst is induced by CaM antagonists (W7, TFP, SKF-7171 and Calmidazolium (A). W5 is a weak analogue of W7 and is less efficient in activating the Ca-burst (B). Pretreatment with one CaM-antagonist abolishes the response of another (C) indicating that the different inhibitors operate on the same cellular targets. Computer imaging of the Ca burst is shown in D. The Ca burst is abolished by the Ca-channel blockers Lanthanum and Gadolinium (E)

D

control

TFP

W-7

TFP
pretreated with W7

W7
pretreated with TFP

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Table 1. Arabidopsis genes whose expression is significantly up-regulated by a cytosolic $[Ca^{2+}]_{cyt}$ burst

locus	Description	EST	Fold induction	Control
AT1G03220	Putative extracellular dermal glycoprotein precursor (EDGP)	H76724	2.1 ± 0.3	1.1 ± 0.2
AT1G03730	unknown protein	H37232	1.9 ± 0.3	1.18 ± 0.12
AT1G03740	putative cdc2 protein kinase	T20464	2.3 ± 0.4	1.30 ± 0.05
AT1G11310	Putative Mlo2 protein	T88073	1.84 ± 0.14	1.08 ± 0.14
AT1G11530	Putative thioredoxin-h 4	R65313	2.1 ± 0.4	1.12 ± 0.15
AT1G18570	MYB51 - R2R3-MYB transcription family	T22593	3.0 ± 0.4	1.5 ± 0.2
AT1G19180	Unknown protein	T42340	3.2 ± 0.3	1.2 ± 0.3
AT1G20440	cor47 – cold regulated gene similar to late embryogenesis abundant proteins	N96955	2.0 ± 0.3	1.0 ± 0.2
AT1G21110	Putative O-methyltransferase 1	T46659	3.4 ± 2.0	1.5 ± 0.3
AT1G21730	kinesin-related protein	N38368	1.8 ± 0.2	0.92 ± 0.10
AT1G28380	unknown protein	R30143	2.0 ± 0.4	1.16 ± 0.12
AT1G31130	similar to Na/Alanine symporter	T20423	2.3 ± 0.3	1.2 ± 0.2
AT1G33600	LRR protein family	T20493	2.0 ± 0.3	1.4 ± 0.2
AT1G34430	Putative dihydrolipoamide S-acetyltransferase	T42217	1.8 ± 0.3	0.87 ± 0.13
AT1G36310	putative methyl transferase	R65236	1.9 ± 0.2	0.93 ± 0.12
AT1G42990	bZIP family transcription factor	N97053	1.8 ± 0.2	0.96 ± 0.08
AT1G47380	putative PP2C	T44777	1.9 ± 0.3	1.2 ± 0.2
AT1G51700	adof1 - dof zinc finger protein	N97077	2.1 ± 0.5	0.99 ± 0.13
AT1G52890	similar to NAM (no apical meristem)	N65888	2.1 ± 0.3	1.2 ± 0.2
AT1G55670	Putative photosystem I subunit V precursor	T43953	2.0 ± 0.2	1.13 ± 0.12
AT1G59820	chromaffin granule ATPase II homolog, putative	N96155	2.3 ± 0.4	1.04 ± 0.09
AT1G62660	beta fructosidase	W43492	1.9 ± 0.3	1.1 ± 0.2
AT1G66260	Putative RNA and export factor binding protein	T45888	1.9 ± 0.3	0.98 ± 0.12
AT1G69080	unknown protein	N38009	1.9 ± 0.3	1.09 ± 0.03
AT1G69840	unknown protein	R90080	2.3 ± 0.4	1.15 ± 0.07
AT1G70090	putative glycosyl transferase	N38288	2.6 ± 0.5	1.1 ± 0.2
AT1G72450	expressed protein	T44776	1.9 ± 0.2	1.14 ± 0.13
AT1G72930	Putative disease-resistance protein (TIR class)	N65692	2.4 ± 0.3	1.1 ± 0.2
AT1G74100	similar to flavonol 4'-sulfotransferase	T44722	3.7 ± 0.9	1.4 ± 0.2
AT1G79900	Mitochondrial carrier protein family similar to carnitine acylcarnitine translocase	T46024	2.1 ± 0.3	1.1 ± 0.2
AT2G01270	Unknown protein	T22047	2.5 ± 0.3	1.16 ± 0.11
AT2G01670	Unknown protein	T20807	2.0 ± 0.2	1.23 ± 0.09
AT2G05710	Cytoplasmic aconitate hydratase	T44218	2.9 ± 0.3	1.3 ± 0.2
AT2G05940	putative protein kinase	H76238	1.4 ± 0.5	2.8 ± 0.5
AT2G22500	Mitochondrial carrier protein family	AA06758 1	2.4 ± 0.3	1.28 ± 0.09
AT2G23120	Unknown protein	T21007	3.2 ± 0.8	1.3 ± 0.2
AT2G23810	Unknown protein	T43684	2.5 ± 0.8	1.3 ± 0.2
		N97214	2.3 ± 0.4	1.21 ± 0.10

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locus	Description	EST	Fold induction	Control
AT2G26190	Unknown protein	R90092	2.1 ± 0.2	1.0 ± 0.2
AT2G28840	putative RING zinc finger ankyrin protein	T22042	2.0 ± 0.2	1.14 ± 0.14
AT2G29960	Cyclophilin	T46293	2.0 ± 0.3	1.24 ± 0.14
AT2G30470	putative VP1/ABI3 protein	T22510	4.4 ± 0.7	1.16 ± 0.06
AT2G30740	putative protein kinase	T76002	2.1 ± 0.4	1.2 ± 0.2
AT2G30870	ERD13 - Glutathion-S-Transferase - Early Responsive Dehydration	R65251 T43250	2.4 ± 0.4 2.6 ± 0.7	1.3 ± 0.2 1.14 ± 0.12
AT2G32240	putative myosin heavy chain	H76467 W43572	2.4 ± 0.4 2.0 ± 0.4	1.2 ± 0.3 0.9 ± 0.2
AT2G36220	Unknown protein	T22218	2.17 ± 0.14	1.4 ± 0.2
AT2G40000	putative nematode-resistance protein	N65731	2.3 ± 0.4	1.1 ± 0.2
AT2G40140	putative ankyrin-repeats CCCH-type zinc finger protein	T43596	4.7 ± 0.4	1.6 ± 0.4
AT2G41100	TCH3 - calmodulin-like protein	N38224 N97207	2.8 ± 0.2 3.4 ± 0.4	1.4 ± 0.2 1.5 ± 0.2
AT2G41430	ERD15 - Early Responsive Dehydration	AA042759	2.0 ± 0.2	1.38 ± 0.09
AT2G45820	remorin - a non-specific DNA binding protein	T76318	1.9 ± 0.2	1.21 ± 0.06
AT3G01690	unknown protein	R65234	3.5 ± 0.9	1.2 ± 0.3
AT3G07180	unknown protein	R90439	2.9 ± 0.5	1.1 ± 0.2
AT3G11820	AtSYR1 - syntaxin related protein	R90507	2.0 ± 0.3	1.05 ± 0.11
AT3G16530	putative lectin	T75902	2.6 ± 1.3	1.5 ± 0.2
AT3G16720	similar to RING-H2 zinc finger protein ATL6	N38413	1.91 ± 0.10	1.1 ± 0.3
AT3G19260	longevity factor-like protein	T21493	2.2 ± 0.3	1.19 ± 0.13
AT3G44720	putative chloroplast prephenate dehydratase	N96696	2.4 ± 0.3	1.3 ± 0.2
AT3G45640	AtMPK3 - mitogen-activated protein kinase 3	N65559	2.3 ± 0.5	1.3 ± 0.2
AT3G51550	putative receptor-protein kinase	R64794	3.5 ± 1.4	0.9 ± 0.2
AT3G55980	PEI1 - ankyrin-repeats zinc finger transcription factor	T22041	6.5 ± 1.4	1.4 ± 0.2
AT3G57530	CDPK32 - calcium-dependent protein kinase	N96364	2.3 ± 0.2	1.3 ± 0.2
AT3G60220	RING-H2 zinc finger protein ATL4 (ATL4)	R89979	2.2 ± 0.2	1.09 ± 0.08
AT3G62720	alpha galactosyltransferase-like protein	H76189	2.0 ± 0.4	1.0 ± 0.2
AT4G02380	late embryogenesis abundant protein - similar to small stress induced proteins	H37120	2.0 ± 0.2	1.13 ± 0.08
AT4G17090	glycosyl hydrolase family 14 (beta-amylase)	H37046	2.0 ± 0.4	0.70 ± 0.11
AT4G22710	CYP706A2 - putative flavonoid 3,5 -hydroxylase - cytochrome p450 family	N65907	2.4 ± 0.2	1.4 ± 0.2
AT4G25030	unknown protein	N65831	2.0 ± 0.2	1.17 ± 0.06
AT4G30530	unknown protein	T43728	2.2 ± 0.2	1.0 ± 0.2
AT4G31500	cytochrome p450 family - tryptophan biosynthesis and auxin homeostasis	T75944	3.0 ± 1.7	1.4 ± 0.3
AT4G33070	pyruvate decarboxylase-1 (Pdc1)	N97215	1.8 ± 0.2	1.07 ± 0.10
AT4G35480	RHA3B - RING-H2 finger protein	T45602	2.0 ± 0.3	1.0 ± 0.2
AT4G38550	pEARL14 - Phospholipase like protein	R65028	1.9 ± 0.3	1.18 ± 0.12
AT4G39670	unknown protein	R30050	2.8 ± 0.4	1.1 ± 0.2
AT4G39950	CYP79B2 - converts Trp to indo-3-acetaldoxime a	T42902	3.2 ± 0.7	1.6 ± 0.3

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locus	Description	EST	Fold induction	Control
	precursor to IAA - cytochrome P450 family			
AT5G03380	similar to farnesylated protein ATFP2	T20408	1.83 ± 0.09	1.09 ± 0.14
AT5G06320	NHL3 - harpin induced NDR1/HIN1-like protein 3	H37034	2.2 ± 0.4	1.0 ± 0.3
AT5G11670	NADP dependent malic enzyme - like protein	N65762	1.8 ± 0.2	1.13 ± 0.09
AT5G13420	transaldolase - like protein	N38293	4.6 ± 1.6	1.5 ± 0.2
AT5G15970	KIN2 - cold regulated protein COR6.6	T21841	5.0 ± 1.3	1.1 ± 0.3
AT5G24140	SQP2 - squalene monooxygenase 2	T44667	2.80 ± 0.11	1.23 ± 0.12
AT5G24300	Putative starch synthase	T22050	3.0 ± 0.3	1.26 ± 0.12
AT5G26030	ferrochelatase-I	N38420	3.3 ± 0.4	1.56 ± 0.11
AT5G35735	unknown protein	T43614	2.7 ± 0.4	1.1 ± 0.2
AT5G42050	unknown protein	T21358	2.4 ± 0.6	1.1 ± 0.2
AT5G42380	calmodulin like protein	R30557	5.0 ± 0.6	0.8 ± 0.3
AT5G42650	CYP74 - allene oxide synthase in JA biosynthetic pathway -cytochrome p450 family	N65720	2.9 ± 0.4	1.1 ± 0.2
AT5G48480	unknown protein	T46263	2.0 ± 0.5	1.3 ± 0.2
AT5G53350	CLPX - ATP-dependent Clp protease ATP-binding subunit	T20819	1.98 ± 0.14	0.9 ± 0.2
AT5G56980	unknown protein	T21530	2.4 ± 0.5	1.03 ± 0.12
AT5G57560	TCH4 - xyloglucan endotransglycosylase	T76325	2.0 ± 0.5	1.08 ± 0.07
AT5G59550	CIP8 - COP1-interacting protein	R30129	2.3 ± 0.4	1.2 ± 0.2
Unknown	Unknown	N97187	2.3 ± 0.4	1.18 ± 0.06
Unknown	Unknown	N97200	2.4 ± 0.2	1.3 ± 0.2
Unknown	Unknown	T45312	1.8 ± 0.3	1.21 ± 0.12
Unknown	Unknown	T76754	1.9 ± 0.3	0.74 ± 0.09

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Table 2. Arabidopsis genes whose expression is significantly down-regulated by a cytosolic $[Ca^{2+}]_{cyt}$ burst

locus	Description	EST	Fold reduction	Control
AT1G66270	beta-glucosidase - glycosyl hydrolase family 1	N65342	2.3 ± 0.4	0.8 ± 0.2
		N97158	2.2 ± 0.5	0.8 ± 0.3
AT1G66280	glycosyl hydrolase family 1	N65443	1.8 ± 0.3	0.7 ± 0.3
AT1G73260	putative trypsin inhibitor	R30257	5.3 ± 1.2	1.0 ± 0.2
AT2G36830	putative aquaporin - gamma tonoplast intrinsic protein	N64968	3.0 ± 0.7	1.3 ± 0.2
AT3G01420	feebly-like protein	H37095	2.8 ± 0.8	0.9 ± 0.2
AT3G16420	jacalin-like lectin, similar to jasmonate inducible protein - myrosinase binding protein	N65032	1.9 ± 0.3	1.0 ± 0.2
		N65775	1.8 ± 0.2	0.9 ± 0.2
AT3G16460	jacalin-like lectin, similar to jasmonate inducible protein - myrosinase binding protein	W43253	2.3 ± 0.2	1.02 ± 0.09
		T46036	2.4 ± 0.3	0.97 ± 0.08
AT3G23190	unknown protein	T20932	2.2 ± 0.7	0.9 ± 0.3
AT3G26510	unknown protein	N65790	3.4 ± 0.6	1.4 ± 0.5
AT3G26520	putative aquaporin - gamma tonoplast intrinsic protein	AA06753 2	2.0 ± 0.4	1.1 ± 2
AT3G26740	light regulated protein, putative	N65497	1.8 ± 0.3	0.99 ± 0.13
AT3G49070	unknown protein	N65390	2.6 ± 0.3	1.00 ± 0.14
AT3G51370	protein phosphatase 2C -like protein	T46496	2.1 ± 0.3	0.97 ± 0.15
AT3G51730	unknown protein	T43972	2.0 ± 0.4	0.88 ± 0.07
AT3G54040	photoassimilate-responsive protein PAR-1b -like protein	T44090	1.8 ± 0.3	0.80 ± 0.09
AT4G11650	osmotin precursor	H76850	3.9 ± 1.3	0.9 ± 0.2
		N97229	4.1 ± 1.6	0.90 ± 0.13
AT4G12420	pectinesterase (pectin methylesterase) family	N38363	2.0 ± 0.7	0.7 ± 0.3
AT4G12470	pEARL1 1-like protein	N37508	2.6 ± 0.7	0.7 ± 0.2
AT4G14630	germin precursor oxalate oxidase	N65240	2.2 ± 0.3	1.1 ± 0.2
AT4G26090	disease resistance protein RPS2 (CC-NBS-LRR class)	T88149	5.1 ± 0.6	1.06 ± 0.13
AT4G30170	putative peroxidase	T21036	2.4 ± 0.5	1.2 ± 0.2
AT4G39090	RD19A - cysteine proteinase	N65892	2.6 ± 0.4	1.3 ± 0.3
		T41787	3.2 ± 0.9	1.2 ± 0.3
AT5G17820	putative peroxidase	T45353	2.0 ± 0.3	1.2 ± 0.2
AT5G19890	putative peroxidase	H37593	1.9 ± 0.3	1.06 ± 0.08
AT5G43370	APT1, PHT2 - inorganic phosphate transporter	T46507	1.8 ± 0.2	1.06 ± 0.07
AT5G44610	unknown protein	T21724	3.7 ± 0.5	1.4 ± 0.2
		T22213	4.1 ± 0.6	1.1 ± 0.3
AT5G49360	xylosidase - glycosyl hydrolase family 3	H37097	1.9 ± 0.3	1.1 ± 0.3
AT5G63600	flavonol synthase family	T75976	2.1 ± 0.7	0.86 ± 0.05
AT5G64100	putative peroxidase	N65288	2.3 ± 0.5	1.0 ± 0.2
		T44766	2.3 ± 0.6	0.9 ± 0.2
AT5G65210	bZIP transcription factor, TGA1	R90199	2.16 ± 0.12	1.1 ± 0.2

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Table 3: Early stress responsive genes are the common denominator of the genes upregulated by the cytosolic $[Ca^{2+}]_{cyt}$ burst

	locus	EST	ratio TFP/DMS O	ratio W7/DMS O	ratio W7/W7+L a	ratio(control W7+La/La	description
1	AT1G09070	T21700	3.4	4.3	2.2	1.1	similar to src-induced by cold drought heat and wounding
2	AT2G30470	T22510	5.0	7.0	5.3	1.1	putative seed specific VP1/ABI3 family regulatory protein
3	AT1G27730	R29923 R90419	5.4 4.4	8.7 5.7	2.6 2.1	1.7 1.4	ZAT10 - salt, ABA and cold induced C2H2 zinc finger protein
4	AT3G45640	N65559	3.0	3.3	2.5	1.4	ATMPK3 - mitogen-activated protein kinase 3 - A gene encoding a mitogen-activated protein kinase kinase kinase induced simultaneously with genes for a mitogen-activated protein kinase and an S6 ribosomal protein kinase by touch, cold, and water stress
5	AT5G57560	T76325	2.9	3.0	2.3	1.1	xyloglucan endotransglycosylase (TCH4)
6	AT1G65310	N37583	2.6	3.3	2.3	1.2	xyloglucan endotransglycosylase, putative - Similar to TCH4
7	AT4G02380	H37120	2.5	2.9	2.2	1.1	late embryogenesis abundant protein -related - similar to several small proteins (~100 aa) that are induced by heat, auxin, ethylene and wounding such as Phaseolus aureus indole-3-acetic acid induced protein ARG
8	AT2G40140	T43596	10.5	12.1	4.8	1.8	Putative cch-zinc finger transcription factor contain ankyrin repeat
9	AT3G55980	T22041	12.2	21.5	8.3	1.4	an embryo specific cch-zinc finger transcription factor (PEI1) contain ankyrin repeat
10	AT2G41100	N97207 N38224	4.6 6.1	11.5 11.5	3.8 3.0	1.3 1.3	ATCAL5 - calmodulin-like protein (TCH3)
11	AT2G41430	W43612 AA042759	2.5 2.2	2.2 2.8	2.7 2.1	1.3 1.3	ERD15 - Early Responsive Dehydration
12	AT3G15210	N65389 T76090	2.9 2.8	2.8 2.7	1.9 2.0	1.5 1.3	rap2.5 - ethylene responsive element binding factor (AtERF4) induced by cold drought and salt
13	AT5G42380	R30557	4.9	6.3	5.1	0.7	calmodulin like protein

RnI - upregulated more than 1.9 fold

Bold - upregulated more than 1.6 fold

Figure 3. SOS3 promoter-GUS is expressed in lateral root primordia.

Fig. 4: SOS3 is not inducible by NaCl