

# EFFECTS OF SALINITY CONCENTRATIONS ON ARABIDOPSIS FUNCTIONAL TRAITS



MOHAMAD ALI TOUFIC NAJIA  
School of Biomedical Engineering  
Georgia Institute of Technology



DR. CARA GORMALLY  
School of Biology  
Georgia Institute of Technology

“**E**xcessive soluble salts in the soil are harmful to most plants. In fact, no toxic substance restricts plant growth more than salt does on a world scale. Understanding the mechanisms of plant salt tolerance will lead to effective means to breed or genetically engineer salt tolerant crops. Salt tolerance research also represents an important part of basic plant biology, contributing to our understanding of subjects ranging from gene regulation to ion transport, osmoregulation and mineral nutrition. Using a survey of published literature, we asked whether salinity mitigates a functional response, examined the form of responses, and surveyed the evidence for saline effect on functional traits. Our primary goal was to seek general patterns of saline effects on Arabidopsis for broad categories of functional traits. This research review is aimed at answering these general questions: 1) Does salinity affect phenotypic expression? 2) How does salinity affect reproductive fitness? 3) Can salt inhibit germination? 4) Whether saline disrupts ion transport through root structures? 5) Is there variation in salinity tolerance among the ecotypes? We surveyed nine peer-reviewed journals from 1999 to 2010 and organized the articles we found (12) into categories that best answered one of our five questions. Our overall findings suggest that saline does have a pertinent effect on Arabidopsis and we go into further detail, in regards to the answers to our questions. Ultimately, this review is significant because we show that Arabidopsis is adaptive to increase its salt tolerance. Also, these results can beneficially impact the agricultural sector in increasing crop yields or vegetative output.”

## I. INTRODUCTION

Plants need essential mineral nutrients to grow and develop. However, excessive soluble salts in the soil are harmful to most plants. In fact, no toxic substance restricts plant growth more than salt does on a world scale (Xiong et al. 2002). It is estimated that salinity affects at least 20% of world's arable land and more than 40% of irrigated land to various degrees (Rhoades and Loveday 1990). In extreme cases, productive agricultural land could no longer sustain agricultural production and had to be abandoned. This may have contributed to the decline of some human civilizations in history. Soil salinization is also one of the driving forces of land degradation throughout the world and has a formidable impact on the agricultural industry (Zhang et al. 2010).

Based on their capacity to grow on high salt mediums, plants are traditionally classified as glycophytes or halophytes (Flowers et al. 1977). Halophytes are tolerant to high concentrations of sodium chloride; some can withstand salts that are more than twice the concentration of seawater. Most plants, including the majority of crop species, are glycophytes and cannot tolerate high salinity. For glycophytes, salinity imposes ionic stress, osmotic stress, and secondary stresses such as nutritional disorders and oxidative stress (Zhu 2001a). Sodium toxicity represents the major ionic stress associated with high salinity. Additionally, some plant species are also sensitive to chloride, the major anion found in saline soils. The low osmotic potential of saline solutions hampers plant water uptake, resulting in "physiological drought." For halophytic plants that are tolerant of sodium toxicity, osmotic stress may be the main cause of growth inhibition.

Understanding the mechanisms of plant salt tolerance will lead to effective means to breed or genetically engineer salt tolerant crops. Salt tolerance research also represents an important part of basic plant biology, contributing to our understanding of subjects ranging from gene regulation and ion transport, to osmoregulation and mineral nutrition. Additionally, some aspects of salt stress responses are intimately related to drought and cold stress responses (Zhu 2001b). Using a survey of published literature, we asked whether salinity mitigates a functional response, examined the form of responses, and surveyed the evidence for saline effect on functional traits.

## Salt Stress and Arabidopsis

Our review focused primarily on the glycophytic plant *Arabidopsis thaliana* because of its ubiquity, use as a model organism, and ecotypic variation in salinity tolerance. Although salt sensitivity among genetically different geographic varieties (ecotypes) of *Arabidopsis* exists, a systematic comparison among different ecotypes has not been reported. This comparison between ecotypes may localize salt tolerance functional traits if relatively large differences in salt tolerance exist between ecotypes. For this research review, we did not limit our definition of salinity to purely sodium chloride.

Research with other glycophytic plant species has shown that upon exposure to high salinity, plants may exhibit a reduced growth rate, accelerated development or death if the stress is severe or prolonged (reviewed by Lazof and Bernstein 1999). Like many other glycophytes, the sensitivity of *Arabidopsis* to salt stress is exhibited at all stages of development. Thus, functional traits are pertinent in characterizing specific *Arabidopsis* developmental characters, affected under saline conditions.

## Definition of Functional Traits

In reviewing current scientific literature, derivatives for the definition of a functional trait were ubiquitous. In the broadest sense, a functional trait can be defined as any phenotypic character that influences organismal fitness through biochemical, physiological, morphological, developmental, or behavioral mechanisms (Geber and Griffen 2003). Most often, a functional trait affects fitness through performance measures, such as growth rate, competitive ability, herbivore resistance or tolerance, attractiveness to pollinators, and so on. Table 1.0 synthesizes common derivations of traits definitions used in this review.

In practice, the distinctions between functional and performance traits and between performance and fitness components are difficult and subjective because the designations will often differ between researchers investigating different levels of function. For example, leaf size is often considered a functional trait by ecologists, whereas a developmental biologist might view it as a performance measure because it is the outcome of leaf meristem size and rates of cell division and expansion. Leaf photosynthetic rate is also considered a functional trait by ecologists, but as a measure of net carbon gain it can also be viewed as a performance trait that is

		<b>Definition</b>	<b>Application</b>
<b>Functional Trait</b>	(1) Physiological processes: photosynthesis, respiration (Calow 1987)	Individual	Individual
	(2) Life history processes: germination, growth production (Weiher et al 1999)	Individual	Individual/ population
	(3) Individual Fitness (Reich et al 2003)	Individual	Individual
	(4) Performance measures (Geber and Griffen 2003)	Individual	Individual
<b>Performance Trait</b>	Fitness components: growth, reproduction, survival (Geber and Griffen 2003).	Individual	Individual
<b>Response Trait</b>	Response of a plant to environmental changes (Keddy 1992)	Individual	Individual
<b>Effect Trait</b>	Effect of a plant on ecosystem functioning (Diaz and Cabido 2001)	Individual	Ecosystem
<b>Functional Marker</b>	Function s.l. at any organization level (more easily measurable than the function itself) (Garnier et al. 2004)	Individual	Any organization level

Table 1. Examples of plant functional traits found in literature, while the function, component or process they are supposed to capture the levels of definition and application.

determined by biochemical and transpiration properties of leaves (Geber and Dawson 1997).

In our review, we focus on traits related to vegetative function that affect survival, vegetative growth and size, and fertility. We do not address sexually selected traits.

#### Review Goals

Our primary goal was to seek general patterns of saline effects on *Arabidopsis* for broad categories of functional traits (i.e. physiology, morphology) and fitness measures (i.e. vegetative fitness, fertility). We addressed five questions of general significance to studies of *Arabidopsis* salt tolerance. This research review is aimed at answering these general questions:

1. Does salinity affect phenotypic expression?
2. How does salinity affect reproductive fitness?
3. Can salt inhibit germination?
4. Whether saline disrupts ion transport through root structures?
5. Is there variation in salinity tolerance among the ecotypes?

Our article provides a comprehensive review of saline effects on *Arabidopsis* functional traits and is one of the few papers that formally investigate saline variations among ecotypes.

## II. METHODS

### Literature Survey

We conducted a broad literature review of three online databases (ISI Web of Science, MEDLINE, and PubMed) accessible through the Georgia Tech Library. The search yielded twelve peer-reviewed journal articles from nine journals ranging in date from 1999 to 2010. These the journals include: Journal of Plant Ecology, The American Society of Plant Biologists, Plant Molecular Biology, Journal of Experimental Botany, Journal of Plant Nutrition, Plant Cell and Environment, Journal of Plant Physiology, Plant and Soil, and Acta Physiologiae Plantarum.

The articles were sorted into categories that best answered one of our five questions. Note: a particular article could have been sorted into two of the question categories if we felt that it was applicable and offering an alternative/supplementing viewpoint.

## III. RESULTS

Our overall findings suggest that saline does have a profound effect on *Arabidopsis* and we go into further detail, in regards to the answers to our inquiries.



### Question 1: Does salinity affect phenotypic expression?

The literature reviewed indicated across the board that salinity does affect phenotypic expression. In comparison to 11 other Brassicaceae species, Orsini et al. 2010 presented the variability that *Arabidopsis* phenotypic expression takes. A first comparison between different species was aimed at assessing their performance in saline environments in terms of both general growth and survival. Leaf traits and height were common functional traits that varied. *A. thaliana* and *T. salsauginea*, the latter known to tolerate very high NaCl concentrations (Inan et al. 2004), were used as controls. Under the imposed experimental conditions at 150 mM NaCl, leaf area was significantly reduced by the stress in *A. thaliana* (Figure 1). Similarly, *Arabidopsis* root growth was significantly inhibited at 150 mM NaCl, while others were less affected. Significantly tolerant root systems were found for *M. triloba* and *T. parvula* (Figure 1).

The NaCl lethal dose of 50% to the population (LD50NaCl) was used to assess plant survival to salt stress. Most species revealed their halophytic nature since their survival threshold was between 200 and 400 mM NaCl. This was much higher than *Arabidopsis*, whose LD50NaCl was 150 mM (see Appendix IA). Knowledge

of the dose-response relationship establishes causality that the NaCl has in fact induced the observed phenotypic effects.

After germination, seedling growth is also very sensitive to NaCl (Xiong 2002). Two-week-old Columbia ecotype seedlings growing in the soil were irrigated with 0, 50, 75, and 100 mM NaCl, respectively. Xiong et al. (2002) observed the bleaching of leaves, retarded growth, and delayed development of seedlings treated with higher concentrations of the salt. Specifically, at concentrations higher than 50 mM, NaCl statistically correlated ( $p < 0.01$ ) to the degradation and death of *Arabidopsis*.

The manner in which NaCl affects performance traits in *Arabidopsis* is striking. Why is leaf area more profoundly affected than root length? (Figure 1) Counterintuitive? Actually, no.

The imino acid, proline, has been reported to accumulate in plants subjected to salt stress (Mansour 2000). Proline, which accumulates in larger amounts than any other amino acid (Abraham et al. 2003), contributes to membrane stability and mitigates the effect of NaCl on cell membrane disruption (Mansour 1998). Total free amino acids in the leaves have been reported to be higher in salt tolerant than in salt sensitive ecotypes of *Arabidopsis* (Ashraf and

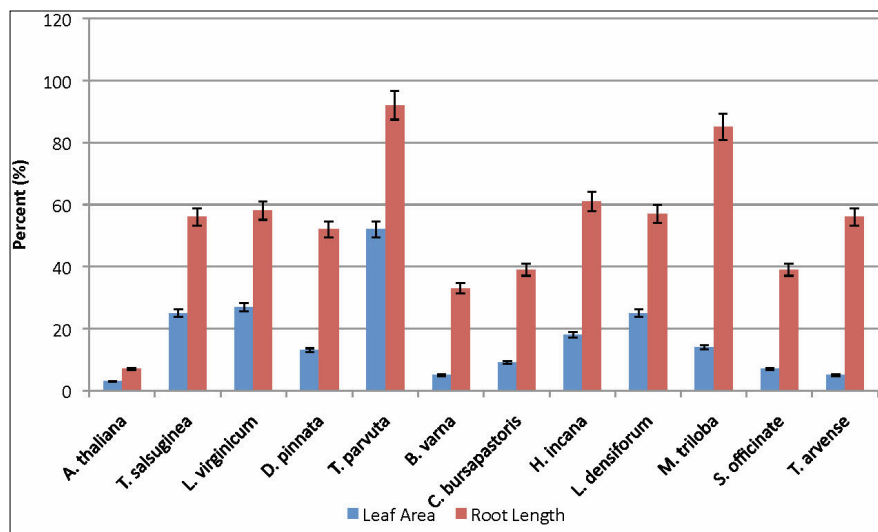


Figure 1. Effect of 150 mM NaCl stress on leaf area and root length of different *Arabidopsis* species synthesized from several articles. Salt treatments were administered when plants were 4-6 cm tall. Leaf area and root length were measured using a scanner and image processing software. Values are expressed as a percentage (%) of leaf area and root length in non-salinized plant controls.

Species	Response to salinity	References
<i>Oryza sativa</i>	decrease	Alamgir and Ali (1999)
<i>Vicia faba</i>	decrease	Gadallah (1999)
<i>Amaranthus tricolor</i>	decrease	Wang and Nil (2000)
<i>Bruguiera parviflora</i>	decrease	Parida et al. (2002)
<i>Pancreatium maritimum</i>	increases at low salinity; decrease at high salinity	Khedr et al. (2003)
<i>Arabidopsis thaliana</i>	increase	Quintero et al. (1996)
<i>Fragaria ananassa</i>	increase	El-Baz et al. (2003)

Table 2. Changes in proline in response to salinity

Tufail 1995). Petrusa and Winicov (1997) demonstrated that salt tolerant *Arabidopsis* ecotypes rapidly doubled their proline content in roots, whereas in most *Arabidopsis* ecotypes the increase was slow in leaves.

There are two alternative routes in proline biosynthesis in higher plants: the L-ornithine and the L-glutamate pathways. It is also known that, as in plants, both ornithine and glutamate are precursors of proline biosynthesis in microorganisms and mammals. Delauney et al. (1993) showed that two enzymes: pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR), play major roles in proline biosynthetic pathway. Plants over-expressing P5CS have shown increased concentration of proline and resistance to both drought and salinity stresses (Kishor et al. 1995). However, whether proline accumulation in these transgenic plants resulted in increased stress tolerance through osmotic adjustment or other mechanisms is unknown (Sharp et al. 1996). Table 2 presents the physiological reaction of several model plants to salt stress, in regards to their proline formation.

Transgenic approach to improve plant stress tolerance has appreciable results. Overproduction of proline by genetically manipulated *Arabidopsis* ecotypes showed tolerance to NaCl (Hong et al. 2000). Nanjo et al. (2003) demonstrated that introduction of antisense proline dehydrogenase cDNA in *Arabidopsis* over expresses proline and showed tolerance to salinity (600 mmol NaCl).

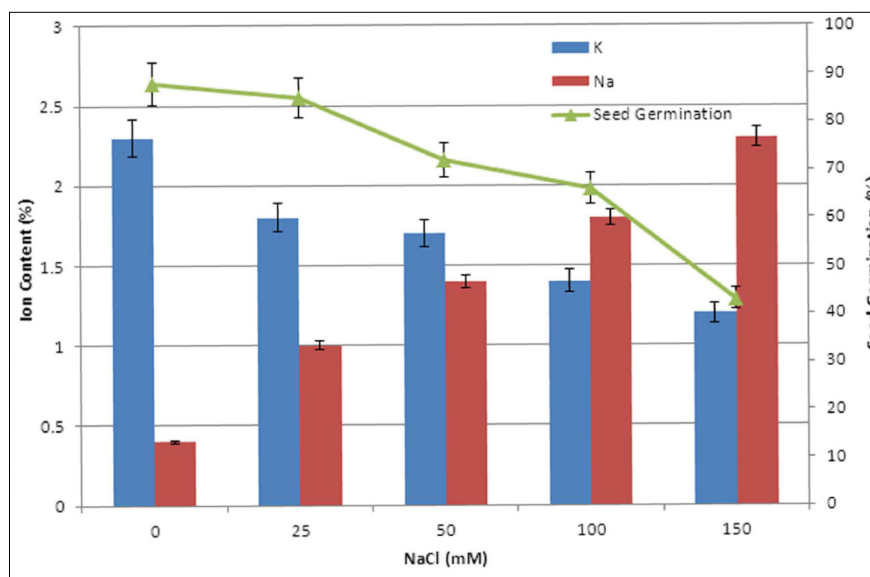
### Question 2: How does salinity affect reproductive fitness?

Salt accumulation has detrimental effects on seed maturation (Labidi et al. 2005). For their study, the diversity of some effects of salinity on rosette growth, seed production, and seed viability in *Arabidopsis thaliana* was explored.

There was a large inter-ecotype variability of the effect of salt on all factors contribution to reproduction (number of flower per axis, flower fertility, and seed viability). Among the five ecotypes, those with highest levels of Na<sup>+</sup> and Cl<sup>-</sup> ions in the silique valves produced the less viable seeds. The increased presence of sodium ions up-taken by *Arabidopsis* limited potassium nutrition; thus, limiting size and quantity of seeds produced (Xiong et al. 2002). Under increased saline stress and lower potassium absorption, reproductive functional seed traits were impaired (Figure 2).

The potassium ion is the preferred inorganic cation of living cells, and *Arabidopsis* is no exception to this rule; yet almost invariably the concentration of K<sup>+</sup> in the soil solution is lower than the cytosolic K<sup>+</sup> concentration (100-200 mM), meaning that *Arabidopsis* must actively take up and concentrate K<sup>+</sup> using various types of ion transporters (Rodriguez et al. 2000). Because Na<sup>+</sup> is similar to K<sup>+</sup>, and many K<sup>+</sup> transporters do not discriminate sufficiently between these cations, excess external Na<sup>+</sup> cannot only impair K<sup>+</sup> acquisition, but also lead to accumulation of Na<sup>+</sup> in *Arabidopsis* cells. In order to avert Na<sup>+</sup> toxicity most glycophytes rely on restricting Na<sup>+</sup> intake, but because the cell's interior is electronegative relative to the extracellular space, and because cation transporters in cell membranes are somewhat permeable to Na<sup>+</sup>, there is constant influx of Na<sup>+</sup> down this electrochemical gradient that cannot be completely prevented (Amtmann et al. 1999, Hasegawa et al. 2000). Moreover, the outcome of long-

Figure 2. Salt stress impairs K nutrition in Arabidopsis. With increased concentration of NaCl in the culture medium, Na<sup>+</sup> content in plants increases whereas K content decreases. Arabidopsis seedlings (ecotype Columbia) growing for two weeks were treated with NaCl. Seedlings were allowed to grow for 14 days before harvesting and analyzing ion contents (dry weight basis). Source: Xiong et al. 2002. The reproductive success of the seedlings can be represented by the percent of germinated seedlings that the Columbia ecotypes produced. The general trend is that as the salt concentrations increase, seedling germination decreases and consequently the ecotype's reproductive fitness. Source: Berthomieu et al. 2003.



term inhibition of K<sup>+</sup> acquisition by competing Na<sup>+</sup> is chronic K<sup>+</sup> deficiency. Such deficiencies are the biochemical explanations to the decreasing percent seed germination along a salt gradient, reflected in Figure 2, and consequently decreased reproductive fitness.

### Question 3: Can salt inhibit germination?

Seed germination behavior of Arabidopsis ecotypes were closely related to the salinity level of the habitats over which they were distributed. Ecotypes from the habitats with higher salinity had generally higher final germination proportions, but shorter mean times to germination than those from the habitats with lower salinity (Zhang et al. 2010). The inhibition of germination could be due either to NaCl-induced seed mortality or to unfavorable external conditions (Debez et al. 2004). Figure 2 underscores that inherent correlation between salt concentrations and the seed's ability to successfully germinate. As explained previously, sodium ions biochemically inhibit potassium ion uptake. Chronic potassium deficiency arrest cell growth and germination processes from undergoing. Particularly, Debez et al. (2004) observed that saline inhibited germination without damaging the seeds, which could recover their high capacity to germinate, when transferred to pure water. Hence, the main factor involved in the salt induced

dormancy of Arabidopsis seems to be the low water potential of the saline medium.

### Question 4: Whether saline disrupts ion transport through root structures?

Saline inhibition of germination stems from the realization that NaCl inhibits certain minerals from absorption by the roots. Hence, salinity tolerance can be attributed to three different mechanisms: Na<sup>+</sup> exclusion from the shoot, Na<sup>+</sup> tissue tolerance and osmotic tolerance (Jha et al. 2010). Jha et al. found that not only are genes differentially regulated between ecotypes, the expression levels of the genes can also be linked to the concentration of Na<sup>+</sup> in the plant. An inverse relationship was found between a particular gene expression in the roots and total plant Na<sup>+</sup> accumulation, supporting a role for that particular root gene in Na<sup>+</sup> efflux from the plant. Similarly, ecotypes with high expression levels of this gene in the roots had lower root Na<sup>+</sup> concentrations, due to the hypothesized role of the gene.

This new evidence supplements older theories that excessive sodium ions at the root surface may disrupt plant potassium nutrition that is vital for the maintenance of cell turgor, membrane potential, and the activities of many enzymes (reviewed by Lazof and Bernstein 1999). Because this particular gene expression



inhibits the majority of  $\text{Na}^+$  uptake, the sodium ions then act as competitive inhibitors of potassium ion uptake. Sodium ions are not required for the growth of most land plants. Land plants do not seem to have transport systems specifically for  $\text{Na}^+$  uptake. However,  $\text{Na}^+$  can still enter plant cells via several routes. Since the concentration of  $\text{Na}^+$  in the soil solution is usually much higher than that in the cytosol of root cells,  $\text{Na}^+$  movement into root cells is passive. Current evidence suggests that  $\text{Na}^+$  enters root cells mainly through various cation channels (Xiong 2002). These channels could be voltage dependent cation channels and due to the similarity between  $\text{Na}^+$  and  $\text{K}^+$ ,  $\text{Na}^+$  could enter the roots in place of  $\text{K}^+$  causing differential expression of functional traits (reviewed in Blumwald et al. 2000).

**Question 5: Is there variation in salinity tolerance among the ecotypes?**

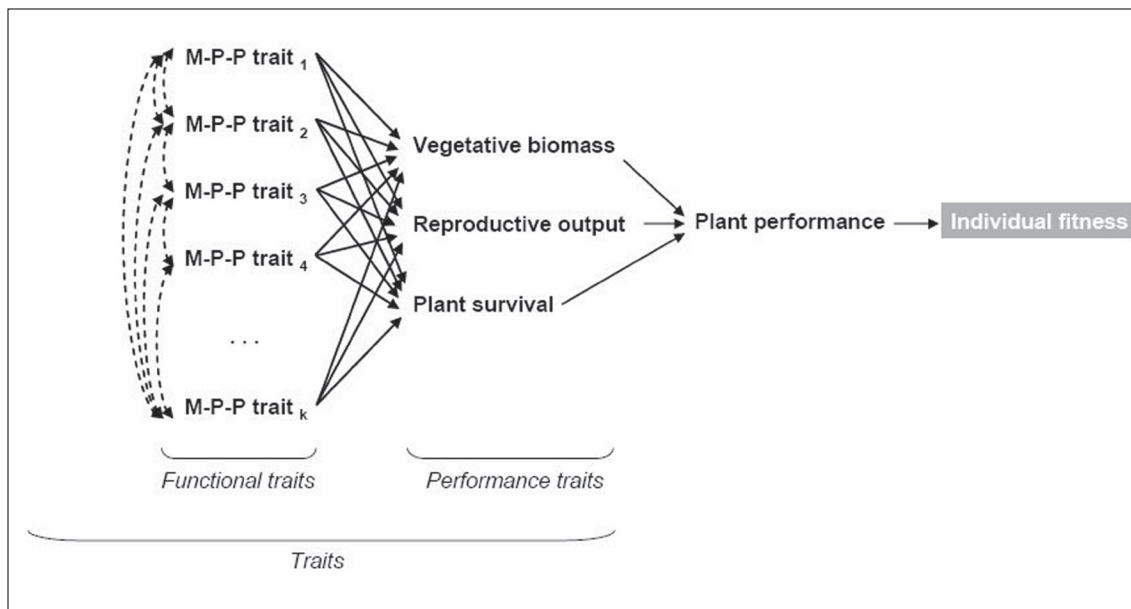
All the literature we reviewed contained experimental designs that compared *Arabidopsis* ecotypes or genetically similar species.

As well, in all cases there was statistically significant variation in functional traits between the ecotypes. Yet, underscoring this mantra was Katori et al.'s (2010) experiment where 350 *Arabidopsis thaliana* accessions large-scale soil pot experiments were performed to understand the natural variability in salt tolerance. The evaluation revealed a wide variation in the salt tolerance among accessions on the 35th day of 500 mM NaCl treatment. Salinity treatments on agar plates renders immediate salinity shock to plants, whereas the treatment using soil pots exposes plants to a gradual increase of NaCl stress because the water contained in soil is gradually substituted with saline water. Thus, treatments in soil pots stratified *Arabidopsis* responses, with gradual accumulation to high saline concentrations.

#### IV. DISCUSSION

Our primary goal was to seek general patterns of saline effects on *Arabidopsis* for broad categories of functional traits and

Figure 3.0 The current paradigm of trait, performance and fitness interconnectivity. This figure reflects current, widely accepted theories augmented with Arnold's (1983) framework of plant ecology. Morpho-physio-phenological (M-P-P) traits (from 1 to k) modulate one or all three performance traits (vegetative biomass, reproductive output and plant survival) that determine plant performance and individual fitness. M-P-P traits may be inter-related (dashed double-arrows).



demonstrate that this literature is pertinent in identifying and synthesizing knowledge for agricultural applications.

As Zhang et al. (2010) studied, soil salinization is a leading cause of land degradation, an urgent problem in the agricultural industry, where soil salinities can be high enough to impede optimal growing conditions. Although data on functional trait fitness are well-appreciated by community ecologists, stressors on these traits have largely been overlooked by population biologists focusing on the demography of a single species. Similarly, this review provides in depth research on inter-special variation. Solutions to the ever mounting battle against salinity in the agriculture industry can be achieved through differentiating glycophytes or halophytes plants. Genetic engineering and gene manipulation also provides an avenue for phenotypic plant alteration and adaption to high saline environments.

Additionally, we have shown that saline stress influences phenotypic expression, and more specifically *Arabidopsis*' reproductive trait expressions. Germination, the resultant of these trait expressions, was also shown to be inhibited, along with ion transport—the metabolic ignition for germination. Yet, more significantly, saline is a stressor of functional traits. These traits then assume particularly important roles as determinations for survival and, more long term, an individual's fitness (Figure

3). Thus, this research review becomes of significant importance because it has critical implications for real world applications. Scientists and geneticists are now enabled to create better fit individuals, grown in a specific habitat, to increase crop yields or vegetative output.

Because *Arabidopsis* is a glycophyte and is very sensitive to salt, one might assume that this plant is not suitable for studying the mechanisms of salt tolerance. However, previous studies with cultured glycophytic plant cells indicated that these cells could be adapted to tolerate high concentrations of salt that would kill un-adapted cells (Xiong et al 2002). Additionally, this review is necessary in the field of botany because our results for the model organism, *Arabidopsis*, can be applied to the general realm of glycophytic plants. The fact that adaptation can increase plant salt tolerance suggests that glycophytes do have salt tolerance machinery that may not be operating effectively in un-adapted conditions. Thus, further research is needed to invent adaptive machinery in glycophytes to allow optimal growth in salt saturated sectors of the planet. Therefore, the difference in salt tolerance between glycophytes and halophytes appears to be quantitative rather than qualitative, and basic salt tolerance mechanisms are probably conserved in all plant species. Our research review on *Arabidopsis* salt tolerance has provided the preliminary and

APPENDIX IA: *Arabidopsis* Ecotypic Response to Salinity Stressors

	Leaf Area Reduction (%)	Root Length Reduction (%)	Lethal Dose NaCl Response (mM)	K Ion Content % (@ 100 mM NaCl)	Na Ion Content % (@ 100 mM NaCl)
<i>A. thaliana</i>	3	7	145	1.7	1.5
<i>T. salsuginea</i>	25	56	591	5.7	5.3
<i>L. virginicum</i>	27	58	500	4.9	4.7
<i>D. pinnata</i>	13	52	223	3.7	4.5
<i>T. parvuta</i>	52	92	600	8.4	9
<i>B. varna</i>	5	33	263	3.3	4.3
<i>C. bursapastoris</i>	9	39	343	4.1	4.4
<i>H. incana</i>	18	61	307	4.5	4.6
<i>L. densiflorum</i>	25	57	498	5.2	2.3
<i>M. triloba</i>	14	85	600	8.9	7.6
<i>S. officinate</i>	7	39	339	3.4	3.9
<i>T. arvense</i>	5	56	296	1.9	1.6



confirmatory evidence for other specialized fields, such as genetic agricultural engineering, to apply our results and create adaptive mechanisms to optimize growth. Further research is needed in this field to determine the specific differences in salt sensitivity/tolerance and genetic markers for predisposition towards salt tolerance.

## V. REFERENCES

### Studies in Review

Attia H; Arnaud N; Karray N; Lachaal M. (2008, March). Long-term effects of mild salt stress on growth, ion accumulation and superoxide dismutase expression of *Arabidopsis rosette*

leaves. *Acta Physiologiae Plantarum*, 132(3), 293-305.

Blumwald, E.; Aharon, G.; Apse, M.P. (2000). Sodium transport in plant cells. *Biochim. Biophys. Acta*, 1465. 140-151.

Debez, Ahmed et al. (2004). Salinity effects on germination, growth, and seed production of the halophyte *Cakile maritima*. *Plant and Soil*, 262.179–189.

Inan G; Zhang H; Li P; et al. (2004). Salt cress. A halophyte and cryophyte *Arabidopsis* relative model system and its applicability to molecular genetic analyses of growth and development of extremophiles. *Journal of Plant Physiology*, 135. 1718–1737.

Jha, D.; Shirley, N.; Tester, M.; Roy, S. J. (2010, May). Variation in salinity tolerance and shoot sodium accumulation in *Arabidopsis* ecotypes linked to differences in the natural expression levels of transporters involved in sodium transport. *Plant Cell and Environment*, 33(5), 793-804.

Katori, T; Ikeda, A; Iuchi, S, et al. (2010, January). Dissecting the genetic control of natural variation in salt tolerance of *Arabidopsis thaliana* accessions. *Journal of Experimental Botany*, 61(4).1125-1138.

Labidi, N.; Hajji, M.; Grignon, C. (2005, January). Variability of the Effects of Salinity on Reproductive Capacity of *Arabidopsis thaliana*. *Journal of Plant Nutrition*, 27(9), 1561-1573.

Lazof, D.B.; Bernstein, N. (1999). The NaCl induced inhibition of shoot growth: the case for distributed nutrition with special consideration of calcium. *Adv. Bot. Res.*, 29. 113-189.

Orsini, Francesco et al. (2010). A comparative study of salt tolerance parameters in 11 wild relatives of *Arabidopsis thaliana*. *Journal of Experimental Botany*, 61(13). 3787–3798.

Wang, Weiquan et al. (2010). A large insert *Thellungiella halophila* BIBAC library for genomics and identification of stress tolerance genes. *Plant Molecular Biology*. 72. 91-99.

Xiong, Liming; Zhu, Jian-Kang (2002). Salt Tolerance. *The American Society of Plant Biologists*, 10(11), 1-22.

Zhang, X.; Xu, W.; Yang, B. (2010, September 8). Seed germination traits of two plant functional groups in the saline deltaic ecosystems. *Journal of Plant Ecology*, 3(3).

### Literature Cited

Amtmann A, Sanders D. (1999). Mechanisms of Na<sup>+</sup> uptake by plant cells. *Adv Bot Res.*, 29. 75–113.

Flowers, T.J.; Troke, P.F.; Yeo, A.R. (1977). The mechanism of salt tolerance in halophytes. *Journal of Plant Physiology*, 28.89-121.

Geber MA; TE Dawson (1997). Genetic variation in stomatal and biochemical limitations to photosynthesis in the annual plant, *Polygonum arenastrum*. *Oecologia*, 109. 535–546.

Geber, Monica A.; Griffen; Lauren R. (2003). Inheritance and Natural Selection on Functional Traits. *International Journal of Plant Science*.164 (3). S21–S42.

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. (2000). Plant cellular and molecular responses to high salinity. *Annu Rev Plant Physiol Plant Mol Biol.*, 51. 463–499.

Lazof, D.B., and Bernstein, N. (1999). The NaCl induced inhibition of shoot growth: the case for distributed nutrition with special consideration of calcium. *Adv. Bot. Res.*, 29. 113-189.

Rhoades, J.D.; Loveday, J. (1990). Salinity in irrigated agriculture. *Journal of Irrigation of Agricultural Crops*, 30. 1089-1142.

Rodriguez-Navarro A. (2000). Potassium transport in fungi and plants. *Biochim Biophys Acta*, 1469. 1–30.

Violle, Cyrille; et al. (2007). Let the concept of trait be functional! *Oikos*, 116(10). 882-892.

Xiong, Liming; Zhu, Jian-Kang (2002). Salt Tolerance. *The American Society of Plant Biologists*, 10(11), 1-22.

Zhang, X.; Xu, W.; Yang, B. (2010, September 8). Seed germination traits of two plant functional groups in the saline deltaic ecosystems. *Journal of Plant Ecology*, 3(3).

Zhu, J.-K. (2001a). Plant salt tolerance. *Trends Plant Sci*, 6. 66-71.

Zhu J.-K. (2001b). Cell signaling under salt, water and cold stresses. *Current Opinion Plant Biology*, 4. 401-406.