

Review Article

**Halophytic crops: A resource for the future
to reduce the water crisis?**

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Abstract: Water scarcity has been increasing and the problem is more severe in the arid regions and cause poverty and other related social and economic issues. An integrated approach therefore is imperative for the sustained development. Utilization of saline resources to mass produce halophytes of economic importance e.g. as vegetable, forage, and oilseed crops in agronomic field trials, have been used for bio-remediation of salt-contaminated soils and even pharmaceutical values of their products could be one such strategy to address water issue. We intend to explain a new concept of sustainable agriculture with so called “cash crop halophytes” (CCH) irrigated with saline waters (up to seawater salinity). Beside their potential to become cash crops, halophytes can be used in future also as model plants for the development of salt resistant crops from current non-salt tolerant conventional crops. Investigations of salt tolerant mechanisms of halophytes could provide critical clue to improve salt tolerance. Therefore we need to screen the potential of CCH with methods such as the quick check system (QCS). This is merely the first step to develop sustainable irrigation systems with saline water. This paper will discuss mainly the first step of the screening procedure. The QCS enables a detailed record of general tolerance criterion at reproducible conditions. Irrigation farming is expanding fast and many fields have reached a soil salinity level which prevents farmers from raising common crops and even the use of halophytes is not without consequences and a sustainable utilization is *sine qua non*! The further use of halophytes is the only available way for a sustainable utilization and is an efficient resource for the reduction of the water crisis.

Key words: water crisis, halophytes, salt resistance, sustainable use, breeding, cash crop halophytes

المحاصيل الملحية: مورد للمستقبل للحد من أزمة المياه

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المخلص: تفاقمت مشكلة ندرة المياه وأصبحت أكثر حدة في المناطق القاحلة مسببة الفقر وغيره من القضايا ذات الصلة الاجتماعية والاقتصادية. وكان لزاما أن ننحو نحو نهج متكامل لتحقيق التنمية المستدامة. وتعتبر الاستفادة من الموارد المائية المتملحة لإنتاج نباتات ملحية ذات أهمية اقتصادية كما في الخضروات والأعلاف والمحاصيل الزيتية وفي مناطق التجارب الميدانية الزراعية التي تم استخدامها للمعالجة البيولوجية للتربة الملوثة بالملوحة. وكذلك لها أهمية دوائية طبية مما يؤكد أهمية هذه الإستراتيجية بان تكون المحاصيل الملحية تلعب دورا في معالجة قضية المياه. ومن خلال الورقة الاستعراضية يتم شرح مفهوم جديد للزراعة المستدامة بما يسمى (النباتات الملحية هي محاصيل نقدية) بين (CCH) المروية بالمياه المالحة حتى ملوحة البحر. إلى جانب قدرتها على أن تصبح محاصيل نقدية يمكن استخدامها في المستقبل أيضا كنباتات نموذجية لتطوير محاصيل مقاومة للملوحة من المحاصيل التقليدية الغير مقاومة. يمكن أن تكون دراسة مكثفة لآليات مقاومة الملوحة للنباتات الملحية ويمكن أن تقدم دليلا حاسما لتحسين مقاومة الملوحة لذا نحن في أمس الحاجة إلى آلية لفرز الأصناف (CCH) المتحملة للملوحة مع منهجية واضحة لآلية سريعة لنظام سريع للفرز (QCS) وتعتبر هذه مجرد خطوة أولى لتطوير نظم الري المستدام باستخدام المياه المتملحة. وفي هذه الورقة التي تناقش بشكل مباشر الخطوة الأولى لإجراءات الفرز السريع (QCS) يمكن شرح مفصل للمعايير المقاومة العامة خاصة في مراحل البزوغ والإستنساخ. المزارع ذات نظم الري الحديثة بدأت تتوسع بشكل سريع في السنوات الأخيرة مما أدى إلى وصول الملوحة إلى مستويات أثرت على الإنتاجية مما يمنع المزارعين من التوسع في زراعة المحاصيل. وحتى استخدام النباتات الملحية لا يخلو من عواقب مما يجعل الاستخدام المستدام حل لا غنى عنه. في المستقبل ستكون زراعة المحاصيل الملحية هي الحل الوحيد المتاح لاستخدامها على نحو مستدام واستخدام متوازن للموارد للحد من أزمة ندرة المياه.

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Introduction

Water, of all natural resources is the major factor of the increasing worldwide concern over sustainable development, since various critical environmental threats with global implications have links to water crises (Gleick, 1994, 2000). Particularly, water is one of the essential resources in arid and semi-arid regions, where one-sixth of the world population lives and possesses the highest population (World Bank, 1999; UNDP, 1999). Rapid population growth increasingly generates pressure on existing cultivated land and other resources, and induces migration to the marginal land of the arid and semi-arid areas in many developing countries, such as Tanzania, Sudan, Egypt and Mexico (Bilsborrow and Delargy, 1991, Darkoh, 1982, Ericson et al., 1999; Findlay, 1996). Population migration to those arid and semi-arid areas increase the problems of water shortage and worsens the situation of land degradation in the destination, and in turn cause severe problems of poverty, social instability, and population health (Moench, 2002). Consequently, the enforced out-migrants from arid and semi-arid areas account for a large share of 13-26 million environmental refugees annually in the world (Bates, 2002). It has become clear that population growth, water shortage and land degradation in the arid and semi-arid regions are interlinked and jointly cause the problems of poverty, social insecurity, and environmental refugee situations.

The water crisis or better most of the water shortage problems arise from the following aspects (Koyro et al., 2006):

1) Fresh water is mainly available in the countries of the northern part of the world at ample amounts, while it is scarce especially in developing countries, where about 40% of the world's population live.

2) Water consumption has increased by more than 600% during the last century. This means that it is increasing twice as fast as population growth. Therefore, it is expected that 50% of mankind will experience scarcity of fresh water by the year 2025.

3) Due to global climate change, drastic draw-backs can be expected during this century

in Mediterranean countries, while increased rainfall is expected in other areas of the world.

4) Currently 70% of water worldwide consumed for irrigation. The area of irrigated land has increased from 1.5 mio km² in the year 1966 to 2,700,000 km² in the year 1998. This indicates that about 20% of arable lands have been under irrigation by the end of the last century. On this area 40% of all crops have been produced.

5) Water consumption of irrigation systems is increasing progressively with the augmentation of the irrigated area. This demand of extra irrigation water due to increase in arable areas, where blue water is already scarce or not available any more.

Water scarcity and desertification could critically undermine efforts for sustainable development, introducing new threats to human health, ecosystems and national economies of several countries. Therefore, an integrated approach for solutions is required through economic, social and environmentally sustainable developmental opportunities (Duda and El-Ashry, 2000).

Shortage of fresh water resources and soil salinization

A major aim is to evaluate the potential of local halophytes for wide economic use in arid and semiarid regions in the light of the progressive shortage of fresh water resources and soil salinization. Major research topics are to identify and select plant species tolerant to salt stress by selecting and using biomarkers to characterise halophytes (but also salt-tolerant glycophytes), to evaluate the possible use of non conventional water such as sea water, to select halophytes and tolerant glycophytes of a potential importance in the field of human or animal nutrition.

It is also an aim of this review to explain a practicable concept of sustainable agriculture with so called "cash crop halophytes" irrigated with saline waters (up to seawater salinity). A major advantage of this concept is that oceans contain most of the water on earth. Natural saline habitats occur along bodies of saltwater, e.g., coastal salt marsh, and inland within high-evaporation basins, saline lakes, and lowlands

of dryland and desert topography. However, a major problem of this concept is the high salinity itself and the electrolytes sodium (a cation) and chloride (an anion) being toxic to men, animals and most plants at relatively low soil water concentrations. Thus, it is neglected in most water management calculations. Nevertheless, even if we are reluctant to use seawater then we need urgently a solution for the problem of salinization. Irrigation water contributes to salinization of the upper layer of the soil in arid and semiarid regions. "No one is really certain of the figures, but it seems that at least 8 percent of the world's irrigated land is affected," says FAO water expert Julián Martínez Beltrán. "In the arid and semi-arid regions, it's somewhere around 25 percent." (<http://www.fao.org/worldfoodsummit/english/newsroom/focus/focus1.htm>). When soils in arid regions of the world are irrigated, solutes from the irrigation water can accumulate and eventually reach levels that have an adverse effect on plant growth. Of the current 230 million ha of irrigated land, 45 million ha are salt-affected (19.5 percent) and of the 1,500 million ha under dryland agriculture, 32 million are salt-affected to varying degrees (2.1 percent).

Sustainable utilization of saline lands

Along the path of plant domestication, many crop species have lost resistance mechanisms to various stress conditions (Serrano, 1996), including salt stress (Munns, 1993). Thus, most crop plants do not fully express their original genetic potential for growth, development, and yield under salt stress, and their economic value declines as salinity levels increase (Läuchli and Epstein, 1990; Maas, 1990). Improving salt resistance of crop plants is, therefore, of major importance in agricultural research. A potent genetic source for the improvement of salt resistance in crop plants resides among wild populations of halophytes (Glenn et al., 1999; Serrano et al., 1999; Khan et al., 2009). These

can be either domesticated into new, salt-resistant crops, or used as a source of genes to be introduced into crop species by classical breeding or molecular methods.

Generally, the introduction of alternate crops lead to reducing water consumption, is advisable in areas of limited water availability. Currently some of these plants produce lower yields as compared to well-established crops such as maize, soy bean, rice, etc. Therefore, they will not be accepted in areas, where high yield crops can be grown on a reliable scheme.

However, there are already several examples known for the utilization of halophytes for industrial, ecological, or agricultural purposes (Figure 1). Because of their diversity, halophytes have been tested as vegetable, forage, and oilseed crops in agronomic field trials. The most productive species yield 10 to 20 t ha⁻¹ of biomass on seawater irrigation, equivalent to conventional crops. The oilseed halophyte, *Salicornia bigelovii*, yields 2 t ha⁻¹ of seed containing 28% oil and 31% protein, similar to soybean yield and seed quality (Glenn et al., 1999). Halophytes grown on seawater require a leaching fraction to control soil salinity, but at lower salinities they outperform conventional crops in yield and water use efficiency. Halophytic forage and seed products can replace conventional ingredients in animal feeding (Table 1a and b) systems, with some restrictions on their use due to partially high salt content and antinutritional compounds present in some species (Khan et al., 2009). An animal feeding trial conducted at ISHU, Pakistan comparing conventional green fodder (maize) with a halophytic grass (*Panicum turgidum*) fed to cow calves showed that the weight gain over a period of four months was similar in the two cases with somewhat better quality meat i.e. higher protein and lower fat in meat of animals consuming halophytic grass (Table 1a and b).

Table 1. Use of *Panicum turgidum* green, grown with saline irrigation waters, as cattle feed.
a) *Panicum turgidum* green as an alternate to maize in cattle feed.
(Diet constituents in Kg fed twice daily).

Feed constituents	Maize	Panicum
Wheat straw	05.0	05.0
Maize	03.0	00.0
Panicum	00.0	03.0
Wheat bran	02.0	02.0
Concentrates	02.0	02.0
Total	12.0	12.0

b) Observations recorded at the termination of trial (Mean ± Standard Error).

Observations	Maize	Panicum
Live weight initial (kg)	139.0±5.0	138.0±7.4
Live weight at slaughter (kg)	199.0± 2.0	192.0±10
Weight gain from initial (%)	043±3.10	038.0±3.40
Weight gain per week (kg)	03.75±0.50	3.38±0.91
Carcass weight (kg/animal)	96.1±2.40	91.2±1.90
Protein in meat (%)	64.4±5.70	70.3±2.80
Fat in meat (%)	28.2±0.98	24.9±0.88
Dressed meat (%)	49.7±2.85	47.6±0.97

Possibilities for halophyte utilisation

Table 1: Utilisations of halophytes already existing and utilisation purposes that are investigated.

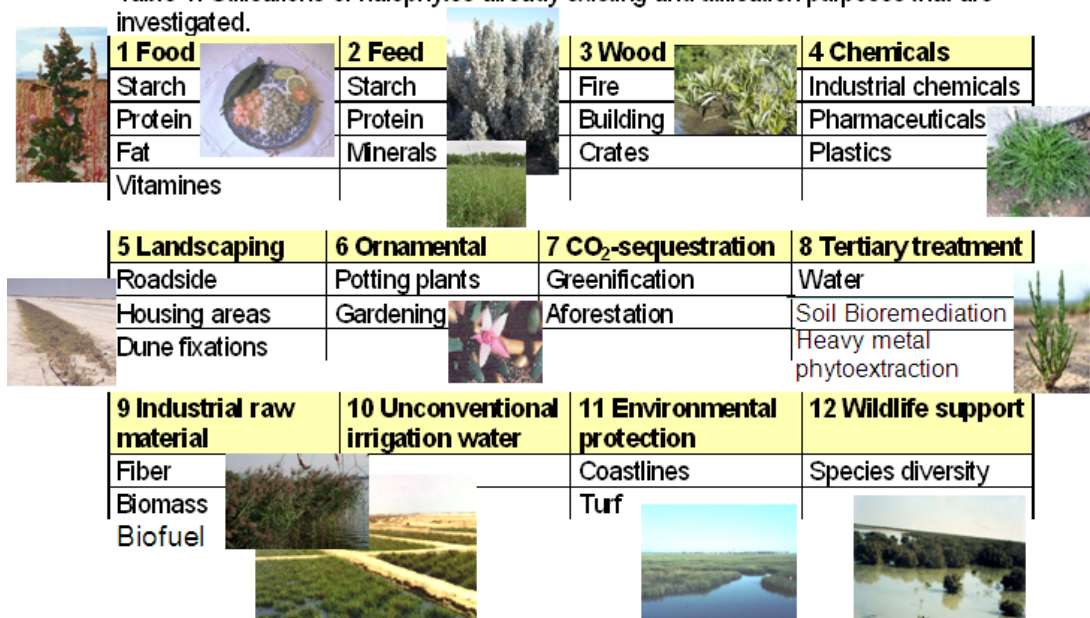


Figure 1. Already existing halophyte utilisations and utilisation purposes that are under investigation.

In several countries, specific plant species are used for waste water treatment. It has been observed that plants differ in their capacity to remove or precipitate contaminations. Moreover, some coastal plants (see below halophytes or xerohalophytes) found to survive under seawater irrigation have been used as crops in the past or have been subjected to breeding concepts to improve yield (Figure 1). Some halophytes can be used for bio-remediation of salt-contaminated soils and even pharmaceutical values of their products are described. It has been demonstrated that silage from such plants can be successfully used as fodder for ruminants.

Classification of halophytes

A halophyte is a plant that naturally grows and completes their life cycle where it is affected by salinity in the root area or by salt spray, such as in saline semi-deserts, mangrove swamps, marshes and sloughs, and seashores. Adaptation to saline environments by halophytes may take the form of salt tolerance (see halotolerance) or salt avoidance. Plants that avoid the effects of high salt (e.g. completes its reproductive life cycle during rainy season) even though they live in a saline

environment may be referred to as facultative halophytes rather than obligate halophytes.

Obligate halophytes (xerohalophytes are the desert species of halophytes) are plants that thrive when given water having greater than 0.5% NaCl (Koyro and Lieth, 1998). Halophytes are often classified as secretor/secretor versus succulents or as excluders versus includers. A small number of plant lineages in numerous, related families have evolved structural, phenological, physiological, and biochemical mechanisms for salt resistance.

General strategies of salt resistance

Salt resistance is the reaction of an organism to salt stress. Resistance can involve either salt tolerance or salt avoidance. Salt tolerance involves physiological and biochemical adaptations for maintaining protoplasmic viability as cells accumulate electrolytes. Salt avoidance involves structural with physiological adaptations to minimize salt concentrations of the cells or physiological exclusion by root membranes. In principle, salt tolerance can be achieved by salt exclusion or salt inclusion (Figure 2).

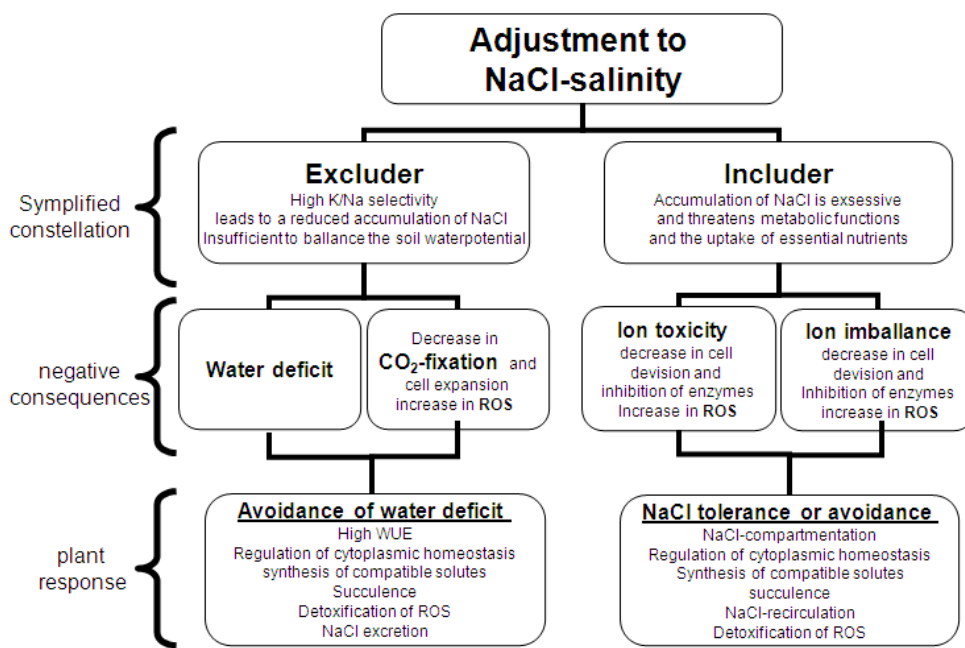


Figure 2. Flow chart showing the possible mechanisms of vascular halophytes to adjust at high external NaCl salinity [Modified after Marschner, 1995].

Physiological and biochemical investigations have shown that salt resistance in halophytes depends on a range of adaptations embracing many aspects of a plants physiology, including; ion compartmentalisation, osmolyte production, germination responses, osmotic adaptation, succulence, selective transport and uptake of ions, enzyme responses, salt excretion and genetic control.

Several physiological mechanisms are described in literature which avoid salt injury (and to protect the symplast) are known as major plant responses to high NaCl-salinity (Marschner, 1995; Mengel and Kirkby, 2001; Munns, 2002; Koyro, 2004):

1) Adjustment of the water potential, decrease of the osmotic and matric potential and enhanced synthesis of organic solutes. Most halophilic and all halotolerant organisms spend energy to exclude salt from their cytoplasm to avoid protein aggregation ('salting out'). To survive the high salinities, halophiles employ two differing strategies to prevent desiccation through osmotic movement of water out of their cytoplasm. Both strategies work by increasing the internal osmolarity of the cell. In the first specific low molecular weight organic compounds are accumulated in the cytoplasm – these are known as compatible solutes. These can be synthesised again or accumulated from the environment. The most common compatible solutes are neutral or zwitterionic and include amino acids, sugars, polyols, betaines and ectoines, as well as derivatives of some of these compounds.

2) Regulation of the gas exchange (H_2O and CO_2), high water use efficiency (H_2O - loss per net CO_2 -uptake) or/and switch to CAM-type of photosynthesis,

3) Ion-selectivity to maintain homeostasis especially in the cytoplasm of vital organs e.g. by selective uptake or exclusion (e.g. salt glands), by selective ion-transport in the shoot, in storage organs, to the growing parts and to the flowering parts of the plants, retranslocation in the phloem or by compartmentation of Na and Cl in the vacuole

4) High storage capacity for NaCl in the entirety of all vacuoles of a plant organ,

generally in old and drying parts (e.g. in leaves supposed to be dropped later) or in special structures such as hairs. The dilution of a high NaCl content can be reached in parallel by an increase in tissue water content (and a decrease of the surface area, succulence).

Morphological adjustment to salinity

In many cases various mechanisms and special morphological structures are advantageous for halophytes since they help to reduce the salt concentrations especially in photosynthetic or storage tissue and seeds. These morphological adjustments include salt excreting system and increasing succulence in halophytes.

Excreting halophytes have glandular cells capable of secreting excess salts from plant organs (Marschner, 1995). Excreting salt glands distributed in numerous unrelated plant groups and some grasses. A simple system with two-celled trichomes have evolved as collecting chambers for salts in the cordgrasses (*Spartina alterniflora*, *S. patens*), alkali grass (*Puccinellia phryganodes*), saltgrass (*Distichlis spicata*), and shoregrass (*Monanthochloe littoralis*). Also a complex type of salt glands is known in *Frankenia* (*Frankeniaceae*), *Tamarix*, (*saltcedar*, *Tamaricaceae*) and in several common mangroves. *Atriplex* (saltbush) has on the surfaces of the leaf vesiculated trichomes (hairs). The leaves sequester excess electrolytes in the bladder cells, which release the salt back into the environment when they are ruptured. Additionally leaves of *Atriplex* have a silvery reflectance, due to the presence of this layer of trichomes, which has also been shown to prevent some ultraviolet light from reaching the leaf tissues and therefore minimizing the development of reactive oxygen species (ROS).

Succulence is demonstrated in many genera of halophytes that inhabit saline environments. Succulents use higher water content within large vacuoles to minimize salt toxicity. By depositing ions of salts in vacuoles, the toxicity is partitioned from the cytoplasm and organelles of the cells. Salts are removed from the plant when the leaf or stem segment is shed. Common examples of succulence are found in *Allenrolfea*,

Arthrocnemum, *Batis*, *Chenopodium Halimione*, *Nitrophila*, *Salicornia*, *Suaeda* and *Zygophyllum*.

Basis for the screening of cash crop halophytes

Many halophytic species can tolerate high sea water salinity without possessing special morphological structures. To achieve salt tolerance three interconnected aspects of plant activity are important for plants with or without saltglands. Damage must be prevented, homeostatic conditions must be re-established and growth must resume. Growth and survival of vascular plants at high salinity depends on adaptation to both low water potentials and high sodium concentrations, with high salinity in the external solution of plant cells producing a variety of negative consequences. It is the exception that a single parameter is of major importance for the ability to survive at high NaCl-salinity. A comprehensive study in a Quick check system (QCS) with the analysis of at least a combination of several parameters is a necessity to get a survey about mechanisms constitution leading at the end to the salinity tolerance of individual species (Koyro, 2003). These mechanisms are connected to the major constraints of plant growth on saline substrates water deficit, restriction of CO₂ uptake, ion toxicity and nutrient imbalance.

Salt exclusion minimizes ion toxicity but accelerates water deficit and deminishes indirectly the CO₂-uptake. Salt absorption (inclusion) facilitates osmotic adjustment but can lead to toxicity and nutritional imbalance (Figure 2).

The presence of soluble salts can affect growth in several ways (Mengel and Kirkby, 2001). In the first place plants may suffer from water stress, secondly high concentrations of specific ions can be toxic and induce physiological disorders and thirdly intracellular imbalances can be caused by high salt concentration.

Screening Procedure of halophytes

The quick check system is merely the first step to develop sustainable irrigation systems with saline waters.

At least 4 steps are needed essentially for future testing the potentials of halophytes: A Quick check system in climate chambers to study the salt tolerance of a plant under ideal conditions, green house experiments using local substrates to select and propagate promising sites, lysimeter studies on field sites to study additionally the water consumption and ion movement and plantation in coastal areas or at inland sites to test economic feasibility.

This paper will discuss mainly the first step of the screening procedure. The Quick check system enables a detailed record of general tolerance criterion at reproducible conditions and is the first step on the way to the sustainable use of halophytes (Figure 3). Major goal of the QCS is the comparative research about the physiology of salt tolerance in many species to provide detailed scientific information about the limits of resistance and to uncover the individual mechanisms. The limit of salinity-tolerance is defined physiologically as the NaCl-salinity at which the yield of a crop under saline conditions relative to its yield under non-saline conditions reaches less than 50% (Kinzel, 1982).

The limit of salt resistance can easily be detected at growth and development stages of halophytes under different salinities (Figure 4).

Halophytes are plants growing on or surviving in saline conditions, such as marine estuaries and salt marshes. They respond to salt stress at three different levels; cellular, tissue and the whole plant level (Epstein, 1980). Therefore, in order to successfully understand salt tolerance in plants, the mechanisms at each level must be studied separately. To uncover the individual mechanisms for salt resistance and the adjustment it is essential to evaluate the major constraints of plant growth on saline substrates (s.a. Figure 2). The reactions of species to these constraints give an overall survey about the individual salt resistance mechanisms as shown in the next chapters.

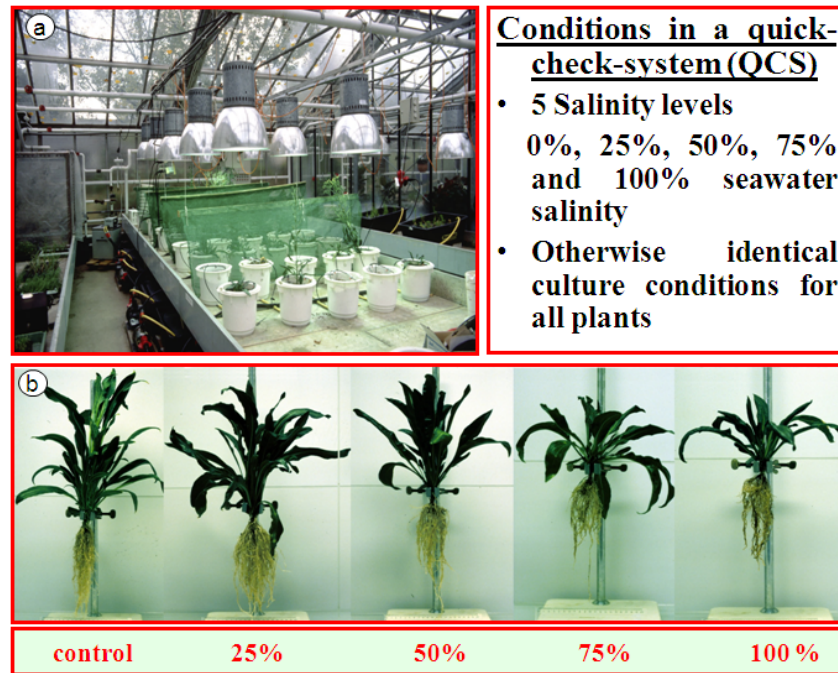


Figure 3. A quick-check-system (QCS) of *Aster tripolium* under photoperiodic conditions in a growth cabinet.

a) Gravel/hydroponic quick check system with automatic drip irrigation. b) Habitus of *Aster tripolium* plants grown in different salinity levels. Control plants (ctr) are visible on the left side, plants of the sea water salinity treatment (500 mol*m⁻³ NaCl) on the right side.

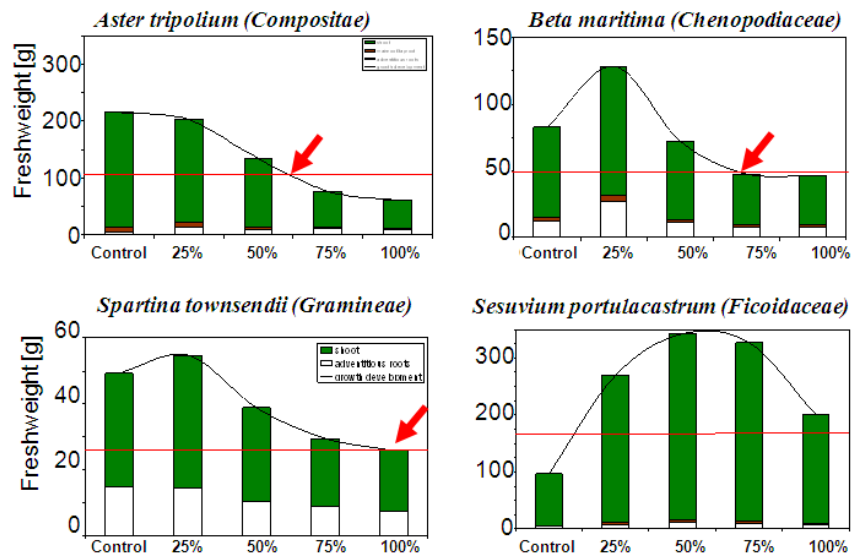


Figure 4. Development of the plant freshweight at treatments with different percentages of sea water salinity.

The crossover of the red and the black lines reflects the NaCl-salinity where the growth depression falls down to 50 % of the control plant (threshold of NaCl-salinity according to Kinzel, 1982). a), *Aster tripolium* 60 % sea water salinity; b) *Beta vulgaris* ssp. *maritima* 75 % sea water salinity; c) *Spartina townsendii*: 100 % sea water salinity; d) *Sesuvium portulacastrum* 150 % sea water salinity 0% sea water salinity = control, 25% = 125NaCl, 50% = 250NaCl, 75% = 375NaCl and 100% = 500NaCl.

Water loss versus CO₂-uptake

Terrestrial plants at saline habitats are often surrounded by low water potentials in the soil solution and atmosphere. It is under these circumstances important to avoid a water loss (e.g. by transpiration) higher than the influx rate. This is only possible if the water potential is lower in the plant in comparison to the soil. Recognition of the importance of time frame led to the concept of a two-phase growth response to salinity (Mengel and Kirkby, 2001; Munns, 1993, 2002). The first phase of growth reduction is essentially a water stress or osmotic phase.

Data of the leaf water potentials demonstrate clearly that leaf water potential of halophytes does not correlate alone as a single factor with salinity tolerance. *Aster tripolium* (Figure 5a), *Beta vulgaris* ssp. *maritima* (Figure 5b), *Spartina townsendii* (Figure 5c), and *Sesuvium portulacastrum* (Figure 5d), have a sufficient adjustment mechanism even at high salinity treatment. The osmotic potentials were sufficiently low for all four halophytes (and many others) at all salinity levels to explain the full turgescence of the leaves (results not shown).

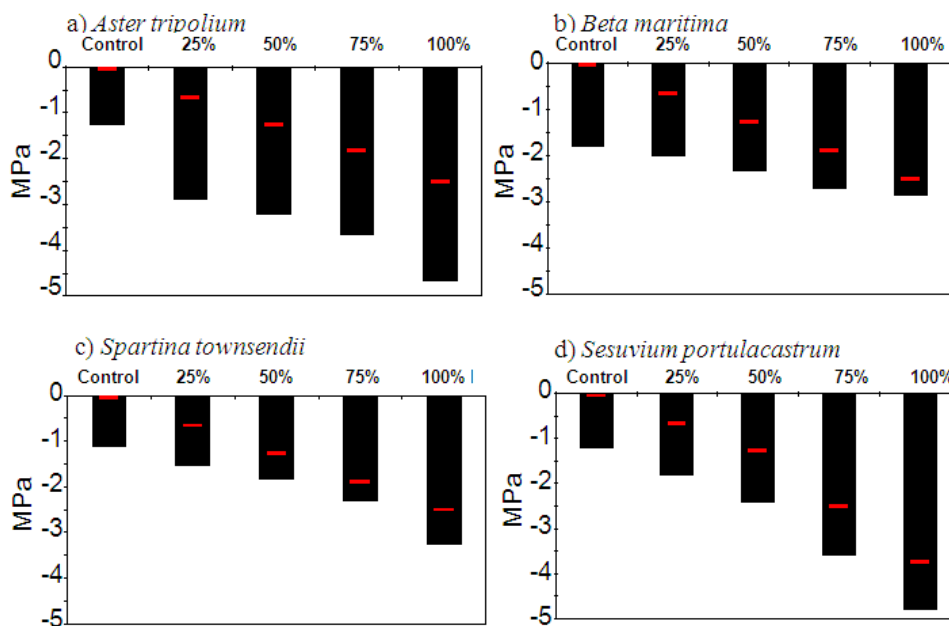


Figure 5. Leaf water potentials (MPa) of (a) *Aster tripolium*, (b) *Beta vulgaris* ssp. *maritima*, (c) *Spartina townsendii* and (d) *Sesuvium portulacastrum*.

The red lines in the bars mark the water potentials in the nutrient solutions. Leaf water potentials were always lower than in the assigned nutrient solution potential. The difference between water potentials in the leaves and in the nutrient solutions decreased with increasing NaCl-salinity. 0% sea water salinity = control, 100% sea water salinity = sea water salinity.

Plant water loss has to be minimized at low soil water potentials, since biomass production depends mainly on the ability to keep a high net photosynthesis by low water loss rates. In this field of tension, biomass production of a plant depends on the energy consumption and the accumulation of carbon (CO₂ net photosynthesis). A critical point for

the plant is reached if the CO₂-fixation falls below the CO₂-production (compensation point). Therefore, one crucial aspect of the screening procedure is the study of growth reduction and net photosynthesis especially at the threshold of salinity tolerance (Figure 6).

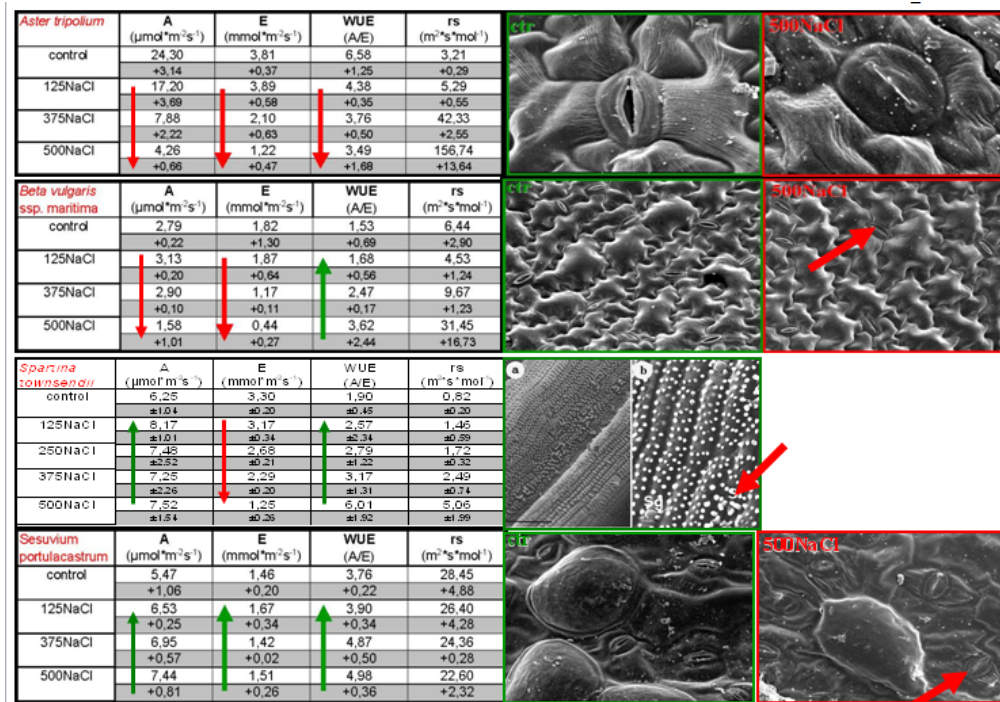


Figure 6. Influence of NaCl-salinity on the apparent photosynthesis (A), the adaxial transpiration (E), the wateruse efficiency (WUE) and the stomatal conductance (rs) of *Aster tripolium*, *Beta vulgaris* ssp. *maritima*, *Spartina townsendii* and *Sesuvium portulacastrum*.

The ultrastructures (SEM-micrograph) of the leaf surfaces (left side controls, right side seawater salinity treatments) are presented next to the responding table.

Many plants such as *Aster tripolium*, *Beta vulgaris* ssp. *maritima* or *Spartina townsendii* reveal at their threshold salinity tolerance a combination of low (but positive) net photosynthesis, minimum transpiration, high stomatal resistance and minimum internal CO₂-concentration (Koyro and Huchzermeyer, 2004). However there is a big range among halophytes. Especially succulent halophytes such as *Sesuvium portulacastrum* or *Avicennia marina* have alternatives if the water balance is still positive (water uptake minus water loss) and not limiting factor for photosynthesis. In case of *Sesuvium* net photosynthesis and WUE increase but stomatal resistance decreases. These results show that it is quite important to discuss the regulation of gas-exchange at high salinity in relation with other parameters (such as water relations). Water deficit is one major constraint at high salinity and can lead to a restriction of CO₂-uptake. The balance between water loss and CO₂-uptake is another basis for assessment of their potential of utilization.

Ion toxicity versus ion imbalance

There is a second phase of growth response to salinity which takes time to develop, and results from internal injury (Kirkby and Mengel, 2001; Munns, 1993, 2002). It is due to excessive salt accumulation in transpiring leaves. Ion toxicity and nutrient imbalance are two major constraints of growth at saline habitats and therefore of special importance for the salt tolerance of halophytes. Data from other scientific studies have shown that halophytes exhibit different ways of adjustment to high NaCl-salinity. Generally, salt tolerant plants differ from salt-sensitive ones in having a low rate of Na⁺ and Cl⁻ transport to leaves (Munns, 2002). However, some halophytes (see above salt includers and Figure 2) even need an excess of salts for maximum growth and for attaining low solute potentials (Flowers et al., 1977, Greenway and Munns, 1980). Alternatively, high concentrations can be avoided by filtering out most of the salt. These halophytes so-called salt

excluders adapt to saline conditions by ion exclusion so that osmotically active solutes have to be synthesized endogenously to meet turgor pressure requirements (Mengel and Kirkby, 2001). This adaptive feature can be of importance even in species that have salt glands or bladders. However, NaCl-salinity is discussed in the literature mainly as if a common reaction of both ions (Na^+ and Cl^-) is leading to a salt injury. This is not always the case! For example in maize, Schubert and Lauchli (1986) did not find a positive correlation between salt tolerance and Na^+ exclusion. It is quite important to distinguish between both ions to uncover the individual mechanisms for salt tolerance.

Halophytes are able to distinguish precisely between the metabolic effects of both ions Cl^- and Na^+ : Some halophytes such as *Scirpus americanus*, *Avicennia marina* (with salt glands) or *Rhizophora mangle* are able to exclude Na and Cl (see literature in Kinzel, 1982) from the leaves, *Laguncularia racemosa* (with salt glands) on the other hand is a typical Na-excluder but with high Cl-accumulation in the leaves (Koyro et al., 1997), *Suaeda brevifolia*, *Suaeda vera*, *Limoneastrum monopetalum*, *Allenrolfea occidentalis*, or *Spartina townsendii* are typical Cl-excluder with high Na-accumulation in the leaves (Kinzel, 1982; Koyro and Huchzermeyer, 1999). *Salicornia rubra* *Salicornia utahensis*, *Suaeda occidentalis*, *Atriplex vesicaria*, *Atriplex nummularia*, *Atriplex papula*, *Atriplex rosea* or *Inula crithmoides* accumulate Na and Cl in the leaves in a range above the saline environment (salt-includers). Typical halophytic adaptations include in this case leaf succulence in order to dilute toxic ion concentrations (Kinzel, 1982; Mengel and Kirkby, 2001).

In Na^+ and/or Cl^- excluding species (a-c), however, a lack of solutes may result in adverse effects on water balance, so that water deficiency rather than salt toxicity may be the

growth limiting factor (Greenway and Munns, 1980; Mengel and Kirkby, 2001). To achieve a low water potential and/or a charge balance the solute potential in these species is decreased by the synthesis of organic solutes (Figure 7a and b) such as sugar alcohol (e.g. mannitol in leaves of *Laguncularia racemosa*; see also Figure 7a), soluble carbohydrates (e.g. sucrose in tap roots of *Beta vulgaris* ssp. *maritima*; see also Figure 7b), organic acids (including amino acids) or by reducing the matric potential (e.g. with soluble proteins in leaves of *Beta vulgaris* ssp. *maritima*; results not shown). However, the synthesis of organic solutes is energy demanding and the formation of these solutes decreases the energy status of the plant. Thus for plant survival, growth depression is a necessary compromise in Na^+ and /or Cl^- excluding species and not a sign of toxicity or nutrient imbalance.

Compartmentation and selectivity

In order for a species to succeed in the saline environment the destruction of the metabolism by Na^+ or Cl^- has to be avoided. Therefore, the protection of the responsible enzymes is of major importance. The ability of plant cells to maintain low cytosolic sodium concentrations is an essential process for halophytes (Borsani et al., 2003). Leaves being fed by the transpiration stream, receive large quantities of sodium, which must be regulated. Plant cells respond to salt stress by increasing sodium efflux at the plasma cell membrane and sodium accumulation in the vacuole. For such a reason, the proteins, and ultimately genes, involved in these processes can be considered as salt tolerance determinants. The cloning of Na^+/H^+ antiporters have demonstrated the role of intracellular sodium (Ohta, 2002) compartmentalisation in plant salt resistance. Such compartmentalisation of sodium and chloride in leaf vacuoles can only be attained with an active transport into the vacuole and low tonoplast permeability to these ions.

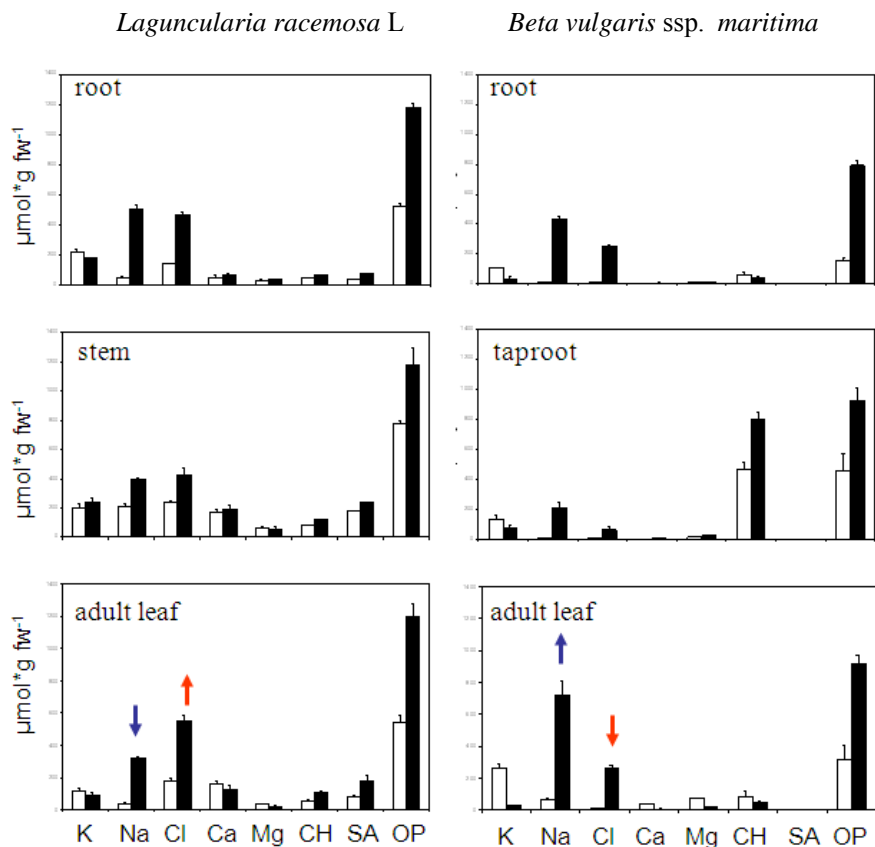


Figure 7. Composition (K, Na, Cl, Ca, Mg, CH and SA) of the solute potential (OP) in different plant tissues of *Laguncularia racemosa* and *Beta vulgaris ssp. maritima*.

Sucrose accumulation is important for osmotic adjustment in taproots of *Beta vulgaris ssp. maritima* and mannitol in leaves of *Laguncularia racemosa*. CH: soluble carbohydrates; SA: sugaralcohol.

The transport of ions across the plasma membrane and tonoplast requires energy, which is provided by vacuolar and plasma membrane ATPase (Koyro and Huchzermeyer, 1997; Leigh, 1997). Sodium ions exchanged for hydrogen ions across a membrane membrane Na^+/H^+ antiporters take advantage of a proton gradient formed by these pumps. Salt stress was shown to increase Na^+/H^+ activity in glycophytes and halophytes (Apse and Blumwald, 2002). The activation of such antiporters is likely to be operating to reduce sodium toxicity in salt tolerant plants under saline conditions.

Learning from halophytes to improve the salt resistance of glycophytic crops

Beside their potential to become cash crops, halophytes can be used in future also as

model plants for the breeding of salt resistant out of glycophytic crops. On basis of the detected salt resistance mechanisms (as shown above) strategies to improve salt tolerance can be developed. A common molecular approach used to define salt tolerance mechanisms in plants is to identify cellular processes and genes whose activity or expression is affected by salt stress (Hasegawa et al., 2002a, b), which has led to a better understanding of the complexity of salt tolerance in higher plants. Three mechanisms of halophytes are in front of the actual research. 1). Sodium extrusion and SOS pathway enabling ion homeostasis in the cytoplasm; 2) Vacuolar compartmentalization and 3) Sodium uptake and recirculation

To 1) Since Na toxicity is the principal stress component in saline soils, much research has focused on the identification of ion

transporters and regulatory mechanisms that mediate Na^+ homeostasis and maintenance of a high cytoplasmic K^+/Na^+ ratio. It was shown that a salt-sensitive rice cultivar that expresses the vacuolar-type Na^+/H^+ antiporter gene from the halophytic plant *Atriplex gmelini* (AgNHX1 = vacuolar Na^+/H^+ antiporter) was much more salt resistant as the wild type rice (Ohta, 2002), indicating that over expression of the Na^+/H^+ antiporter significantly enhances transgenic rice salt tolerance. Extending such research could improve crop plant salt tolerance in the near future if successful genetic transfer can occur on a large scale. The Salt Overly Sensitive (SOS) signaling pathway, composed of the SOS1, 2 and 3 proteins, has emerged as a key factor in the detection of and tolerance to salt stress. Evidence suggests that a protein kinase complex of SOS3 and SOS2 is activated by a salt stress elicited calcium signal (Zhu, 2003). This protein kinase complex phosphorylates and activates various ion transporters, such as the plasma membrane Na^+/H^+ antiporter SOS1 responsible for excreting Na^+ into the apoplast.

To 2) The tonoplast Na^+ transport may also be regulated through SOS3-like calcium binding proteins. Vacuolar compartmentalization of Na^+ ions is beside the excretion across the plasmalemma (s.a. SOS1) an efficient mechanism to maintain a lower concentration of Na^+ in the cytosol. Transport of Na^+ into the vacuole is mediated by a Na^+/H^+ antiporter. The proton-motive force for this transport is provided by both an ATPase and a H^+ -pyrophosphatase. Overexpression of a vacuolar H^+ -pyrophosphatase (AVP1) and of the tonoplast Na^+/H^+ antiporter, AtNHX1 enhanced sequestration of Na^+ into vacuoles and led to increased salt tolerance (Gaxiola et al., 2001).

To 3) It has also been defined a gene locus that corresponds to the HKT1 gene, which is a sodium influx transporter. The HKT1 expression is restricted to the phloem tissue in all organs strongly reducing sodium concentration in the phloem sap. HKT1 is probably involved in the recirculation of sodium from the shoots to the roots by

mediating sodium loading into the phloem sap in shoots and unloading in the roots. The high-affinity carrier HKT1, a Na^+/K^+ symporter, is also required for continued K^+ uptake during salt stress (Uozumi et al., 2000). High external Na^+ concentrations inhibited HKT1-mediated K^+ influx (Rubio et al., 1995) and transgenic wheat with reduced HKT1 expression exhibited significantly less Na^+ uptake and enhanced tolerance to salinity (Laurie et al., 2002). This suggests that HKT1 is an important determinant of salt tolerance (Katiyar-Agarwal, 2005). However, attempts to improve the salt tolerance of crops through conventional breeding programmes have met with very limited success, due to the complexity of the trait: salt tolerance is complex as well genetically as physiologically. The quick check systems of salt resistance mechanisms together with these molecular studies have the potential to uncover approaches to improve the performance of crop plants under saline conditions.

Conclusion

Tolerance to salinity quite varied among plants and conventional crops generally do not survive 30% seawater salinity. Halophyte, however, could survive above seawater salinity through compartmentalization, water use efficiency and ion selectivity which is clearly superior than conventional crops (Waisel, 1972). Still all the mechanisms responsible are not clearly understood. Genes which are up or down-regulated due to introduction salinity may be identified either through the analysis of RNA (Kawasaki et al., 2001) or proteins (Salekdeh et al., 2002) and finding a key gene for salinity tolerance is still farfetched. Therefore engineering a salt tolerance plant may take much longer than anticipated. Irrigation farming which is wide spread in arid and semi-arid regions of the world has resulted in increasing soil salinity of prime agricultural lands rendering them not suitable for conventional agriculture. There is no time to wait for salt tolerant conventional crops but rather sustainable use of cash crop halophytes to utilize salinized lands and also utilize huge resources of brackish or seawater. This may

help us to successfully negotiate water and food crises simultaneously.

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