Importance of the Diversity within the Halophytes to Agriculture and Land Management in Arid and Semiarid Countries

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Abstract

Freshwater resources will become limited in near future and it is necessary to develop sustainable biological production systems, which can tolerate hyper-osmotic and hyper-ionic salinity. Plants growing in saline conditions primarily have to cope with osmotic stress followed by specific ion effects, their toxicities, ion disequilibrium and related ramifications such as oxidative burst. This is an exclusion criterion for the majority of our common crops. In order to survive under such conditions, suitable adjustments are necessary. Beside the control of the entrance on root level, the ability to secrete ions (excreter) or to dilute ions (succulents) helps to preserve a vital ion balance inside the tissues.

Sadly, traditional approaches of breeding crop plants with improved abiotic stress resistance have met limited success so far. Failures were due to two problem areas, lack of easy to detect traits and too many genes that had to be transferred at a time. These arguments underline the advantage of utilizing suited halophytes as crops on saline lands and to improve their individual crop potential. Because of their diversity, halophytes have been regarded as a rich source of potential germplasm. A variety of halophytic plant species already has been utilized as nonconventional cash-crops. Lieth H, Mochtchenko M (Cash crop halophytes: recent studies. Tasks for vegetation science, vol 38. Kluwer, Dordrecht, 2003) described the

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utilization of halophytic species for the improvement of sustainable agriculture as well as sources of income.

However, knowing that saline irrigation always comprises the risk of increasing salinity up to levels where no plants (even no halophytes) can exist anymore, it is important to achieve sustainable conditions. Therefore it is essential to study the interaction among soil salinity, individual species (to study heterogeneity within the halophytes and plant diversity), biotic interactions, and atmosphere at distinct conditions before application.

The heterogeneity within halophytes (biotic factor) is often ignored but biotic interactions can be in this context an ideal accessory to stabilize sustainable populations on saline lands. The aspect, that dicotyledonous halophytes, when grown in saline soils, generally accumulate more NaCl in shoot tissues than monocotyledonous halophytes (especially grasses) has several consequences on their suitability as crops and their culture conditions (procedure to apply salinity). The implementation of an intercropping system (halophyte culture) is such a way to use saline land and brackish water for producing an economically viable and environmentally sound agriculture. It was estimated that 15 % of undeveloped land in the world's coastal and inland salt deserts could be suitable for growing crops using saltwater agriculture. This amounts to 130 million hectares of new cropland that could be brought into human or animal food production chain - without cutting down forests or consuming more scarce freshwater for irrigation.

1 Introduction

There is overwhelming evidence that the ancestors of modern land plants evolved in aquatic environments, most probably in saline oceans where they existed and diversified over millions of years [1, 2]. However the plants growing on land have a distinct advantage over their counterparts in water in that about two-thirds of total annual photosynthetic CO_2 uptake takes place on land, and one-third in the rivers and oceans while land plants contain nearly 200 times as much carbon as aquatic plants [3]. Hence, low availability of carbon dioxide coupled with its high diffusion resistance in water may have forced these plants to move onto land and adjust their according to the prevailing conditions. Analysis of fossils suggests that by the Early Devonian, about 400 million years ago, plants were drought and probably salt resistant [4]. However, most of the plants lost the ability to resist high salt concentrations of the soil and cannot be grown on a salt affected land any more [5]. Such plants are known as non-salt resisting plants, non-halophytes or glycophytes. Only 2 % of the plants have still the ability to grow under salinity due to the presence of different mechanisms in them for salt resistance; such plants are known as salt resisting plants, salt tolerating plants or halophytes [6]. However all plants experiencing salinity stress face three major constraints: (a) water deficit arising from the low water potential, (b) ion toxicity on the basis of excessive uptake of Na^+ or Cl^- leading also to oxidative stress and (c) nutrient imbalance by depression in uptake of essential nutrients [7].

Freshwater resources will become limited in near future [8] and it is necessary to develop sustainable biological production systems, which can tolerate hyperosmotic salinity. A precondition is the identification and/or development of salinity-resistant crops. The arguments listed above demonstrate the advantage of utilizing suited halophytes as crops on saline lands and to improve their individual crop potential. However, knowing that saline irrigation always contains the risk of increasing salinity up to levels where no plants (even no halophytes) can exist anymore, it is important to achieve sustainable conditions. Therefore it is essential to study the interaction between soil salinity, individual species (to study heterogeneity in between halophytes and plant diversity), biotic interactions, and atmosphere at distinct conditions before application. The heterogeneity between halophytes (biotic factor) is often ignored but biotic interactions can be in this context an ideal accessory to stabilize sustainable populations on saline lands. It is necessary to understand the mechanism operating at each level in full detail so as to develop a complete understanding of salt resistance in plants and utilizing this knowledge to preserve crops from destruction.

2 Glycophytic Land Plants and Hyperosmotic Salinity

2.1 Primary Stress Factors

Plants growing in saline conditions primarily have to cope with osmotic stress followed by specific ion effects, their toxicities and related ramifications. In order to survive under such conditions, suitable adjustments are necessary (Fig. 1). The most terrestrial plants growing in saline soils must adjust osmotically to water potentials in the range of −3 MPa. They do this by accumulating a mixture of ions and organic solutes [9]. Plant adaptations to salinity are of three distinct types: osmotic stress tolerance, Na^+ or Cl^- exclusion, and the tolerance of tissue to accumulated Na^+ or Cl^- [10]. Even if terrestrial plants are able to exclude ions from a strong saline solution they must also adjust their water potential to be at least as low as that of the soil in which they are growing. On the other hand, the growth on well (fresh-) watered soils may have even facilitated the evolution of species with relatively low ion contents because of a reduced necessity for the uptake of ions (such as for osmotic reasons) and may have led to the loss or reduction of (a) exclusion or discrimination in favor of K^+ over Na^+ (or NO_3^- over Cl^-), (b) the ability to excrete or compartmentalize toxic ions such as Na^+ or Cl^- in vacuoles and (c) to a reduced regulation of the water balance in the plants.

As a consequence, the interaction of all three factors (see above a to c) can be harmful at saline habitats because the large difference in water potential is not only the driving force for the

Fig. 1 (**a**) Plant with drought symptoms on a dry habitat. (**b**) Plant with salt on its leaves and crusts around the base and on the soil

movement of water through the soil–plant–atmosphere continuum but also for any dissolved solutes that enter the transpiration stream is carried to the leaves where they accumulate in case they cannot be re-circulated or excreted. The exclusion of ions is under these circumstances one possible plant response to avoid ion toxicity but requires for the avoidance of internal water deficit the enhanced synthesis of organic solutes and a decrease in surface area to reduce transpiration [7]. Adverse effects include reduced growth and an upcoming water deficit leading to the closure of stomata and in consequence a decrease in cell expansion, CO_2 fixation and protein synthesis. In other words, the exclusion of ions leads at saline habitats to substantial overlaps with the effects of drought [10].

2.2 The Influence of Drought on Photosynthesis

In any case, 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 moisture tension, biomass production of a plant has always to be seen in concurrence with the CO_2/H_2O-gas exchange, which can be estimated by the water use efficiency (WUE) of photosynthesis.

$$\mathrm{WUE}\left[\mu\mathrm{mol\,mmol}^{-1}\right] = \mathrm{J}_{\mathrm{CO2}}\left[\mu\mathrm{mol\,m}^{-2}\mathrm{s}^{-1}\right] / \mathrm{E}_{\mathrm{H_2O}}\left[\mathbf{mmol\,m^{-2}s^{-1}}\right]$$

WUE = water use efficiency of photosynthesis
J_{CO2} = net assimilation of CO_2
E_{H2O} = evaporation of H_2O

A critical point for the plant is reached if the CO_2 fixation (apparent photosynthesis) falls below the CO_2 production (compensation point, Fig. 2). Therefore, one crucial aspect of the screening procedure (for drought or salinity resistance) is the study of growth reduction, water consumption, and net photosynthesis especially at the threshold of resistance [9].

Substrate salinization as well as drought decrease water availability and water uptake and thus lead to a reduction of turgor of the leaf cells,

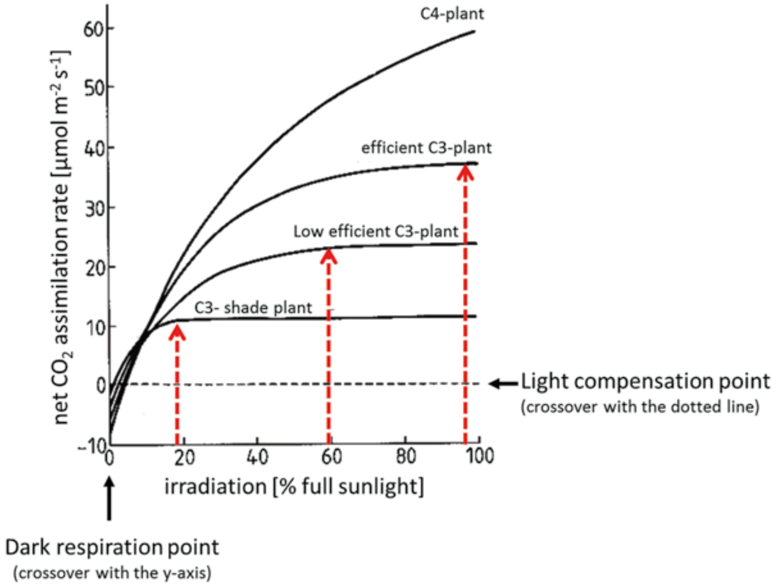

Fig. 2 Idealized light saturation curves of C3 and C4 plants. The light compensation point (crossover with the *dotted black line*), the photosynthetic efficiency (slope at light limiting conditions) and the light saturation point (*dotted red arrows*) are higher for C4 plants higher as for C3 plants. Latter one is for C4 plants often not reached at full sunlight. Light intensities left of light saturation point are light limited and right of it are CO_2 limited

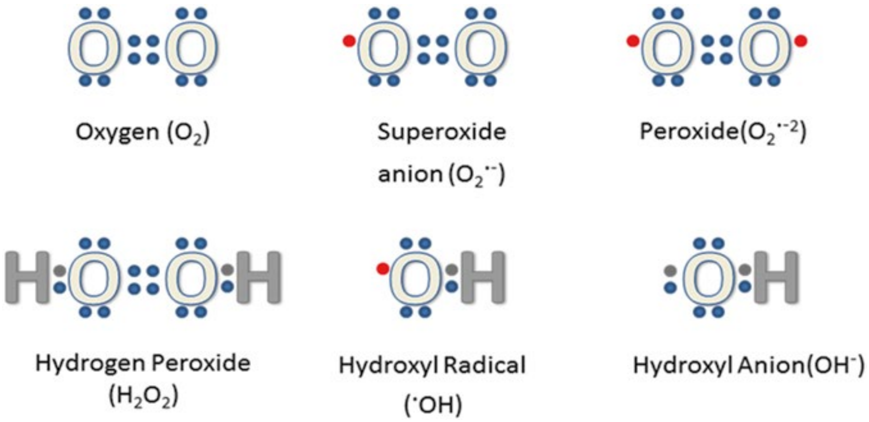

Fig. 3 List of reactive oxygen species (*ROS*) in the form of ions, free radicals, or peroxide

and finally to a reduction of water loss by stomatal closure which affects CO_2 intake. Photosynthetic CO_2 assimilation is the major consumer recycling the both coenzyme molecules (NADP+/NADPH and ADP/ATP) in the reaction sequence of the Calvin cycle. Otherwise, turnover of energy by the electron transport would be inhibited, which would impair electron release from activated chlorophyll and cause the so called secondary stresses [11]. Accordingly, in the literature the occurrence of various forms of ROS is described ([12, 13] Fig. 3). Cytotoxicity may be attributed to oxidative damage of membrane lipids [14, 15] as well as oxidation of proteins and nucleic acids [14, 16]. In the field, salt stress results in severe damage especially in situations when its inhibitory effects occur in presence of high light intensity. In such cases the PSII activity will result in high oxygen concentrations, especially if stomata are closed under stress. Concomitantly, chlorophyll will remain in its active state for a prolonged period of time, as electron transport rate is reduced by inhibited off flow of products. However, any reduction of electron transport rate, especially under high light conditions, will increase the risk of ROS production through transfer of electrons from activated chlorophyll to molecular oxygen to form O_2 radicals and the less reactive ROS H_2O_2 [16]. Concentration of these reactive compounds will build up in the light and eventually will reach concentrations toxic for cells active in photosynthesis. Even if this scenario describes only the action of a secondary stress it can lead to the dieback of plants and a defense will be essential for survival.

2.3 Nondestructive Buffer Capacity of the Plant Against Oxidative Stress

Under conditions that limit assimilation of CO_2, the potential rate of NADPH production exceeds the actual rate of consumption of reductive power. In order to be able to grow under stressful conditions, plants have to be equipped with mechanisms preventing excess reducing power. They lead to a decrease in quantum yield of photosystem II [17]. The principal adaptation mechanism in photosynthesis is the control of thermal dissipation of excess energy within the photosystem II antenna, thus matching physiological needs [18].

In C_3 plants, losses by non-photochemical energy quenching may exceed that caused by photorespiration. For experimental approaches investigating salinity effects, it is important to know that non-photochemical quenching of excitation energy is comprised of a fast and a slow component, qE and qI, respectively. Both reactions are reversible. qI is the quenching parameter puddle model that represents photo-inhibition,

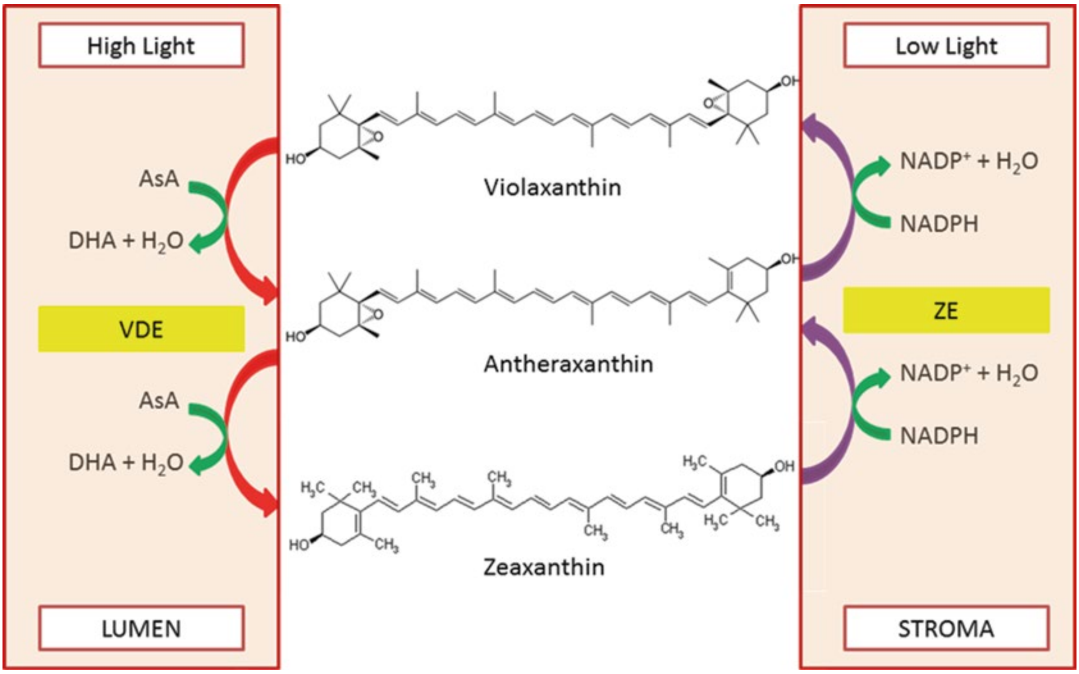

Fig. 4 The xanthophylls cycle. Violaxanthin de epoxidase (*VDE*) catalyses the de-epoxidation of violaxanthin to zeaxanthin in the presence of excess light, and Zeaxanthin epoxidase (*ZE*) catalyses the reverse reaction in *darkness* or *low light*. Zeaxanthin therefore accumulates under light intensities that exceed photosynthetic capacity

photo-damage or photoprotection [19]. The resulting decline in the number of active PSII units and the slow D1 repair both cause a decrease in electron transfer even when excess light is no longer there [20].

The trigger of qE is the ΔpH across the thylakoid membrane sensed by the PsbS subunit of the light-harvesting complex [21, 22] and function on the expense of NADPH. Full expression of qE is associated with the enzymatic de-epoxidation of violaxanthin to zeaxanthin (Fig. 4). This reaction is part of the xanthophylls cycle [23]. Based on current understanding, it can be expected that adverse effects of drought or salinity can be monitored by pigment shifts due to altered ratios of xanthophylls and by detection of qE and qI respectively. At high salinity or drought, several species use the masking of chlorophyll by anthocyanins, to prevent photooxidative damage. They can be identified, because leaf color will vary depending on their growth conditions like it can be observed with *Salicornia* and *Sesuvium* [11].

2.4 Enzymatic and Non-enzymatic Defense Against Oxidative Stress

Plants differ in their capacities to immediately detoxify ROS upon their occurrence and to build up a detoxification potential under stress such as salinity or drought. If the balance between production of ROS and quenching capacity of the respective tissues is upset, oxidative damage will be produced [15, 24]. In experimental approaches, it was demonstrated that enzyme activities of antioxidative pathways increase as a salt stress response [25] and that the maximal level of salt resistance correlated with maximal respective enzyme activities [26–29] suggesting the necessity and importance of a secondary stress response to the salinity reduced low water potential. Ascorbic acid is one of the major antioxidants in plants which detoxifies reactive oxygen species and maintains photosynthetic function. Through its ascorbate recycling function, dehydroascorbate reductase affects the level of foliar reactive oxygen species and photosynthetic activity during leaf development [30, 31]. In chloroplasts, H_2O_2 can be detoxified by an ascorbate-specific peroxidase [32] involved in the ascorbate–glutathione cycle, [12] while in the cytosol H_2O_2 detoxification is catalyzed in a catalase-dependent reaction. Other enzymes involved in detoxification of ROS are superoxide dismutase and several peroxidases [33].

3 Xerophytes and Halophytes

Plants that have adapted to survive in an environment that lacks average or sufficient amounts of water are called xerophytes (Fig. 5). Xerophytes may have adapted shapes and forms (morphology) or internal functions (physiology) that reduce their water loss or store water during long periods of dryness. It is easy to understand that plants excluding the uptake of ions in saline habitats also undergo physiological drought and show similar forms of adjustment as xerophytes. Nevertheless, most studies on water stress signaling have focused on salt stress primarily because plant responses to salt and drought are closely related and the mechanisms overlap. However, high levels of salt induce both hyper-osmotic and hyper-ionic stress leading to secondary stress effects like ion disequilibrium as mentioned above. This is the case for the majority of our common crops [34–36].

Fundamentally, plants cope by either escaping or resisting salt stress. Salt resistance is the reaction of an organism to salt stress. It includes both avoidance and tolerance. Exclusion meets by definition the requirements of avoidance. This means that plants are either dormant during the salt episode (escape), or (i) they avoid high salt concentrations in the plant by exclusion, (ii) they reduce the accumulation in sensitive organs or organelles, (iii) they adjust on cellular level by compartmentation and thus tolerate the saline environment [37].

Salt resistance involves physiological and biochemical adaptations for maintaining protoplasmic viability as cells accumulate electrolytes. Salt avoidance involves structural and physiological adaptations to minimize salt concentrations of the cells or physiological exclusion by root membranes. This led to the classification of halophytes as excluders *versus* includers [7]. Another classification recognizes excreters and succulents. Excreters have glandular cells capable of secreting excess salts from plant organs. Succulents use increase in water content within large vacuoles to minimize internal salt concentration and ion toxicity. By considering the diversity of halophytes and the current understanding

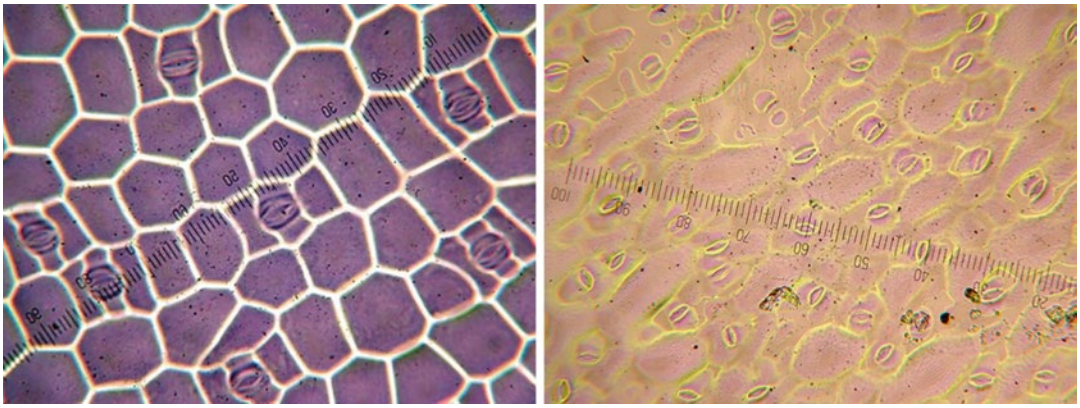

Fig. 5 Morphological adjustment. Surveys of the adaxial leaf surface of *Tradescantia zebrina* (drought sensitive) and *Sesuvium portulacastrum* (drought resistant). Tradescantia is hypostomatic and has few but large stomates. Sesuvium is amphistomatic and has many but small stomates. Latter one is ideal for short gas-exchange phases in times of high water potential in the air

of halophyte salt-resistance mechanisms we can deduce their relevance to efforts to improve crop plants and the status of halophyte agronomy.

4 Development of Specific Traits

The control of the accumulation of ions in distinct tissues or even cell compartments is needed as well in salt including as in salt excluding halophytes. Beside the control of the entrance on root level, the ability to secrete ions (excreter) or to dilute ions (succulents) helps to preserve a vital ion balance inside the tissues [38]. The resistance of plants to sodium chloride is often related to the concentration of sodium in the photosynthetically active tissue [9]. Several traits relating to salt resistance are associated with the absolute ion contents in plants, grown in the presence of salt and with the ratios in-between the monovalent cations (K^+/Na^+) or anions (NO_3^-/Cl^-) [39]. However, for plants growing on saline soils, the distribution of ions between plant tissues or cell compartments, the K^+ homeostasis in the cytoplasm, the maintenance of the $Na^+:K^+$ ratio by favoring the accumulation of potassium over sodium are also crucial for plant growth and development [40, 41].

The uptake of ions can be highly selective. A key property of all ion channels is their selective permeability; i.e., only certain species of ions may pass through a channel. Potassium channels are able to prefer K^+ transport to Na^+ transport, despite only a small difference in their ionic (i.e., Pauling) radii (0.133 nm vs.0.095 nm, respectively). In *Arabidopsis thaliana*, for example, this is accomplished by K^+-selective uptake channels and the sodium-detoxifying SOS system [42]. Genes encoding root K^+ uptake channels were identified in many plant species: AKT1 and AtKC1in Arabidopsis, SKT1 in potato, LKT1 in tomato, KDC1in carrot and ZMK1 in maize (see literature cited in [43]). However several channels, activated when the membrane potential is depolarized, are less selective and could be one means by which sodium enters cells [44–47].

Three classes of low-affinity K^+ channels, identified as K^+ inward rectifying channels (KIRC); K^+ outward rectifying channels (KORCs) and Voltage-independent cation channels (VIC) respectively K^+ outward rectifying channels (KORCs) could play a role in mediating the influx of Na^+ into plant cells. These channels, which open during the depolarization of the plasma membrane, could mediate the efflux of K^+ and the influx of Na^+ ions. Na^+ competes with K^+ uptake through Na^+–K^+ co-transporters and may also block the K^+ specific transporters of root cells under salinity [42, 48]. In particular, the regulation of the low-affinity K^+ channels is essential for plants to survive on saline habitats and therefore an important trait as well.

The cellular response to hyperosmotic salinity also includes the synthesis and accumulation of a class of osmoprotective compounds known as compatible solutes (Fig. 6). One of the essential functions of compatible substances is the substitution of ions to avoid protein precipitation and the counterbalance of the osmotic potential in the cytoplasm against the vacuole. In addition to the conventional role of these compatible solutes in cell osmotic adjustment or osmotic substitution of sodium [49], they are also suggested to act as low-molecular-weight chaperones, stabilizing the photosystem II complex, protecting the structure of enzymes and proteins, maintaining membrane integrity and scavenging ROS (see references in [50]). However, controversies exist as to whether hyper-accumulation of compatible solutes such as glycine betaine and proline is essential for improving salinity resistance, or whether it is just a symptom of salt stress in overlap with effective ROS scavenging. Their essentiality for salt resistance is therefore still not clear.

5 Utilization of Halophyte Crops for Transferring Resistant Traits in Glycophyte Crops *via* Breeding

As freshwater resources will become limited in near future [8], it is necessary to develop sustainable biological production systems, which can resist hyperosmotic salinity. A precondition is the identification and/or development of salinity

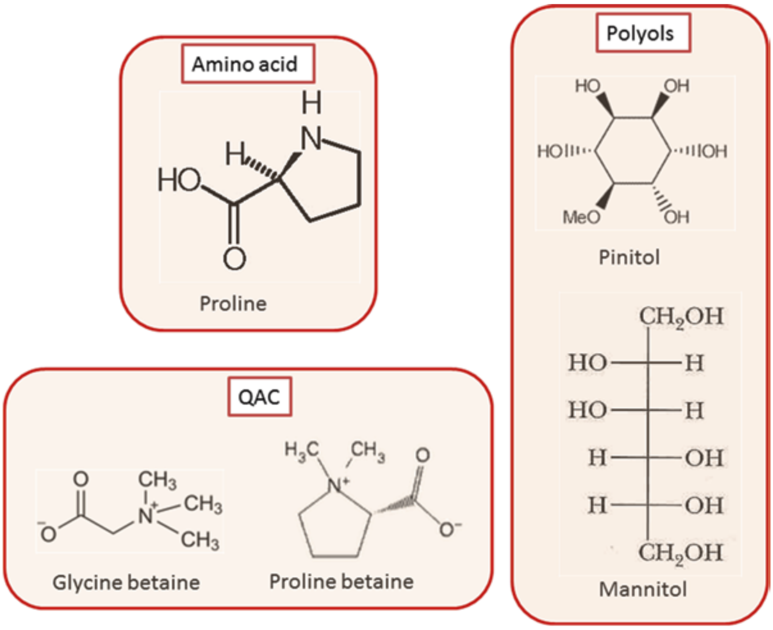

Fig. 6 Examples for compatible solutes

resistant crops. Almost all our modern crops are derived from glycophytes, plants apparently lacking the genetic basis for salt tolerance. Although the terms glycophytes and halophytes inseminate the impression that there are general qualitative differences in adaptation, in reality things are less complex. There is a fluent passage between these two groups and all plants rely on multiple adaptation mechanisms (see above) to cope with high salinity. But, the adjustment to salinity is a complex phenomenon that is characterized by ecological complexity, structural changes and physiological adjustment of gene expression, protein synthesis, stress signal transduction or regulation of catalytic activities of enzymes [48] and a number of factors, including climatic conditions and phenophases.

5.1 Breeding for Salt Resistance in Glycophytes

Knowing that a large number of halophytes are closely related to crop species, and that desired traits can only be introduced from closely related species [47] it is logical to conclude that gene transfer or genetic modification of plants can make them more salt resistant. Classical breeding for salt tolerance has been tried but with limited success. In tomato transgene have been inserted into its genome successfully, the main target was that tomato plant should be able to survive under salt stress while the taste must not be affected, however not much success in this regard has so far been achieved [51, 52]. NaCl resistance was observed in plants in which expression of a sodium transporter, HKT1, was reduced by antisense [53]. Grass has been made salt resistant by transforming it with rice vacuolar membrane Na^+/H^+ anti porter gene via the Agrobacterium-mediated transformation. The resultant plant species had a better resistance to hyperosmotic salinity [54, 55] showing at the same time a correlation between Na exclusion and Na tolerance. Recent strategy is to produce salt tolerant plants through genetic engineering and genes which are important for salt resistance are under investigation [56]. However, it has been questioned whether any cultivars bred for salt resistance have been commercially successful [57]. For a further progress a better understanding of how naturally adapted plants (halophytes) handle salts and how the mechanisms interact seems to be necessary.

5.2 The Potential of Halophyte Crops

Traditional approaches of breeding crop plants with improved abiotic stress resistance have so far met limited success because of several problems:

1. the focus has been on yield rather than on specific traits,
2. the difficulties in breeding for resistance traits due to the complexity of the multigenic trait. Selecting for salt resistance is genetically and physiologically complex because of the relatively infrequent use of simple physiological traits as measures of resistance and
3. desired traits can only be introduced from closely related species [47].

Halophytic crops have the potential to meet the requirements of all three problems:

to 1. Halophytes have been tested as vegetable (food), forage, fodder and oilseed crops in agronomic field trials and for chemical and ornamental uses. The most productive species yield 10–20 ton/ha of biomass on seawater irrigation, equivalent to conventional crops [57, 58]. Halophytes grown in an agronomic setting can be used to evaluate the overall feasibility of high-salinity agriculture, which depends on more than finding a source of tolerant germplasm. Halophytes may become a direct source of new crops.

to 2. Halophytes possess a wide range of adaptations and it is not necessary to breed for resistance traits. The mechanisms by which halophytes survive and maintain productivity on saline water can be used to define a minimal set of adaptations required in tolerant germplasm.

to 3. Halophytes show immense diversity in habitat and response to resist the abiotic stress conditions with uneven distribution across the taxa of flowering plants [59]. The largest number of halophyte species is found among the *Chenopodiaceae* (now called Amaranthaceae); over half of its 550 species are halophytic. The three families, *Poaceae* (grasses), *Fabaceae* (legumes), and *Asteraceae* (composites), also have large numbers of halophytes [57]. These four families solely contain a great number of closely related crop species as well.

Aronson listed ~1,550 species [60]; whereas a total of 2,600 species was recorded [61, 62] as salt-resistant based on their capacity to survive a salt concentration of more than 80 mM NaCl (equivalent to EC 7.8 dS m^{-1}). This knowledge can help to focus the efforts of plant breeders and molecular biologists working with conventional crop plants.

A further advantage of halophytes is that they are not a single taxonomic group, but are represented by a large diversity:

– Halophytes belong to the group of forbs, grasses, shrubs and trees,
– some can be found only in salt marshes and other grow in the desert,
– they are distributed form coastal areas to mountains and lowland deserts,
– they occupy important niches in many ecosystems often in diverse and generally harsh environments in a wide range of saline to alkaline habitats

A variety of halophytic plant species has been utilized as a source of nonconventional cash-crops [63]. Lieth et al. (2003) [64] described the utilization of halophytic species for the improvement of sustainable agriculture as well as sources of income. Using halophytes provides opportunities of introducing completely new options, e.g.:

1. The potential of plants to accumulate enormous salt quantities (salt includer, hyperaccumulating plants, [65]) could be of high significance particularly in the arid and semi-arid regions where insufficient precipitations and inappropriate irrigation systems are unable to reduce the salt burden in the soil and suitable physicochemical methods are too expensive [66].
2. In the course of evolution from marine to freshwater habitat, halophytes are found to be most successful group of plants which have shown adaptations to a variety of abiotic stresses, resistance to heavy metal stress is one of these. Several examples of halophytic

plant species used for the purpose of phytoremediation of areas polluted with heavy metals are listed [58].

3. Marsh land and mangroves have provided ecological benefits in terms of shoreline stabilization, reduction in wave and wind energy against shorelines thus protecting inland structures, supporting coastal fisheries and support wildlife. Therefore, new planting, restoration, and re-vegetation of coastal halophytes has become important for the development of sustainable agriculture and to avoid the destructive natural calamities. Research in this field has demonstrated the potential of salt-resistant plants and halophytes on barren lands and wetlands along the coastal regions [67–69].

5.3 Heterogeneity in within the Halophytes

Because of their diversity, halophytes have been regarded as a rich source of potential new crops. However, it should not be ignored that halophytes are an extremely heterogeneous group. Between monocotyledons and dicotyledons there are great differences not only in development and anatomy but also in mechanisms to tolerate hyperosmotic salinity. For example, when grown in saline soils, dicotyledonous halophytes generally accumulate more NaCl in shoot tissues than monocotyledonous halophytes (especially grasses), which led early researchers to characterize the former as “includers” and the latter as “excluders” (see literature in [57]). This feature was related to the observation that succulence is observed more commonly in dicotyledons than monocotyledons, particularly the grasses [47].

This heterogeneity should be considered much more when breeding for salt resistance in crops. For example a transfer of knowledge from the dicotyledonous plant *Brassicaceae Thellungiella salsuginea* (an extremophile model for abiotic stress resistance studies and a close relative of Arabidopsis) to the most of the monocotyledonous crops makes not much sense [70]. Instead halophytic *Poaceae* are the best sources for cereals to optimize their gene pool. Step changes in resistance may arise from the introduction of *de novo* characteristics that are apparently completely absent from a particular gene pool. Increases in resistance of hyperosmotic salinity may be introgressed into commercial lines from tolerant halophytic *Poaceae* using marker-assisted breeding approaches [71], facilitated by recent successes with positional cloning [72].

The differentiation between includer and excluder may be one major reason why the enhancement of exclusion mechanisms still appears to be the principal strategy of researchers trying to improve the salt resistance of grains (see literature in [57]). However, such generalization can also lead to neglect some promising possibilities. Studies of *Leptochloa fusca* [73], *Puccinellia peisonis* [40], *Spartina alterniflora* and S. *townsendii* [40, 74], *Sporobolus viginicus* [75], *Plantago coronopus* [36], *Triglochin bulbosa* and *T. striata* [76, 77] show that grasses and other monocotyledonous halophytes which use Na^+ uptake into leaves for osmotic adjustment, as do dicot halophytes, should not be ignored. These halophytes could be used to breed for salt accumulating grains. However, because of their lower cell vacuolar volume and leaf water content, grasses do not need as much Na^+ uptake per unit of growth as typical dicotyledonous halophytes, so they still maintain low Na^+: K^+ ratios on exposure to salt [57].

6 Importance of the Diversity of Halophytic *gramineaes* to Agriculture and Land Management

6.1 Combating Desertification and Substitution of Fresh Water Utilization

Besides the use as food or fodder crops, *gramineae* are typically used for revegetation, greenification or as turf grasses. Among these measures, revegetation of the arid lands, using plant species that are more adapted to the harsh and stressful conditions of the deserts is probably the most effective practice because of its potential use in combating

Fig. 7 Photo of a salt resistant turf grasses

desertification. 43 % of the earth's total land surface is arid or semiarid. A mainly perennial vegetation cover is the best protection against desertification [78]. In desert regions perennial vegetation coverage can maintain adequate growth and persistence under variable levels of soil salinity or salinity-laden water over several years. Successful assessment of salinity resistance of perennial, halophytic plants, therefore, should be based on growth at non saline levels. Since the growth rates of the halophytic grasses, such as *Paspalum vaginatum* (seashore paspalum), were affected only under high levels of NaCl salinity and even stimulated under lower and medium levels of salinity, it can be concluded that these halophytic plant species are suitable candidates for growth and production under arid, desert regions and dry-land conditions to effectively combat desertification processes in these regions [78].

Critical water shortages are occurring not only in deserts but also in rapidly growing urban areas, resulting in restrictions on the use of potable water for irrigating turf grass landscape areas [79]. Turf grass landscape irrigation is typically considered a low priority use for fresh water, particularly when water shortages occur [80]. Instead of using fresh water for irrigation of turf, saline water sources can fill this gap. This can include reclaimed water (sewage effluent), brackish groundwater caused either by salt leaching or seawater intrusion, and other sources [79, 81]. Proper turf management techniques are critical in counteracting salinity and long-term solutions require the development and use of salt resistant turf grass genotypes. Most of the turf grasses present high salt sensitivity (such as *Poaannua* or *Eremochloa ophiuroides*) or moderate salt-sensitivity (such as *Lolium perenne*, *Agrostis stolonifera* or *Zoysia japonica*; [79]).

Turf grass salinity resistance is a complex phenomenon, influenced by a number of environmental, edaphic, and plant factors (Fig. 7). One strategy to enhance plants and turf grasses survival and recovery from salinity is to use cultivars with superior salinity resistance [57]. Several highly salt resistant turf grasses are already in use or under development such as *Puccinellia* spp. (alkali grass, EC values between 12 and 46 dS^{-1}), *Cynodon dactylon* (Bermuda grass, dead at EC values of 36 dS m^{-1}) or *Paspalum vaginatum* (seashore paspalum, survives EC values >30 dS^{-1}; [79]). There are also so called true halophytes in use such as *Distichlis spicata* (salt grass) or *Sporobolus virginicus* (marine couch). Both survive full strength seawater salinity ($EC = 54$ dS m^{-1} or 34,560 g L^{-1}) and are offering great potential for land stabilization in highly saline areas [82]. Again diversity and heterogeneity is of importance for the sustainable use of turf grasses at high salinity. It is noticeable that many of the highly salt tolerant turf grasses are crinohalophytes (*Distichlis spicata*, *Sporobolus virginicus*, *Cynodon dactylon*). They have salt glands or bladders, which excrete excess saline ions from shoots [79] that can be eliminated by cutting the grass periodically and disposing it off away from the site.

There are several similarities between the uses of *gramineaes* for revegetation, greenification and as turf grasses if freshwater is not available (see above). If freshwater is a limiting factor it is extraordinary promising to grow the grasses listed above and to attain a win-win situation by combatting desertification and create high net productivity at the same time. The number of halophytic grasses which are suitable as forage crops under these circumstances can be extended [83] and open complete new directions for economic utilization on these wastelands and ecological purposes such as CO_2 segregation. Khan and Weber mentioned [83] that grasses like *Aeluropus lagopoides* and *Urochondra setulosa* present in the vegetation of Pakistan could survive salinity up to 2 times seawater while a number of them survived salinity approaching seawater. The potential of using *gramineaes* for revegetation, greenification and as turf grasses is however not yet fully explored.

6.2 Intercropping Halophyte Culture

Halophytes have been tested as vegetable, forage, and oilseed crops in agronomic field trials (see above). The aspect, that dicotyledonous halophytes, when grown in saline soils, generally accumulate more NaCl in shoot tissues than monocotyledonous halophytes (especially grasses) has several consequences on their suitability as crops and their culture conditions (procedure to apply salinity). This aspect can be explained best by giving an example:

Halophyte forage and seed products can replace conventional ingredients in animal feeding systems. However, there are some restrictions on their use due to high salt content and antinutritional compounds present in some species [57]. The oilseed dicotyledonous halophyte, *Salicornia bigelovii*, accumulates a significant amounts of the supplied salts and yields 2 t/ha of seed containing 28 % oil and 31 % protein, similar to soybean yield and seed quality. The accumulation of salt in the plant tissues helps to control soil salts but reduces its value as a fodder crop. The presence of high contents of ash in such includer species needs to be taken into consideration when formulating diets containing halophytes and or salt-tolerant forages for small ruminants [84]. Sheep raised on a diet supplemented with salt-tolerant dicotyledonous C*henopodiaceae* such as *Atriplex* (saltbush), *Suaeda linearis* (sea blite) and *Salicornia* (glasswort) gain at least as much weight and yield meat of the same quality as control sheep fed conventional grass hay, although they convert less of the feed to meat and must drink almost twice as much water [85]. In contrast, salt excluding *gramineae* do accumulate only small amounts of salt in foliage and could be used advantageously as alternative feed or food on saline land to replace completely common feedstuffs, thus to alleviate feeding cost [84]. Indeed, some halophytes, such as grain from the salt grass *Distichlis palmeri* (Palmer's grass), are used as food [85]. However the accumulation of relative small amounts of salts in their tissues is also favoring an increase of salinity in the soil during their culture and the risk of soil destruction.

This diversity of mechanisms (above shown by an example of an excluder and includer species) can be beneficial if the species are used in an integrated manner. This opens the possibility for an ecologically sustainable and economically feasible

Fig. 8 Example for a successful intercropping culture: *Panicum turgidum* and *Suaeda fruticosa* in a field near the Institute of Sustainable Halophyte Utilization (Karachi, Pakistan; Photo A. Khan)

agriculture of halophytes [86], especially when perennial species are selected (ontogenetic aspect). Perennial plants handle salinity better than annual plants because they do not often exhibit a salt resistant juvenile phase every year [87].

On the basis of these biological parameters first impressive plantings show the reliability of this system ([86], Fig. 8). A search within halophytic plant species to find suitable fodder replacement for calves has been successful in identifying a local salt excluding perennial grass, *Panicum turgidum*, with biomass yields of about 60,000 kg/ha/year (fresh weight) when grown in saline soil (EC 10–15 mS cm^{-1}) irrigated with brackish water (EC 10–12 mS cm^{-1}). *Panicum* was used as a complete replacement for maize in a cattle feeding trial and resulted in equivalent growth and meat production. It has been shown that the cultivation of *Panicum* together with the perennial salt accumulator *Suaeda fruticosa* in adjacent rows and with frequent irrigation was sustainable in terms of soil salt balance, with little change in soil salinity detected.

Implementation of this intercropping system is one way to use saline land and brackish water for producing an economically viable and environmentally sound agriculture. It was estimated that 15 % of undeveloped land in the world's coastal and inland salt deserts could be suitable for growing crops using saltwater agriculture. This amounts to 130 million hectares of new cropland that could be brought into human or animal food production, without cutting down forests or diverting more scarce freshwater for use in [85].

The intercropping (type of polyculture) with *Panicum* and *Suaeda* shown above also provides pest management, nutrient cycling, a greater variety of resource use, yield increases, production of diverse products, and a decrease in the risk of loss due to diseases [88]. It is suited to serve as an argument to transfer the monocultural practices of modern agricultural methods on saline agriculture. Monocultures have been the driving force behind a loss of genetic diversity and a need for expensive inputs i.e. fertilizers, pesticide, seed stock. These practices ultimately pollute the land, the water, and the food they are producing. A compromise between monoculture practices and polyculture could be the incorporation of multiple cropping systems by using rotations, borders, and cover crops. In general, however, the goals are usually the same: to secure food self-sufficiency, to preserve the natural resource base, and to ensure social equity and economic viability.

6.3 Reduction of the Dilemma Between Feed and Fuel by Halophytes

Since the amount of land and water resources that can be used for agricultural production is limited, there is now a widespread fear that the production of biofuels will have a severe impact on natural resources and food security. The diversity of halophytic *gramineae* can also be used to reduce this “dilemma between feed and biofuel” [89]. An unsustainable supply of fossil fuels necessitates the need to look for suitable alternatives [90]. The aim is to create aviation-grade biofuels without using any arable land, freshwater or standard food crops. Even NASA’s green lab research facility is using halophytes to create food and fuel. Crops available for human consumption being used presently as biofuel feedstock may be replaced with halophytes, growing on saline lands and irrigated with brackish water. Some halophytes are being studied for use as “3rd generation” biofuel precursors. Halophytes such as *Salicornia bigelovii* can be grown in harsh environments and typically do not compete with food crops for resources, making them promising sources of biodiesel [85] or bio-alcohol.

Perennial salt resistant grasses like *Halopyrum mucronatum*, *Desmostachya bipinnata*, *Phragmites karka*, *Typha domingensis* and *Panicum turgidum* have also potential as bio-ethanol crops (Fig. 9, [91]). They show considerable high growth rates to produce ligno-cellulosic biomass of good quality (26–37 % cellulose, 24–38 % hemi-cellulose and <10 % lignin) suited for ethanol production. Third-generation biofuel production processes that can convert ligno-cellulosic biomass (from crop residues, grasses and trees grown on marginal land) to produce “cellulosic” ethanol are currently under development [89]. It is expected that third-generation biofuel production may contribute to mitigate eventual pressures on natural resources that can be used to produce food, but for the time being these technologies are not yet commercially viable [92]).

Abideen et al. [91] argue that the unexplored aspects of agronomy of these wild plants are leading again to the requirement of careful studies before large scale cultivation, especially with regards to land degradation and ecological consequences. Latter one might be faciliated by specific properties of *Phragmites*, *Typha* and *Panicum* allowing them to grow on extreme areas well, not suited for conventional crop (food) production but for saline irrigation. This can be seen again as an example of the importance of heterogeneity in halophytes for saline

Fig. 9 Photos of salt resistant grasses like *Panicum turgidum* (**a**) *Phragmites karka* (**b**), *Typha domingensis* (**c**) *Desmostachya bipinnata* (**d**) *and Halopyrum mucronatum* (**e**) have the potential as bio-ethanol crops

Fig. 9 (continued)

sustainable agriculture. These species unlike other cereals can grow well in saline paddy fields and are highly tolerant of excess water stress, from either submergence (in which part or all of the plant is under water) or waterlogging (in which excess water in soil limits gas diffusion). This habitat has similar advantages for saline irrigation as in coastal areas where the irrigation water is permanently renewed. A major advantage of this system is that a fluctuation of the salinity can be minimized in the soil and a precise balance of input and output of salt is less important as in conventional irrigation systems on farmland.

Fig. 9 (continued)

6.4 Ecological Sustainable Ditch Irrigation of Halophytes

The usefulness of heterogeneity or diversity in between extremophytes such as halophytes can be nicely demonstrated with another flooding resistant species, the C-4 marsh grass of the genus *Spartina*. It grows in the upper elevation of the salt marsh at coastal salinity, partially higher than that of seawater, as well as in fresh water. Salt marshes dominated by *Spartina* species are among the most productive ecosystems known, despite nitrogen limitation [40, 93, 94]. *Spartina alterniflora* was introduced first by Lieth in a sustainable halophyte production system for landscaping and fodder, using ditches of about 5 m width irrigated with ocean water of approx. 5 % salinity for 2 h every day ([62], Fig. 10). It is exceptional and impressive how many various ecological and economic benefits emerge with the ecological engineering of *Spartina* plants [95]:

Salt marshes dominated by *Spartina* species

- help to reduce atmospheric CO_2 enrichment [96],
- have a low vulnerability against sea level change and protect the estuaries against the effects of global changes, are 'therefore' an important component of new coastal management practices and useful in developing strategies for the stabilization of deteriorating marshes (in marsh restoration projects) [8, 97–99],
- can tolerate oil spills (its growth is even stimulated by crude oils) and are hosts of microbial degraders promoting oil spill cleanup in coastal wetlands [100–104].
- support biodiversity and the production of marsh fauna (e.g. fish, benthic invertebrates [105–110]),
- support bioremediation of recalcitrant complex carbohydrate biopolymers by marine bacteria [111].

Spartina itself

- is a potential biomass crop (e.g. grown for fodder [8, 112] in poor soil conditions),
- is highly effective in nutrient cycling (e.g. N-fixation, Fe-reduction, sulfate-reduction, sulfide-oxidation, Se-biotransformation to DMSeP, Si reservoir [113–117]),
- reduces toxic metal bioavailability (e.g. Cd, Pb, Cu, Cr, Hg and Zn), by sequestering a larger proportion of its metal burden in its belowground tissues which are likely to be permanently buried [118–121],
- is a bio-monitor for environmental toxicants from municipal and industrial wastes, agricultural

Fig. 10 Spartina alterniflora growing on full strength ocean water (ditch irrigation) in Dhubbayiah/Abu Dhabi (Photo: H. Lieth)

runoff, recreational boating, shipping and coastal development [122–124],
- is used as an indicator for estuarine sediment quality [122],
- can have, in the form of bio-mineral liquid extracts from *Spartina* culms, a number of health functions (e.g. cardiotonic, enhancer of life span); the total flavonoids of *Spartina* can be separated and used to resist blood coagulation and encephalon thrombus [125].

6.5 Complex Systems of Integrated Farming

Saltwater can be used in arid areas for economic purposes in even more complex systems as intercropping. A good example is the integrated farming with multi-species cultivations in Eritrea (Manzanar project): shrimps, fish, mangroves, seaweeds and live-stocks. Wastes from one species are used as nutrients for another species and thus effectively minimized to prevent pollution to the environment [126]. The long-term objective of this farming system is the transforming of the coastal region through sustainable and natural means [126].

In the Manzanar project in Eritrea, artificial mangrove swamps (planted using the fruit and propagules) are created by digging large areas to the depth of 1 ft below the average high tide level. Seawater is channeled from the sea into the mangrove swamps (Fig. 11). These species of trees are highly tolerant of salt and can remove salt from the water and retain it them in root, stem, and leaves. The propagules and leaves, while processed are suitable for human consumption [63] and can be fed directly to live-stocks such as goats and camels [126]. The mangrove trees also provide nourishment and shelter for large numbers of fish, shrimp and crab which feed indirectly from the decomposing leaves. Even the left-over roots help to stabilize the soil against erosion. It is entirely possible that water evaporation from vast-stretches of seawater farm will increase humidity and rainfalls in these areas, bringing in future desirable conditions for other economic activities. Next to the mangrove swamps, deeper ponds are dug which are fertilized with a mixture of camel and goat dung. The algae that grow in

Fig. 11 Photo from a Mangal near Karachi (Pakistan)

this environment supports the growth of an edible fish. The viscera and heads are used to feed crab, shrimp and carnivorous fish that are cultured in other ponds.

Zanella succinctly summarized the basic components of this seawater farming: a shrimp production facility, a mangrove forest, wetland systems [127]. The system can be extended if it feeds to the running approach. Each component must meet specific criteria in the eco-system of the integrated farm. The shrimp production facility must be made in concrete ponds to prevent the seeping and contamination of saltwater into the aquifer beneath. After the seawater is channeled into the shrimp and fish farm, the mangrove forest is flood-irrigated with the effluent from the shrimp and fish farms. Some water is filtered and returns to the sea, while the rest is used to irrigate the wetlands around the mangrove trees. However, in new approaches this irrigation water is also introduced into fields of *Salicornia*. At the peak of its operations, these farms employed almost 800 local people, shipped one metric ton of premium shrimp a week to Europe or the Middle East and cultivated 100 ha of the oil seed crop *Salicornia*, and was completing the planting of 100 ha of seawater forest [128]. Additionally it created a 60 ha wetland and was the home for over 200 species of birds and many other animals in the desert.

The waste water from the shrimp and fish farms offers, in comparison to pure sea water, advantages for the net productivity of the system. Shrimp and fish farming lead to an enrichment of phosphorus and nitrogen in the waste water. This is important because in the majority of cases, the low nitrogen and phosphorus contents limit the net productivity in sea water (although iron limitation has also been detected; [129]). Because nitrate is found in practice to be the most limiting nutrient in surface waters, this led to the conclusion that nitrate rather than phosphate is the main limiting nutrient and that it is the dynamics of the nitrogen cycle which are important for controlling phytoplankton productivity [130, 131]. This enriched seawater can be a valuable nutrient solution also for other halophytes. Strictly speaking is it conceivable that all application explained in the chapters above can be integrated in the complex system of integrated farming.

7 Conclusion

Research on sustainable utilization of halophytes is a very promising field. The diversity in halophytes offers promising options for utilization as shown in this review mainly with thematic priority on *gramineaes*. There is a need of new agronomic approaches as presented above and to revise currently accepted guidelines for water quality evaluation and recommendations for irrigation with saline waters. Only part of the knowledge about conventional agriculture can be used for this purpose. Meeting this challenge may lead to enormous strides towards mankind's well-being and environmental protection in future. However, halophyte agriculture ecosystems are very vulnerable; therefore all environmental issues such as the diversity in between halophytes biodiversity loss, soil and water depletion and salinization should be monitored carefully. The problems to be overcome for an environmentally safe and economically convenient use of saline lands and waters are still formidable and their solution requires a coordinated effort of a vast number of experts in various domains. However, the first steps are encouraging!

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