Tansley review

The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions

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Summary

The effective development of salt tolerant crops requires an understanding that the evolution of halophytes, glycophytes and our major grain crops has involved significantly different processes. Halophytes (and other edaphic endemics) generally arose through colonization of habitats in severe disequilibrium by pre-adapted individuals, rather than by gradual adaptation from populations of 'glycophytes'. Glycophytes, by contrast, occur in low sodium ecosystems, where sodium was and is the major limiting nutrient in herbivore diets, suggesting that their evolution reflects the fact that low sodium individuals experienced lower herbivory and had higher fitness. For domestication/evolution of crop plants, the selective pressure was human imposed and involved humans co-opting functions of defense and reproductive security. Unintended consequences of this included loss of tolerance to various stresses and loss of the genetic variability needed to correct that. Understanding, combining and manipulating all three modes of evolution are now critical to the development of salt tolerant crops, particularly those that will offer food security in countries with few economic resources and limited infrastructure. Such efforts will require exploiting the genetic structures of recently evolved halophytes, the genetic variability of model plants, and endemic halophytes and 'minor' crops that already exist.

I. Introduction

The effects of salinity on plants have been a determining factor in agriculture for more than 6000 yr (Jacobsen & Adams, 1958), and a major economic concern in industrialized agriculture for

> 150 yr (Lawton & Weathers, 1989). In the past half century, with the on-going degradation of millions of hectares of agricultural land by salinization (Munns, 2003; FAO, 2011b), there has been particular interest in plant salt metabolism, especially directed toward (1) making major crop species more

salt tolerant by crossing with wild species or by transferring genes from halophytes, and (2) developing new crops from halophytes (Glenn *et al.*, 1999; Flowers, 2004; Colmer *et al.*, 2005). Both approaches have proved to be quite challenging and progress has been slow (James *et al.*, 2012).

Because there is no quintessential halophyte or glycophyte or crop plant, it is clear that there can be no 'best' or 'optimal' solution to improving crop salt tolerance. Tolerance is multifaceted, a complicated integration of all plant activities (Cheeseman, 2013) and the diversity of successful forms and physiologies confounds generalizations.

Flowers *et al.* (2010) suggested that in order to understand why crop domestication and selection has not produced 'robust and productive' salt tolerant crops, an examination of halophyte evolution should be incorporated. For that, they focused on the phylogenetic relationships of halophytes to angiosperms in general. In this review, I will expand the consideration of halophyte evolution at both the ecological and genomic levels, followed by discussions of the evolution of glycophytes and the evolution/domestication of crop species. I will conclude with some suggestions for experimental approaches to understanding halophyte evolution and for development of salt tolerant crops based on evolutionary precedents.

II. On the evolution of halophytes

1. Halophyte numbers and their phylogenetic distribution

Over a century ago, halophytes were defined simply but usefully as species adapted to perpetually saline conditions (von Marilaun, 1896). More recently, Flowers and co-workers proposed an operational definition as plants which can complete their lifecycles at 300 mM NaCl (Flowers *et al.*, 1977), or later, 200 mM (Flowers & Colmer, 2008). Others have set the cutoff as low as 70 mM (Greenway & Munns, 1980) to 85 mM (Glenn *et al.*, 1999). What this means in terms of numbers of halophytes is not perfectly clear. Glenn *et al.* (1999) have suggested a number as high as 6000 species, whereas the eHALOPH Halophyte Database (Flowers, 2014) currently identifies more than 1500 species as salt tolerant, albeit without labeling them as 'halophyte'. Saslis-Lagoudakis *et al.* (2014) identified a somewhat higher number, 1653, and referred to them as halophytes. In spite of the difference in these last two tallies, most detailed lists represent only *c.* 0.5% of all angiosperms. This may mean that evolution of halophily is difficult, hence rare, but it may also reflect the fact that a relatively small portion of the Earth's surface has naturally saline soils.

Halophytes occur in 37 of the 65 orders of plants (Flowers *et al.*, 1977, 2010). Based on phylogenetic analyses, halophily has apparently evolved no fewer than 59 times (Saslis-Lagoudakis *et al.*, 2014). No families are strictly halophytic although, for reasons that are not clear, some have disproportionately high numbers (e.g. the Chenopodiaceae, now included in the Amaranthaceae). At the level of genus, both halophytes and nonhalophytes frequently co-occur, well-known examples being *Aster*, *Glycine*, *Plantago* and *Solanum*.

2. When did halophytes arise?

In their review, Flowers *et al.* (2010) linked the origin of halophytes to the evolution of land plants (embryophytes) in general as descendants of charophyte algae (Pickett-Heaps, 1979; Lewis & McCourt, 2004). The embryophytes separated from the charophytes *c.* 500 Ma (million years ago) (Sanderson, 2003).

In part because today's charophytes are largely freshwater algae, Flowers *et al.* (2010) suggested that glycophytes arose before halophytes. This scenario is, however, complicated by the fact that even today there are saltwater charophytes, including *Lamprothamnium papulosum, Chara longifolia* and *Nitellopsis obtusa* (Davenport *et al.*, 1996; Winter *et al.*, 1999; Beilby & Shepherd, 2006), and there were more of these in the past (Flowers *et al.*, 2010). Flowers *et al.* also concluded that conditions around freshwater pools would have been less 'stressful' than those bordering saltwater, allowing the land plants to evolve there first.

However, all this may be moot. Whether there are halophytes among the nonvascular plants is still unclear; proximity to coasts by itself does not establish halophily (Sabovljević & Sabovljević, 2007). Thus, with the exception of one fern genus, *Acrostichum,* all known halophytes are angiosperms (Flowers *et al.*, 2010). Embryophytes first appear in the fossil record as microfossils *c.* 470 Ma; the first recognizable fossil land plants date to *c.* 430 Ma. Angiosperms, however, arose another 200–250 Myr later. This is a very long time, as is the 180–230 Myr that have passed since then.

In that very long time, both global climate and global geography have changed immensely. Since the appearance of angiosperms, Pangaea split up and the continents rearranged themselves in major ways. Mountain ranges as high as the Alps appeared and eroded. Ice ages sucked up vast quantities of water from the oceans and returned it – numerous times. Rainforests of the Carboniferous period gave way to deserts in the Permian and a generally wetter Jurassic; a similar drier to wetter change occurred a mere 2 Ma at the beginning of the Quaternary (Valiente-Banuet *et al.*, 2006). Atmospheric oxygen levels increased to near pyrogenic levels in the Permian and declined to about half present levels in the Triassic (Berner, 1999). Atmospheric CO_2 has ranged from as high as 4000 ppm to < 190 ppm (Ekart & Cerling, 1999). As angiosperms arose and diversified, gradually, over 40–80 Myr, they took over much of the world. However, *c.* 60% of the then extant species disappeared during the Cretaceous–Tertiary (KT) extinction (Nichols & Johnson, 2008), further distancing charophytes from the evolution of halophytes.

In the more recent past, during the last *c.* 700 000 yr, glacially related climatic oscillations have been particularly pronounced (Comes & Kadereit, 1998). With each retreat, new habitats opened up, and plants colonized them. Some colonizations involved species moving back from refugia. But some habitats were novel, with no adapted species available to colonize them.

3. How do halophytes (or other edaphic endemics) evolve?

Time, changing climatic conditions and particularly large, unpredictable disruptions such as glaciers or volcanic eruptions create severe habitat disequilibria. In response, species in existing

communities experience differential survival and extinction, either locally or globally. But at the same time, transient opportunities for establishment and survival of new forms appear.

Such disruptions serve as the critical drivers for the evolution of halophily and of edaphic endemism in general (Kruckeberg & Rabinowitz, 1985; DiMichele *et al.*, 1987). The process is summarized in Fig. 1. Beginning with 'habitats momentarily in severe disequilibrium' (DiMichele *et al.*, 1987), the distinctiveness of their eventual flora is established by the severity of the stress (particularly in contrast to neighboring habitats), the extent of the area affected and the proximity to similarly stressed sites with established flora. The severity of the stress determines the number of marginally tolerant individuals suitable for colonization of the disturbed areas, whereas the other two factors determine the potential for migration of species among sites. Stress tolerant species colonizing ecological islands do not generally arise *de novo*, or by natural selection from species otherwise intolerant of the stress (DiMichele *et al.*, 1987). Rather, the founding individuals must be pre-adapted to the stresses, having previously evolved these capacities fortuitously in nonstressful habitats.

Following successful colonization, the ability to reproduce in small or isolated populations and the prevention of gene flow from the great masses of unfit progenitors are critical. The edaphic endemics-to-be often transition from outcrossing to selfing in the process of speciation. Although outcrossers, especially obligate outcrossers, have high genetic variability which allows adaptation to environmental change, the breeding system is poorly suited to small populations where pollinators and suitable mates may be scarce (Rajakaruna, 2004). Phenological changes, particularly a shift in flowering time, also lead to reproductive isolation (McNeilly & Antonovics, 1968). Although these changes may initially be responses to environmental factors, they can rapidly be stabilized by accumulation of genome-level changes (Rajakaruna & Whitton, 2004).

The divergence of the halophyte *Lasthenia maritima* (Gray) M. Vasey (Asteraceae) (Fig. 2a,c) from its progenitor *L. minor* (Fig. 2b, d) is a good example of the speed with which colonization and speciation can occur. With the last retreat of the North American glaciers 15 000–10 000 yr ago and concomitant rising sea levels, a pre-adapted population of *L. minor* was left stranded on islands off the coast of California. Sprayed with salt and colonized by sea birds, these islands became both guano encrusted and saline. *Lasthenia maritima* exemplifies the evolution of halophytes as a result of such major habitat disruptions (Rajakaruna, 2004).

In saying, above, that 'the species colonizing ecological islands do not generally arise *de novo*,' the caveat implied by 'generally' is important. This is demonstrated, for example, by *Helianthus paradoxus* (Asteraceae) (Rieseberg *et al.*, 2003; Edelist *et al.*, 2009). This species (Fig. 2f), a halophyte restricted to a few salt marshes in Texas and New Mexico (USA), is one of three stabilized diploid hybrid derivatives of the less stress tolerant and more widespread species, *H. annuus* and *H. petiolaris* (the other two derivatives are *H. anomalus* (Fig. 2g), found only on sand dunes in Utah and Arizona (USA), and *H. deserticola*, found on dry, sandy desert floors in Nevada, Utah and Arizona). In diploid hybrid speciation, the reproductive barrier allowing expansion in a new environment is associated with rapid chromosomal re-patterning concomitant with niche separation (Rieseberg *et al.*, 2003). As in the case of pre-adapted colonists, the adaptation of fit hybrid genotypes requires that they avoid competition with unfit individuals, a condition made easier by the extreme environments in which they arose (Rieseberg *et al.*, 2003).

There are, of course, numerous other species having populations which differ significantly in the apparent salt tolerance of different populations. These may well prove useful in clarifying the development of halophily and the evolution of halophytes. *Atriplex canescens*, for example, occurs in populations with extremely different levels of sodium accumulation even over small
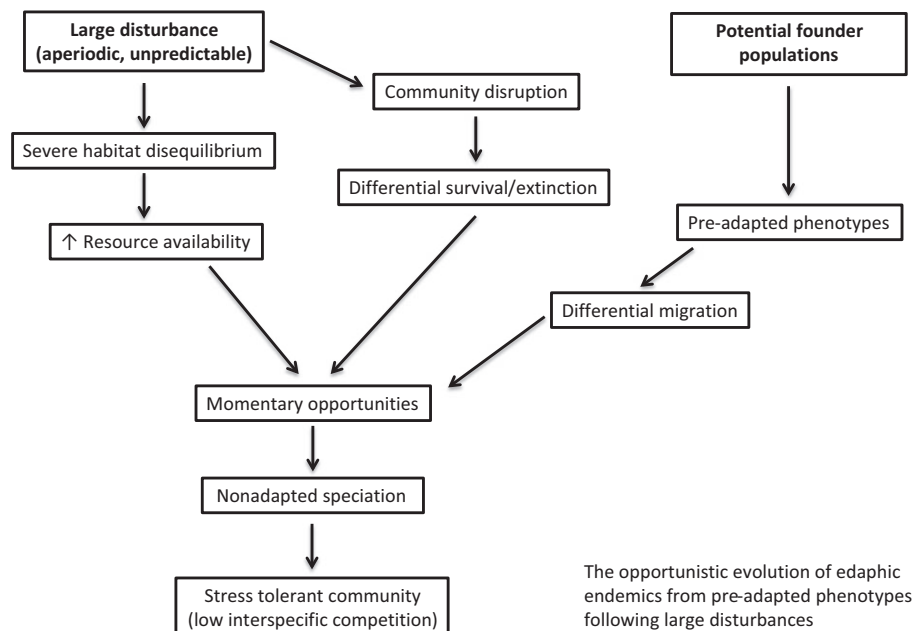

Fig. 1 The opportunistic evolution of edaphic endemics (including halophytes) proceeds from pre-adapted individuals and takes advantage of momentary opportunities made possible by severe habitat disruptions.
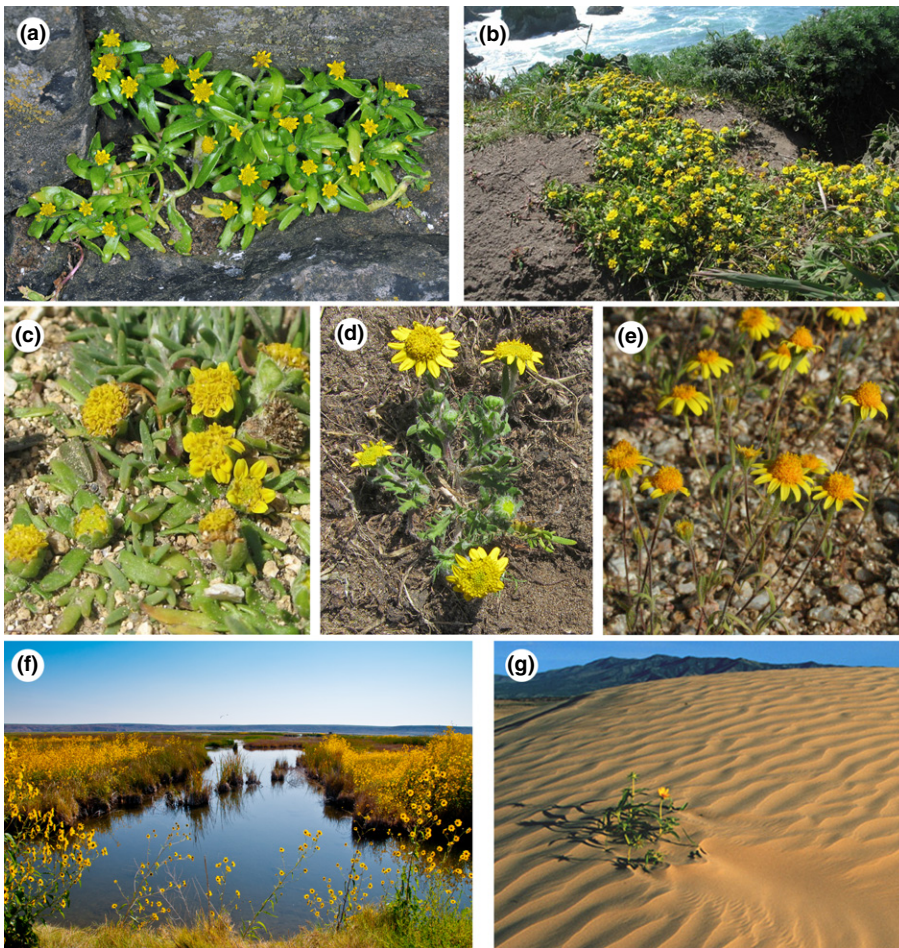
Fig. 2 Recently evolved halophytes and some close relatives. All are in the family Asteraceae. Habitat settings of (a) *Lasthenia maritima* (A. Gray) M.C. Vasey, (Seal Rock State Park, OR, USA) and its putative precursor, (b) *L. minor* (A.DC.) Ornd. (Pt Reyes NS, CA, USA). Inflorescences and leaf forms of (c) *L. maritima*, (d) *L. minor*, and (e) *L. californica* Lindley. Stable diploid hybrids of *Helianthus annuus* and *H. petiolaris* shown *in situ* – (f) *H. paradoxus* Heiser (Bitter Lake NWR, NM, USA); (g) *H. anomalus* S. F. Blake (Little Sahara, UT, USA). For discussion and details, see text. With grateful acknowledgement of the photographers: (a) Gerald D. Carr, (b, c) Robert Steers, (d) Doreen Smith, (e) Elizabeth Makings, (f) Paul Tashjian, and (g) Loren Rieseberg and Jason Rick.

geographic areas (Richardson, 1982; Glenn *et al.*, 1996). Similarly, *Lasthenia californica* (Fig. 2e) in the western United States, especially in Mediterranean climates (Rajakaruna & Bohm, 1999), occurs as at least two different races. Race A is restricted to wet sites with high levels of Na^+ and Mg^{2+} salts, whereas Race C occurs at sites with much lower salinity, but also much less water (Rajakaruna & Whitton, 2004). Race C is, thus, considered drought tolerant whereas Race A is salt tolerant. Comparing Na^+ uptake and translocation between the two races under controlled conditions, Rajakaruna *et al.* (2003), reported that Race A accumulated 20-fold more Na^+ than Race C plants, and translocated a much larger portion to the shoots. One recent study (DeRose-Wilson & Gaut, 2011) has indicated that widely distributed but not particularly halophytic species might, in general, have sufficient genetic variability that localized genotypes pre-adapted to salinity and to other stresses exist. The subject of that study was *Arabidopsis thaliana*.

In summary, it is clear that what *can* evolve in a newly developing habitat depends on what is already present in the vicinity (DiMichele *et al.*, 1987). It is understandable, therefore, that the origin of halophytes is polyphyletic and that they are distributed across so many orders (Flowers *et al.*, 2010; Saslis-Lagoudakis *et al.*, 2014). It is also understandable that orders, families or genera not present at the targets of opportunity do not include halophytes.

And given the relatively small fraction of the total world land area that is naturally saline, and the even smaller fraction that is not also desert, it is also to be expected that as a proportion of all angiosperms, halophytes should be relatively rare.

4. How to make a halophyte: genomic considerations

In addition to having available habitat and the ability to reproduce in small or isolated populations, the pre-adaptation of a mesophyte to salt stress requires a set of 'starter' genes, and conversion to halophytism requires post-colonization changes at the genome level. The archetypal pre-angiosperm ancestral genome likely had *c.* 12000 protein-coding genes (Sterck *et al.*, 2007). Around 320 Ma, there was a genome triplication as angiosperms began to evolve. This was followed, at 190 Ma, by a duplication. Both events are reflected in most of today's angiosperm genomes (van de Peer *et al.*, 2009; Doyle & Egan, 2010; Jiao *et al.*, 2011; Oh *et al.*, 2012) although through gene loss (which begins soon after duplication), today's diploid plant genomes are typically in the range of 24 000 genes, regardless of habitat or life style. Thus, the history of angiosperms provides a rich source of genes and their variants to serve as the starter set.

Genome duplications were, of course, not limited to these two events; hybridization and autopolyploidy continue to occur. They

may, however, have had periods of greater influence and perseverance at some times than at others (Song *et al.*, 1995; Hanada *et al.*, 2008; Edger & Pires, 2009; Khalturin *et al.*, 2009; DeBolt, 2010), possibly conferring increased chances of survival in new or novel habitats (Soltis *et al.*, 2010). This may have been critical, for example, at the KT boundary 66 Ma which cleared many niches and opened many new ones. It has been postulated that the persistence and subsequent expansion of angiosperms across the boundary was associated with a large number of independent genome duplication events (Fawcett *et al.*, 2009).

Although polyploidy may be useful during niche colonization, it need not necessarily be maintained. Not all halophytes are polyploids nor are all polyploids stress tolerant. Partly, this reflects extensive gene loss that begins soon after duplication (Jiao *et al.*, 2011). In some cases, ploidy levels make little difference in salt tolerance (e.g. in $2n$ or $6n$ Buffalo grass; Wu & Lin, 1994). In other cases, autopolyploids are more salt tolerant than diploids (e.g. *Trigonella foenum-graecum*; Marzougui *et al.*, 2010); polyploid wheat is more drought tolerant than diploid (You-Cai *et al.*, 2006). The continued study of stable polyploids at different times after genome duplication events is clearly warranted. In this case, *Atriplex canescens* might be a good subject, having stable 2x, 4x, 6x, 8x,10x, 12x, 14x and 20x chromosome races (Sanderson & Stutz, 2001), at least three of which (2x, 4x and 6x) may co-occur at individual sites (Senock *et al.*, 1991).

Tandem duplications, gene translocations and transposable element insertions can also increase copy numbers of genes useful in stress tolerance. Their rate of occurrence may be accelerated by environmental challenges even in a few generations (Zhang, 2003; DeBolt, 2010). The potential for deciphering and understanding their effects has been increased by the genome sequencing of two *Arabidopsis* relatives, *Thellungiella parvula* (synonyms *Eutrema parvulum*, *Schrenkiella parvula*) and *T. salsuginea* (synonym *Eutrema salsugineum*) (Dassanayake *et al.*, 2011; Oh *et al.*, 2012; Wu *et al.*, 2012; Yang *et al.*, 2013). Thus far, the comparison of *A. thaliana* and *T. parvula* (Fig. 3) has received the greater attention. Because the two lineages diverged only *c.* 12 Ma, macro-synteny still characterizes their genomes, with the *T. parvula* genome interrupted extensively by duplications, translocations and insertions absent in *A. thaliana*. These have resulted in increased numbers of genes putatively associated with membrane-located proton ATPases and with Li^+, Na^+, K^+ and borate management, ions which *T. parvula* must also tolerate in its native environment (Oh *et al.*, 2014). The unrelated salt marsh halophyte, *Limonium sinense*, shows a similar pattern transporter expression at the transcriptome level (Chen *et al.*, 2007), as do two mangroves for which extensive transcriptome data are available (*Rhizophora mangle* and *Heritiera littoralis*; Dassanayake *et al.*, 2009).

In summary, the diversity of halophytes reflects the diversity of ways in which genomes can be modified in response to edaphic or other environmental pressures. Genomic and transcriptomic analyses indicate that their precursors were less well adapted to saline conditions, that is, that the progenitors of halophytes were nonhalophytes. As will be clear from the next section, however, this does not mean halophytes evolved from glycophytes.
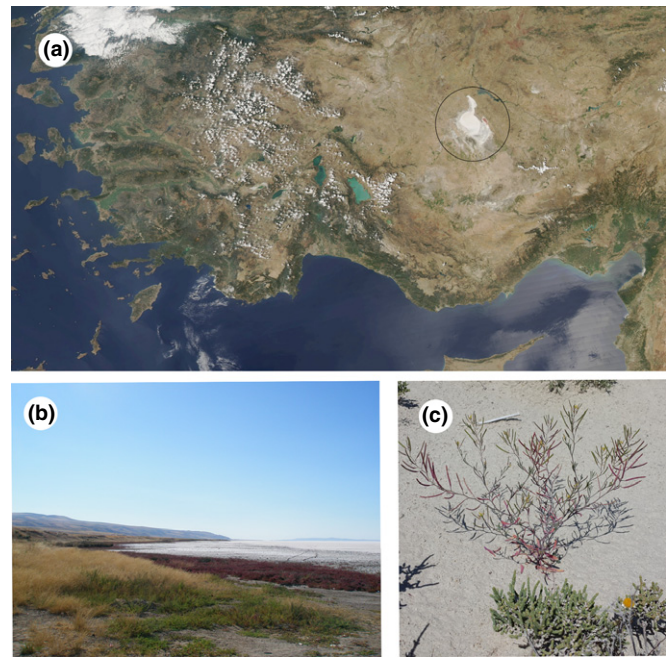

Fig. 3 The halophyte *Thellungiella parvula* is an edaphic endemic from Central Anatolia (Turkey) tolerant of high levels of multiple ions. (a) Satellite image of Turkey showing the location of Lake Tuz (circled). The white appearance is largely crystalized NaCl. Cyprus is visible in the lower right. (b) Ground-level view of Lake Tuz. (c) *T. parvula* at fruiting stage on salt and sand at Lake Tuz. With grateful acknowledgement of the photographers: (a) chelys.eu (http://www.eosnap.com/tag/lake-tuz/page/2/), (b) Sunhee Jeon and (c) Ismail Türkan.

III. Glycophytes – the other salt problem

Saline soil is a powerful driver and selective force, as are drought and other challenging edaphic conditions. There are no similar drivers operational for evolution of adaptation to comparatively benign conditions or evolution of stress *in*tolerance. For most plant physiologists, it is undoubtedly the case that low salt is considered 'normal' and high salt is a 'problem'. There is, however, another problem associated with plants and sodium, namely that many plants actually have *too little* sodium in their leaves.

Understanding the evolution of these plants, which I will call the glycophytes, is arguably more difficult than understanding the evolution of halophytes, and much of what I will say here is by necessity untested and incomplete hypothesis. One of the primary reasons for this is that the mere definition of glycophyte is vague. In general, the assumption underlying studies of 'salt tolerance', sometimes explicitly stated as in the eHaloph database (Flowers, 2014), is that everything that is not a halophyte is a glycophyte. Thus, if there are 350 699 species of angiosperms (The Plant List, 2013), *c.* 349 100 are glycophytes. From that, the absurdity of this 'definition' is obvious. Interestingly, there are no 'glycophyte-like' terms to describe plants which are not, for example, cryophytes, thermophiles, xerophytes or hydrophytes. In general, the term that is most appropriate for all of these 'not-something' species, that is, not specialists in an 'interesting' ecosystem, might be 'mesophyte'. But even 'normal' is more appropriate than 'glycophyte'.

Glycophytes, if they exist, must be defined by something other than by what they are not. They must be specialized in some way, and must be adapted to some set of conditions other than simply 'not-particularly-salty'. Thus, the discussion of glycophyte evolution cannot proceed without clarifying what a glycophyte is.

1. Glycophytes defined

Several respected online dictionaries give identical definitions of glycophyte as 'any plant that will only grow healthily in soils with a low content of sodium salts.' Neither healthily nor low salt content is unambiguous. The Oxford English Dictionary defines glycophyte as 'a plant whose growth is inhibited by saline soil.' In that case, all, or at least nearly all, halophytes are glycophytes. In the physiological literature, there is even the interesting oxymoron of 'salt tolerant glycophytes' (Glenn *et al.*, 1999).

For present purposes, a more useful and accurate definition would be this: a glycophyte is a species which has evolved by adaptation under natural selective pressures in ecosystems with low soil sodium levels and which maintains low sodium levels in its aboveground tissues, especially in its leaves. What constitutes 'low soil sodium levels' and 'low tissue concentrations' needs clarification. With regards to the second stipulation, it is similar to 'natrophobes' as defined by Smith *et al.* (1978). I have chosen to avoid that term because of the connotation that glycophytes somehow 'fear' sodium.

2. What is 'low soil sodium'?

With respect to soils, even in those of marine origin, mineral balances are quickly altered once tectonic movements uplift them. Na$^+$ adsorbs to clay but with lower affinity than multivalent cations or K$^+$, resulting in the preferential leaching of Na$^+$ unless there is an underlying pan layer (Glaze, 1998). Even in areas which experience sea spray, sodium leaches rapidly if annual rainfall is high (Smith & Middleton, 1978).

Because of these edaphic changes, a unifying principle of *all* plants is that they are adapted to conditions in which sodium is not dependably present at high enough concentrations to be reliable for

a central role in cellular metabolism (Cheeseman, 2013). Even among halophytes, the vast majority are capable of growing and reproducing under nonsaline conditions. C$_4$ plants, the only group with a specific sodium requirement, are sated at micronutrient levels.

Sodium is not, however, equally unreliable in all noncoastal terrestrial environments. Some areas are notably depauperate, having surficial sodium contents ranging from < 0.05% to 0.2% (Shacklette & Boerngen, 1984). These include, for example, the southeastern United States (Shacklette & Boerngen, 1984), western Amazonia (Dudley *et al.*, 2011), the Snowy Mountains and Northern Territory of Australia (Blair-West *et al.*, 1968; Cameron, 1997), most of New Zealand (especially South Island; Smith & Middleton, 1978), and weathered, acid soils throughout the tropics (e.g. Holm, 1973; Siddiqi, 1978; Manson, 2000). For now, the level identified by Shacklette & Boerngen (< 0.2%) will serve as a suitable definition of 'low soil sodium'.

3. Low sodium as a selection pressure

In order to consider the evolution of glycophytes, it is important to understand how the extreme exclusion of sodium from leaves and other aboveground tissues (stems, flowers and fruits) could provide them with an advantage in some ecological context. By itself, exclusion does not explain how sodium availability might equate to a selection pressure. Moreover, exclusion is not an obvious default approach; even on low sodium soil, another group of plants transports a seemingly disproportionate amount of sodium to leaves ('natrophiles'; Smith *et al.*, 1978) (see Table 1), and sodium is tolerated in all tissues by enough plants to suggest that in the absence of some advantage, extreme exclusion would not have persisted (Cheeseman, 2013). Thus, to understand the possible origin of glycophytes, we must look beyond the soil–plant system alone. In particular, I will consider the involvement of biotic factors, that is, herbivores.

Because of the herbivory threat, plants are under continual pressure to be poor quality forage. The exclusion of sodium from shoots of plants on low sodium soil has worked so well that sodium is the major limiting mineral nutrient in herbivore diets (Christian,

Table 1 Plants endemic to low sodium soil are classified as glycophytes (natrophiles) according to their major sites of sodium accumulation

Dominant Na accumulation sites	Stubble			Roots		
	Shoots	Stubble	Roots	Shoots	Stubble	Roots
Glycophytes (Natrophobes) Mean sodium (%DM)	0.14	0.35	0.22	0.03	0.15	0.41
Dominant Na accumulation sites	Leaves and stubble			Stubble		
	Shoots	Stubble	Roots	Shoots	Stubble	Roots
Natrophiles Mean sodium (%DM)	0.36	0.35	0.17	0.37	0.53	0.29

The summary is based on 31 species of pasture and fodder plants in New Zealand (Smith *et al.*, 1978). Glycophytes (natrophobes, *sensu* Smith *et al.*) accumulated Na$^+$ in either roots or stubble. Natrophiles accumulated Na$^+$ either equally in leaves and stubble, or at higher concentrations in stubble. Plants were grown in pots with pumice-derived sand, and watered with a solution containing 1 mM Na$^+$. 'Stubble' refers to the lower 5 cm of stem remaining at the soil surface after the aerial parts are harvested. In dicots, it is stem tissue.

1989; Grasman, 1993; McCreedy & Weeks, 1993). Only phosphorous, which is also generally maintained at low concentrations in plant shoots (usually interpreted as its arithmetic inverse, high P use 'efficiency'), has an importance approaching a similar magnitude (Grasman, 1993; Treydte *et al.*, 2007, 2008), but as P is an essential macronutrient for plants as well as animals, its exclusion comes with a higher physiological and fitness cost to the plant itself.

The strategy of sodium exclusion from leaves is effective at determining the foraging behavior of animals ranging in size from elephants (Klaus *et al.*, 1998; Morgan & Lee, 2007) to moose (Ohlson & Staaland, 2001) to mice (Barger & Tannenbaum, 1998). Seasonally, the tissues highest in N and P are those lowest in sodium, that is, buds and inflorescences, fruits, seeds and recently expanded leaves (Jefferies *et al.*, 1994). A mixed diet becomes essential, but it is not always straightforward. The aquatic portion of the moose diet, for example, provides higher levels of sodium, but also potentially toxic levels of heavy metals (Ohlson & Staaland, 2001).

Alternately, herbivores may eat soil to get their sodium (geophagy) (McMillan, 1953) or depend upon natural salt licks (Hebert & Cowan, 1971; Klaus *et al.*, 1998), or, if possible, forage partly at coastal sites (Morgan & Lee, 2007). Insects 'puddle' on salt-enriched mud or on carnivore dung (Arms *et al.*, 1974; Boggs & Dau, 2004). Cattle resort to geophagy, osteophagy or even carnivory when deprived of sufficient sodium (French, 1950; Wallisdevries, 1996). In western Amazonia, herbivores congregate at scattered natural salt licks even though it greatly increases their vulnerability to predators (Dudley *et al.*, 2011). Emmons & Stark (1979) demonstrated that the element sought at those licks is sodium. Tree-dwelling two-toed sloths (*Choloepus didactylus*) have been observed feeding from human latrines, the most plausible explanation being that they were seeking sodium otherwise missing from their diets (Heymann *et al.*, 2011).

The importance of dietary sodium and the limits imposed by plants have also been demonstrated experimentally in both mammals and insects. As shown by Batzli (1986), California voles (*Microtus californicus*) fed only grass seeds produced significantly fewer offspring than those whose diet was supplemented with sodium. Further, Kaspari *et al.* (2009) demonstrated in inland Amazonia that, with the addition of NaCl to leaf litter, the population of termites increased 7-fold and ant populations doubled.

As a point of anthropological interest, salt was critical to westward expansion by European colonizers in the United States. The sodium levels found in the plants grazed by livestock and game were too low to support their growth and reproduction without supplementation, and it was prohibitively expensive to transport salt from production sites on the Atlantic coast to the expanding western frontier (Jones, 1911). Hence, in the late 18th Century, expansion was halted at what is now the border of Indiana and Illinois. Indeed, the first Anglo-Americans to enter the prairies came in search of salt springs, the exploitation of which proved highly profitable. These springs were clearly already known to Native Americans who found them to be easy hunting grounds. The game routes between salt licks from eastern Pennsylvania through to Illinois were easy to follow because they had been heavily trampled by herds of bison (*Bison bison*), sometimes to > 60 m wide. The bison, as well as deer (*Odocoileus virginianus*), and before them mammoths and mastodons (Jakle, 1969), were dependent on the springs for their dietary sodium. The failure of glycophytes to accumulate sufficient sodium to support grazing livestock is still economically significant albeit with an easier technological fix, that is, through the use of salt blocks.

Throughout the world, nutrient deficiency associated with forage quality is a recurring theme in the field of animal husbandry, either involving only sodium (e.g. in the North American prairies – Bonin & Tracy, 2011), or sodium in combination with other minerals, for example, P (Brazil; Agostini & Kaminski, 1976) S (Queensland; Hunter *et al.*, 1979), Cu (Pakistan; Khan *et al.*, 2009; Mirzaei, 2012), Mg (Queensland; Gilbert *et al.*, 1989) or Zn (Uganda; Long *et al.*, 1972). Multiple deficiencies requiring supplementation have also been reported, for example, Na, P, K, Zn and Cu in the Northern Great Plains of the USA (Grings *et al.*, 1996), Na, P, Ca, Mg, S, Cu and Zn in western Intermountain Grasslands of the USA (Wilson *et al.*, 2011), Na, P, Zn and Cu in Northeastern Mexico (Ramirez-Lozano *et al.*, 2010), and various combinations of Na and macronutrients in the Australian Northern Territory (Table 2). The common deficiency in all cases is sodium.

Fertilization with sodium to increase leaf content has had mixed success: both positive (Smith & Middleton, 1978; Mundy, 1984; Chiy & Phillips, 1998) and null (Cushnahan *et al.*, 1996) results having been reported. As might be expected based on the phenology of the plants that are grazed, in some cases the effects are seasonal, with sodium contents being especially low in winter (Khan *et al.*, 2004). Also, as might be expected, the degree of deficiency among animals varies with species and reproductive status. Dairy cows are generally more sensitive than goats or sheep, for example (Smith & Middleton, 1978), and lactating cows are more sensitive than growing cows.

Based on the studies discussed in this section, it is possible to assign a value to 'low sodium' that can be operationally useful in the definition and study of glycophytes. Given the range of leaf and stem sodium concentrations that have been considered minimally sufficient for different grazing animals, the upper limit of 'low sodium' in grazeable tissues can be taken as ranging from less than *c.* 0.08 (Cameron, 1997) to 0.2% (Smith *et al.*, 1978) of dry matter.

4. Not all anti-herbivory strategies involve excluding sodium

Even though herbivores may be physiologically limited by sodium availability, all animals can survive for varying periods on low sodium diets by adjusting their excretory processes to conserve stores and maintain homeostasis (Blair-West *et al.*, 1968; Simpson, 1988; Staaland & Hove, 2000). That there must be more to anti-herbivory defense than sodium exclusion is unquestionable, given that plants and herbivores have co-existed since before the evolution of angiosperms.

In general, there is a trade-off between growth and defense, and some methods of defense are more expensive than others, obligatorily resulting in slower growth (Herms & Mattson, 1992). Defense by the production of secondary compounds

Table 2 Grasses from the 'top end' of the Australian Northern Territory and the mineral nutrients in them which limit cattle growth or reproduction; data from Cameron (1977)

Species	Na	P	Other limitations (1)
Alloteropsis semiolata	All* (2)	Seasonal	N, S
Andropogon gayanus	All*	Variable (3)	N, K, Mg
Aristida spp. (4)	All*	All	N, S, Mg
Astrebla spp. (5)	All*	Seasonal	N (6)
Botriochloa bladhii	All*	All	N, S
Botriochloa pertusa	All*	Seasonal	Mg
Brachiaria decumbens	All*	Seasonal	N, S
Brachiaria humidicola	No	Seasonal	N. K, S
Brachiaria mutica	No	Seasonal	–
Brachiaria spp. (7)	All	Seasonal	N, S
Brachyachne convergens	All*	All	N, S
Cenchrus ciliaris	All	No	N, S
Chloris barbata	No	No	K, Mg
Chloris gayana	No	Seasonal	N, Mg
Chrysopogon spp. (8)	All	Seasonal	N, S, Mg
Coelorharchis rottboelloides	All	All	(6)
Cynodon arcuatus	All	Variable	N
Cynodon dactylon	All*	No	–
Dactyloctenium spp. (9)	Seasonal	Seasonal	–
Digitaria eriantha	Seasonal	Seasonal	N, K, S
Digitaria milanjiana	All	Seasonal	N
Digitaria spp (10)	All*	Seasonal	N, S
Digitaria swynnertonii (11)	No	Seasonal	N, S
Echinochloa colonum	No	–	N (6)
Echinochloa polystachya	Seasonal	No	N
Eragrostis spp. (12)	Seasonal	All	N, S, Mg
Eriachne spp. (13)	Seasonal	All	N, K, S, Ca, Mg
Heteropogon contortus	All*	Seasonal	N, K, S, Mg
Heteropogon triticius	All*	All	N, K, S, Mg
Hymenachne acutigluma	(14)	Seasonal	–
Hymenachne amplexicaulis	All	No	–
Hyparrhenia rufa	All*	All	N, K, S
Iseilema spp. (15)	All*	All	N, S
Leersia hexandra	Seasonal	Seasonal	N
Oryza spp. (16)	No	All	(6)
Panicum maximum	All	Seasonal	N, S
Panicum spp. (17)	Seasonal	All	N, S, Mg
Paspalum notatum	All	Seasonal	N
Paspalum plicatulum	All*	All	N, K, S, (6)
Pennisetum glaucum	All	Seasonal	N
Pseudoraphis spinescens	All	No	N, K, Ca
Setaria spacelata	No	Seasonal	N, K, S, Ca, Mg
Setaria sphacelata	No	No	S, Ca
Sorghum intrans	All	All	N, S, Mg

Table 2 (Continued)

Species	Na	P	Other limitations (1)
Sorghum plumosum	All	All	N, S, Mg
Sorghum spp. (18)	All	No	N, S
Themeda triandra	All	All	N, K, S, Ca, Mg
Urochloa mosambicensis	All	Variable	N, S

'All' indicates that sodium (Na) or phosphorous (P) is below the sufficiency threshold in samples taken throughout the year. 'Seasonal' indicates that a nutrient is below the threshold for some period. Other limiting nutrients tended to be variable, that is, below thresholds in some but not all samples. Sixteen of the 49 species, including two wild *Oryza* spp., had sufficient sodium for cattle production throughout the year. The nutrient contents of the soils from which the samples were collected were not reported.
Notes:
(1) Limiting nutrients based on some samples at some times of year when all months are represented in the data set.
(2) 'All' means that all samples had Na < 0.08% of leaf DW; All* indicates that Na levels were <0.02% of leaf DW.
(3) Dataset included samples with both limiting and nonlimiting levels.
(4) Mixed samples of *A. contorta, A. inaequiglumis, A. latifolia.*
(5) Mixed samples of *A. elymoides, A. pectinata, A. squamosal.*
(6) Data insufficient to classify sufficiency of other elements.
(7) Mixed samples of *B. miliiformis, B. piligera, B. pubigera, B. reptans.*
(8) Mixed samples of *C. fallax, C. latifolius.*
(9) Mixed samples of *D. aegyptium, D. radulans.*
(10) Mixed samples of *D. bicornis, D. brownii, D. ciliaris, D. didactyla.*
(11) Although the authors considered this a synonym for *D. milanjiana,* the Na levels were up to 50-fold higher than in other samples of that species.
(12) Mixed samples of *E. dielsii, E. elongata, E. tenellula.*
(13) Mixed samples of *E. burkittii, E. obtuse.*
(14) Sample Na highly variable, from < 0.01% to 0.23%.
(15) Mixed samples of *I. ciliatum, I. fragile, I. macrathermum, I. membranaceum, I. vaginiflorum.*
(16) Mixed samples of *O. meridionalis, O. rufipogon.*
(17) Mixed samples of *P. cambogiense, P. decompositum, P. mindanense, P. trachyrhachis.*
(18) Forage sorghum mixture.

including anti-nutrients such as tannins and phenolics is in this category, and may be either constitutive or inducible (Iason & Palo, 1991; Jakubas *et al.*, 1995; Dixon *et al.*, 2002; Villalba *et al.*, 2002). Mechanical feeding deterrents reduce digestibility, but also have production costs that can reduce growth and reproduction of the plant (Marquis *et al.*, 2001; Kursar & Coley, 2003; Santiago & Mulkey, 2005). The availability of other nutrients may influence the economics of chemical defense, especially when switching between N-containing or N-free defensive compounds is an option (Craine *et al.*, 2003). However, as exemplified by some plant–fungal symbiotic systems, defensive tasks may be 'outsourced' to the fungus, increasing plant reproductive success despite decreased overall growth (Clay, 1988; Ruotsalainen & Eskelinen, 2011; Schardl *et al.*, 2013).

Herbivory may also have direct positive consequences in some species. Some plants (e.g. *Sporobolus kentrophyllus*, *Ipomosis aggregata*, *Leymus chinensis* and some genotypes of *Arabidopsis thaliana*) respond to herbivory by increased nutrient uptake, increased growth and/or compensatory reproduction (Ruess, 1988; Levine & Paige, 2004; Siddappaji *et al.*, 2013). In some cases, the positive growth response may be a direct result of chemical stimulation through the saliva of the herbivore (Liu *et al.*, 2012). Whether plant sodium metabolism, for example, the partitioning of sodium to leaves in natrophiles (Table 1), is related to the capacity for compensatory growth has yet to be studied.

In summary, the evolution of true glycophytes resulted from very different pressures than the evolution of halophytes; they are not simply different in their levels of salt tolerance or natural distributions in saline and nonsaline environments. Glycophytism may be one strategy of defense against herbivory, particularly under low soil sodium conditions. The correlation remains noncausal,

however; to the best of my knowledge, none of the studies of sodium content and grazing have also included analyses of the soil in which the plants were growing, nor have the effects of salt-block supplementation on susceptibility of specific glycophytes to grazing been examined.

IV. Crops – adaptation with loss of critical functions

When humans transitioned from hunting and gathering to agriculture, they began a new evolutionary pathway for the plants that were their food. Although halophytes reflect evolution from pre-adapted individuals in response to environmental change, and glycophytes putatively reflect evolution by natural selection in response to herbivory, the domestication of crop plants reflects evolution by human selection in response to the breeder's desires. As this process has been recently reviewed in depth, including a recent Tansley review (Hancock, 2012; Meyer *et al.*, 2012; Meyer & Purugganan, 2013), I will consider it only briefly here.

At its initiation, the most critical characteristic allowing crop improvement was genetic variability within available wild populations (Hancock, 2012). Selection for desirable traits, however, obligatorily reduced genetic variability, that is, domestication was a major evolutionary bottleneck. Eventually, as selections stabilized, the loss of variability was sufficient to limit future possibilities. For example, as Hyten *et al.* (2006) noted with respect to soybean, 'when the low sequence diversity present in the wild species was halved (by domestication), 81% of the rare alleles were lost.'

Domestication also reduced fitness under nonagricultural conditions and forced plants into obligate symbiosis, dependent on humans for their continued existence. The resultant suite of characteristics distinguishing today's major food crops from their wild progenitors is referred to as the 'domestication syndrome' (Table 3). As many domestication-related traits are conditioned by recessive, loss-of-function alleles, the alteration of some traits in Table 3 did not require selection on many genes. Control of seed nonshattering in a variety of grains and legumes, for example, reflects the alteration of only one or two genes (Hancock, 2012). Even when many genes or loci were involved, a small number often accounts for most of the effect (Hancock, 2012; Meyer & Purugganan, 2013).

Table 3 The domestication syndrome – common traits in domestic crops reflecting the process of human-directed selection (based on Doebley *et al.*, 2006; Hancock, 2012; Meyer *et al.*, 2012; Meyer & Purugganan, 2013)

- Determinate growth
- Increased resource allocation to reproduction
- Increased size and number of fruits/grains
- Nondehiscent (nonshattering) fruits
- Uniform seed ripening
- Loss of natural seed dispersal
- Early reproduction
- Loss of perenniality (lifecycle shifts)
- Self-pollination
- Change in secondary metabolites (pigments and bitter or toxic compounds)
- Loss of defensive structures
- Reduced genetic variability
- Increased local adaptation

Although important traits may be controlled by small numbers of genes, breeding and selection act on much larger units. Desirable genes are linked to others and selection invariably results in changes in other, nonselected characteristics. This was not a problem so long as the collateral changes were in traits inconsequential for survival or yield under the climatic and edaphic conditions prevailing during domestication. Thus, as the original sites of domestication were not saline, a loss of salt tolerance was neither apparent nor problematic.

Because traits such as salt tolerance are multigenic, single gene transformation approaches to improving it have had little success and the major approach to improving crop salt tolerance today is introgression of genes from still-tolerant wild relatives. However, achieving the goal has also been elusive (Gorham *et al.*, 1986). In wheat, for example, it has been possible to introgress the *Kna1* locus from bread wheat into the durum genome, somewhat increasing salt tolerance, but not without a yield penalty (Munns *et al.*, 2003). This penalty reflects 'linkage drag', that is, the undesired effects of gene linkage to other traits in a QTL or chromosome segment being carried along with the salt tolerance mechanism during breeding (James *et al.*, 2012). Analogous results have been found with maize (Schubert *et al.*, 2009) and rice (Ashraf, 2010).

In summary, the domestication of crop plants represents an evolutionary history quite distinct from that of either halophytes or glycophytes. Nevertheless, the continued existence of salt tolerant wild relatives of the most important seed crops makes it clear that the common practice of referring to crops as glycophytes is without basis. Because the performance of research inevitably depends on the precepts underlying it, this misunderstanding may well stand in the way of understanding and improving crop salt tolerance.

V. Moving forward

The question I will address in this section is this: from this discussion, what experimental opportunities can be identified for better understanding the evolution of halophytes and glycophytes and for directing the evolution of salt tolerant crops? In particular, I will briefly discuss possible approaches exploiting recently evolved halophytes, exploiting the genetic variation within *Arabidopsis thaliana* and other model plants, and exploiting endemic halophytes or minor crops to develop new crops for saline environments.

1. Exploiting recently evolved halophytes

As I discussed earlier, there are at least two examples of recently evolved halophytes that deserve further study at the molecular and physiological levels, especially in comparison with their nonhalophytic precursors or differently stress-tolerant relatives. These were illustrated in Fig. 2 because they are otherwise virtually unknown to physiologists and molecular biologists. Through such studies, we can expect to better understand the relationship between genomes, transcriptomes, proteomes, metabolomes and stress tolerance. For example, by sequencing *Lasthenia maritima* and its progenitor *L. minor*, species which diverged only 10 000–15 000 yr ago (Chan *et al.*, 2001), and following the related changes at the metabolome

and proteome levels, the changes associated with adaptation of *L. maritima* to its island habitat may be understandable at a level of detail not possible by analysis of relatives which diverged millions of years ago (e.g. *Arabidopsis thaliana* and *Thellungiella* spp.). Studies of the stable diploid hybrids of *Helianthus annuus* and *H. petiolaris*, that is, *H. paradoxus*, *H. anomalus* (Fig. 2) and *H. deserticola* would be equally informative (Rieseberg *et al.*, 2003; Edelist *et al.*, 2009). As noted earlier, from similar parents, these three new species are differentiated by the niches to which they are restricted.

2. Exploiting the genetic variation within model plants

The objective of these studies would be to utilize the short generation time of model systems to experimentally test genetic changes relating to (1) domestication of crops and (2) evolution of halophytes. Some of the potential tools include *Arabidopsis thaliana* (DeRose-Wilson & Gaut, 2011), *A. lyrata* (Sletvold & Ågren, 2011), *Brachypodium distachyon* (Bakker *et al.*, 2009) or *Mimulus guttatus* (Lowry *et al.*, 2008, 2009). As with the *Lasthenia californica* example highlighted earlier (Rajakaruna & Whitton, 2004), whereas divergence of the ecotypes or races into species has not yet occurred, adaptation to differing ecological niches is well under way. Hancock (2012) noted that with modern breeding techniques, the domestication process should require only 20–30 generations, a period easily accessible with these species. The kinds of genetic variations, reproductive systems and (in the case of *B. distachyon*) polyploidies that make these successful weedy species are the same that characterize potential halophytes or, forced in the other direction, crops (Bakker *et al.*, 2009). Thus, a program could be undertaken that revisits the kind of breeding and selection that gave rise to our current major crops, selecting for 'agronomic traits' such as early flowering, large seeds, etc. (Table 3), and following genome-level changes by resequencing at each generation. Alternately, a program might use selection on saline soil to create a new halophyte exploiting adaptations already present in the global population. Again, progress could be monitored by resequencing the genome and transcriptome as well as by monitoring phenotypic changes. Indeed, these two projects could be combined, selecting for 'agronomic traits' at high salinity.

3. Exploiting endemic halophytes or minor crops

The objective of this effort would be to develop local or regional food and fodder crops to feed people most at risk for food insecurity due to soil salinity or ground water salinization. Although the conclusion that salinity has not been important enough to have warranted the effort to develop new salt tolerant cultivars (Flowers & Yeo, 1995) may still apply today to countries with extensive, industrial agriculture and supporting infrastructure, the situation in the developing countries most affected by salinity and salinization-related land degradation is different. In Bangladesh, India and Pakistan, for example, local nutrition and food security demand solutions to salinity problems. One alternative in such areas may be to develop new crops for local consumption, that is, to go through the whole domestication process again. Conceivably, the wild, salt tolerant relatives of rice, wheat or barley could be the crops of the

future (as opposed to genetic resources for improving existing crop varieties). Colmer *et al.* (2006), for example, list 38 species in the Triticeae which have been proposed as sources of salt tolerance for wheat and these could be appropriate starting points.

However, *de novo* domestication is not the only possibility. There are a large number of plants already used for foods that have received very little attention in the scientific literature. Harlan (1992) provides a list of 88 genera harvested for food by native Australians. At least 60 of the genera include one or more species domesticated somewhere other than Australia, including *Chenopodium*, *Ficus*, *Glycine*, *Ipomoea*, *Musa*, *Oryza*, *Solanum*, *Vigna* and *Vitis*. He also provides an 11 page 'short list' of *c.* 250 plants cultivated in other regions of the world. Prescott-Allen & Prescott-Allen (1990), using FAO data, list 103 species contributing 90% of the world's food supply, but consider this a significant underestimate because some of the commodities are agglomerations of several species (e.g. pulses, or roots and tubers), and because a number of countries were missing from the FAO dataset (e.g. Ethiopia which has a long and unique agricultural history). One species, *Chenopodium quinoa,* is an excellent example of an indigenous crop that has experienced rapid expansion and acceptance because it is highly nutritious, it can be substituted for other grains in many uses, and its domestication has not proceeded to the point at which genetic variation losses compromise the development of new cultivars (FAO, 2011a). It is also highly salt tolerant (Ruiz-Carrasco *et al.*, 2011).

In some cases, preliminary efforts essentially comprising domestication under saline conditions in countries with high levels of food insecurity have been underway for 30 yr and more. Although they have not eliminated the insecurity, they have helped. The efforts have generally been local. An interesting result of this is that although studies proclaiming the *promise* of halophyte agriculture are reasonably well represented in the international scientific literature, reports of their local, small scale but *successful implementations* are not. However, some of them have been reviewed recently, and include the use of halophytes for food, fuel and fodder (Panta *et al.*, 2014), and for bioremediation of salt affected soils (Hasanuzzaman *et al.*, 2014).

VI. Concluding remarks

The effects of salinity on plants and the mechanisms they employ to survive have been studied for > 100 yr, albeit more intensively in the last 20–30. In contrast to what I have said in discussing climate change and the evolution of halophytes, this is *not* a long time. Even shorter, however, is the time we have to actually use our knowledge to solve food production problems, especially in poor, developing countries. If we do not, we can expect to suffer increasingly dire consequences. Clearly, one important forcing agent is the pace of current climate change (IPCC, 2014). However, as or more important and too often ignored in discussing agricultural productivity, is increasing human population. The projected increase in the next 35 yr (i.e. to 2050) is nearly equal to the current combined populations of China and India (United Nations, 2013).

Poverty and limited food availability already affect > 800 000 000 people, and degradation of soil resources in the

most food-limited regions of the world is ongoing. Unfortunately, or perhaps because of this, it is also true that the greatest needs are in some of the least politically stable regions and in countries with very limited infrastructure and economic resources. It is, therefore, arguable that (1) increases in the ability of crops to perform on saline soils are absolutely necessary and (2) this is a major and compelling reason to investigate the molecular, physiological or organismal level biology of plants under saline conditions.

The comfortable search for single genes under the control of strong promoters that will confer increased 'salt tolerance' on *Arabidopsis* growing semi-heterotrophically on eutrophic media for several weeks in sterile culture was an interesting approach when it was first developed, but it is no longer tenable as either a mechanism for crop improvement or as a viable approach to understanding salt tolerance. Understanding the mechanisms, at the genome level, by which halophytes evolve and by which domestication of crops proceeds, will facilitate the development of new crops. In the meantime, however, crops that can be grown on coastal or degraded soils should be considered the top priority in salinity related plant research. The characteristics of halophyte, glycophyte and crop evolution discussed here can help direct that effort.

Acknowledgements

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