Halophytes as forages in saline landscapes: interactions between plant genotype and environment change their feeding value to ruminants

Reporters:

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Key words: southern Iraq, central Iraq, spatial distribution, remote sensing, irrigation, salinity mapping.

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Halophytes as forages in saline landscapes: interactions between plant genotype and environment change their feeding value to ruminants

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Summary

This report focuses on three factors that affect livestock production using halophytes – biomass production, nutritive value (NV) of the biomass and voluntary feed intake (VFI). The growth of halophytic forages is widely recognized as a means for using saline land and water, but this study aim to assess the factors affecting the utilisation of this biomass by ruminants such as sheep, cattle and goats. Biomass production depends on plant species, genotype, the degree of abiotic stress (salinity, waterlogging), agronomic management and the interaction between genotypes and the abiotic environment. Production in irrigated systems is about 10-times that of dryland systems. NV relates to the efficiency of nutrient use by animals and is influenced by plant species, genotype and genotype x environment interactions. Halophytes typically contain lower metabolisable energy than traditional forages and most do not have enough energy for liveweight maintenance. Chenopods generally have high crude protein, sulphur and minerals, which are critical to ruminant production. However oxalate, mineral toxicities and induced deficiencies can have adverse effects on animals. Antioxidants that halophytes synthesise to detoxify reactive oxygen species may provide precursors of vitamins A and E, helping to alleviate deficiency and improve meat quality. VFI refers to the amount of feed that can be ingested by grazing animals. It is regulated by complex feedback between the stomach and central nervous system. VFI may be restricted by high concentrations of indigestible fibre, salt, and minerals and toxins, such as oxalate and nitrate. The productivity of saline agricultural systems may be improved by increasing halophyte feeding value. Increasing metabolisable energy is the most important factor. Measurement of relative palatability by grazing animals may assist in identifying genotypes with higher NV.

Highlights

- We review the factors affecting livestock production using halophyte fodders.
- We focus on biomass production, nutritive value and voluntary feed intake.
- Halophytes have lower metabolisable energy concentrations than other fodders.
- Voluntary feed intake is also decreased by high indigestible fibre, salt and oxalate.
- Improving metabolisable energy concentrations is a realistic plant selection goal.

Keywords: Salinity; herbivore; salt-tolerant; *Atriplex*; *Maireana*; *Distichlis*; *Puccinellia*; *Melilotus*

1. Introduction

The growth of salt-tolerant forage species for ruminant production offers a major opportunity to use land and water resources that are too saline for conventional crops and forages (Malcolm, 1996; Swingle et al., 1996). It is estimated that 5% of the world's land surface is cultivated salt-affected land, which includes 19.5% of irrigated agricultural land (Flowers and Yeo, 1995; Ghassemi et al., 1995). Halophytes, representing ~1% of the world's flora, are plants that can grow and complete their lifecycles in environments with high concentrations (greater than 200 mM) of electrolytes (mostly Na^+ and Cl^-, but also SO_4^{2-}, Mg^{2+}, Ca^{2+}, K^+ and CO_3^{2-}) in the root medium (Flowers et al., 1977; Flowers and Colmer, 2008). Some authors further distinguish between euhalophytes (plants that show some increase in growth with salinity) and miohalophytes (salt tolerant plants that have their highest growth when irrigated with fresh water) (Glenn and O'Leary, 1985).

The list of halophytes used for ruminant feeding systems is dominated by grasses and chenopods (Table 1). Halophytic forages are often used as a drought reserve or to fill annual feed shortages within grazing systems (Le Houérou, 1992; Ben Salem et al., 2010). For example, *Atriplex* species are used to fill the summer/autumn feed gap typical of Mediterranean-type climates in southern Europe (Papanastasis et al., 2008), Syria (Osman et al., 2006) and Australia (Malcolm and Pol, 1986), and to fill an early winter feed shortage in the Mendoza plain area of Argentina (Guevara et al., 2003). Halophytic grasses can be used to replace conventional hays in feeding systems (Al-Shorepy et al., 2010) and seed meal from *Salicornia bigelovii* has been used as an alternate protein supplement in mixed rations (Swingle et al., 1996). The incorporation of halophytes into farming systems may also have other advantages such as the lowering of the watertables causing secondary salinity (Barrett-Lennard, 2002; Barrett-Lennard et al., 2005) and improving soil stability (Le Houérou, 1992).

Achieving grazing value from saline systems is not straight-forward. The reported levels of salt tolerance of forage species can vary widely (Masters et al., 2007) and production is affected by other abiotic stresses such as waterlogging (Barrett-Lennard, 2003; Colmer and Flowers, 2008; Jenkins et al., 2010), sodicity (Qureshi and Barrett-Lennard, 1998) and aridity (Le Houérou, 1992). In dryland systems, spatial heterogeneity in salinity and associated abiotic stresses may lead to a wide variety of functional niches where individual species are unlikely to dominate or thrive at all locations (Norman et al., 2003). Reported levels of annual biomass production vary widely, from as little as 0.4 t edible dry matter (DM)/ha for *Atriplex* growing in a highly saline and waterlogged environment to 40 t DM/ha for *Distichlis spicata* irrigated with saline water (Pasternak et al., 1993; Norman et al., 2008). However achieving growth of biomass with saline resources is only one component of saline grazing systems; major challenges remain for the conversion of this biomass into animal products.

The vast majority of literature regarding salt-tolerant forages reports physiological mechanisms and agronomic traits such as biomass growth; there are fewer studies that examine utilisation by ruminants. To illustrate this point, we conducted literature searches using the Web of Knowledge^{SM} search engine. ‘Halophyte and growth’ yielded almost 1000 references and ‘halophyte and biomass’ 250 references. ‘Halophyte and sheep or goat’ returned only 29 references and adding the terms ‘nutritive value’, ‘feeding value’ or ‘feed intake’ resulted in less than 5% of the total number achieved for ‘halophyte and biomass’. Why is this area of halophyte research so uncommon when use by ruminants is the key to profitability? One explanation may be that halophytic forages are not considered unique and ruminants will be expected to use them in the same way as conventional forages. Our view is that this is not true: interactions between ruminants and saline forages can be complex and there are further difficulties in conducting feeding experiments with forages of low nutritive value or with high levels of anti-nutritional factors.

The framework of this review is summarised in Fig. 1. To achieve a better understanding of the impact of halophytic forages on ruminants, we need to understand the influence of the growth environment on traits beyond biomass production, namely nutritive value (NV) and voluntary feed intake (VFI). This review therefore emphasises the importance of biomass, VFI and NV, exploring how interactions between halophytes and their environment change the feeding value to ruminants, and therefore the productivity of the livestock system (Fig. 1). Many of the mechanisms that plants use to survive in saline environments have an impact on what grazing animals choose to eat, the quantity of forage eaten and the animal's ability to meet its nutritive requirements while managing toxins. The vast majority of the halophytes used in agricultural systems are 'wild' types and when plant improvement has occurred, it has focussed mostly on selection for survival and biomass growth (e.g. Malcolm and Swaan, 1989). We conclude by focusing on the opportunity to improve the productivity of saline agricultural systems by selecting species and genotypes of species with higher feeding value.

** Fig. 1 near here – REPRODUCE IN COLOR ON WEB, BLACK AND WHITE IN PRINT **

2. Biomass production

From the perspective of feeding value to ruminants, biomass production is the starting point. Biomass production by halophytes is affected by the salinity of the growth medium (Greenway and Munns, 1980; Flowers and Colmer, 2008), the presence of waterlogging (Colmer and Flowers, 2008; Bennett et al., 2009; Jenkins et al., 2010) and a wide range of agronomic factors such as cutting frequency (Bustan et al., 2005) and deep ripping and fertiliser application (Barrett-Lennard et al., 2003). Biomass production by halophytes has been recently reviewed (Masters et al., 2001; 2007; Colmer and Flowers, 2008) so only a few key points will be made here.

2.1. Impact of salinity

A saturated solution of NaCl contains ~360 g/L at 25^{o}C (ie. 6.16 M NaCl; Pinho and Macedo, 2005); this is about 11-times the salinity of seawater. In terrestrial environments, higher plants start to appear in saline landscapes as NaCl concentrations in the rooting medium fall below about one third of saturation (~ 2 M NaCl)[1], but in practical terms, substantial halophytic biomass is not produced until NaCl concentrations in the soil solution fall below ~600 mM, or EC_e values in moist soil of ~30 dS/m.[2]

Chenopods are generally more salt tolerant than halophytic grasses and legumes, with many chenopod species having optimal growth at NaCl concentrations between 25 and 200 mM NaCl (Greenway and Munns, 1980; Flowers and Colmer, 2008); typical chenopods found on saltland in Australia are *Tecticornia pergranulata*, *A. nummularia* and *A. amnicola* (growth responses in Fig. 2). In contrast, halophytic grasses have a growth optimum of less than 100 mM NaCl or show decreasing growth with any increase in salinity; typical fodder examples are *T. ponticum* and *D. spicata* (Fig. 2). *Melilotus siculus* (an exceptionally salt

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[1] One of the best indicators of the salinity limits that terrestrial plants can withstand can be obtained by measuring the seasonal changes in the osmotic potential of the leaf sap of halophyte species growing on the edges of playa lakes in arid environments. The soils in such landscapes will experience extreme salinities in the soil solution as the soil dries in summer. English (2004) reported that the lowest osmotic potential found in the expressed leaf sap of *Tecticornia pergranulata* growing on the edge of Lake Lefroy near Kalgoorlie in Western Australia was -10.7 MPa. Other samphire species had lowest leaf osmotic potentials around -5 MPa. Using the conversion factors of Lang (1967) a water potential of -10 MPa occurs with a NaCl solution of ~2 M. 2 M NaCl is about ~1/3 of saturation (6 M NaCl – cf. Pinho and Macedo 2005).

[2] The salinity of the soil solution depends on the concentrations of salt and moisture in the soil. Soil salinity is widely measured as the electrical conductivity of the saturation extract (EC_e). Our conversion between NaCl (in mM) and EC_e (in dS/m) is based on: (a) at field capacity the $EC_{soil\ solution}$ is ~2 times the EC_e, and (b) NaCl concentrations (in mM) are ~10 times the EC (in dS/m) (Bennett et al. 2009).

tolerant pasture legume – Rogers et al., 2008) has a similar response to salinity as the halophytic grasses. Despite their salt tolerance the DM production of all halophytes is limited by high salinity; 4 of the 6 examples in Fig. 2 have data for 400 mM NaCl, and at this concentration shoot DM was decreased by 30–75% compared with low salt controls (Fig. 2).

**Fig. 2 near here – REPRODUCE IN COLOR ON WEB, BLACK AND WHITE IN PRINT **

One important aspect of halophyte growth in the field is the major difference in productivity of non-irrigated (dryland) compared with irrigated systems (even when irrigated with saline water). For example, with *Atriplex* species under non-irrigated conditions in southern Australia (330–370 mm of annual rainfall per annum), annual leaf yields are commonly around 0.4–0.7 t DM/ha (Malcolm and Pol, 1986; Malcolm et al., 1988; Norman et al., 2008). In contrast, annual leaf yields of 10–20 t DM/ha have been achieved with *Atriplex* species irrigated with water of salinity (EC_w) 9–10 (Watson et al., 1987) and ~55 dS/m (Pasternak et al., 1985). Similar differences in production also occur with grasses. Under dryland salinity conditions in southern Australia, annual biomass production of grasses typically ranges from 0.2 to 1.0 t DM/ha (Nichols et al., 2008), whereas with irrigated systems, annual biomass production of halophytic grasses can reach 40 t DM/ha with an EC_w of 9.5 dS/m (Pasternak et al., 1993).

The slow growth of halophytes under dryland conditions is at least partly caused by the accumulation of high salt concentrations in the root-zone. Halophytes typically take up water ~10 times faster than Na^+ and Cl^- (Munns et al., 1983); over periods of 2-3 years this can substantially increase the salinity of the bulk of the soil. As an example, at a field site with shallow (0.5–1.2 m deep) saline (EC_w 16–62 dS/m) groundwater, the planting of 5 *Atriplex* species at a range of spacings caused chloride accumulation in the soil profile equivalent to the evapotranspiration of ~60-100 mm of groundwater. Over two years the growth of plants increased average Cl^- concentrations from 0.3 to 0.4 % dry soil at 0.4 to 0.6 m depth in the soil profile; this accumulation was proportional to the *Atriplex* leaf DM per m^2 soil surface area (Malcolm et al., 1988; Barrett-Lennard and Malcolm, 1999).

2.2. Impact of waterlogging

Much of the world's saline land is also subject to waterlogging (saturation of the soil) (Barrett-Lennard, 2003; Colmer and Flowers, 2008; Bennett et al., 2009). This arises because salinity is caused by the presence of shallow watertables or decreased infiltration of surface water due to sodicity. In many higher plants, waterlogging under saline conditions causes increased Na^+ and Cl^- concentrations in the shoot, which has adverse effects on plant growth and survival (reviewed by Barrett-Lennard, 2003; Colmer and Flowers, 2008). However, halophytes may be more tolerant to this combination of stresses than non-halophytes. In a survey of 24 higher plants, 17 species had a decrease in shoot DM with waterlogging under saline conditions, but seven species (all halophytes) had increased growth with waterlogging under saline conditions, and for three of these species (all from the genus *Puccinellia*) the ratio of shoot DM under saline-waterlogged conditions to shoot DM under saline-drained conditions ≥ 2.5 (Jenkins et al., 2010).

3. Defining feeding value

Feeding value is defined as 'the animal production response to grazing a forage under unrestricted (i.e. unlimited biomass) conditions' (Ulyatt, 1973). Feeding value therefore impacts on production of meat, milk and wool. It is a function of voluntary feed intake (VFI, what the animal chooses to eat and the quantity eaten) and nutritive value (NV) of ingested biomass. Determining the feeding value of forages is complicated by the fact that when given a choice, herbivores rarely eat monocultures of a particular feed and individual animals can meet their needs through different feed combinations (Provenza et al., 1995). For grazing systems, it is therefore important to consider possible interactions between halophytes, annual non-halophytes that exist in the same environment and opportunities to supplement animals with complementary feeds to meet nutritional requirements. Although provision of supplements to ruminants can be used to overcome constraints in feeding value, supplementation involves varying economic, labour and transport costs. Where possible, agronomists should aim to maximise the feeding value of halophytes in order to reduce reliance on supplementary feed. To illustrate this point, whole-farm bio-economic modelling by O'Connell et al. (2006) suggested that the most critical factor influencing the profitability of extensive saltland pasture systems in southern Australia was their NV. They estimated that a 10% increase in digestibility (energy value) of halophytic shrubs would lead to a doubling of pasture profitability on saltland. Furthermore, improving digestibility by 10% was 3-times more profitable than increasing biomass production by 10% or reducing the economic cost of pasture establishment by 10% (O'Connell et al., 2006).

In intensive, confined feeding systems, the digestibility of forage may not be considered as important if it is provided in a mixed ration as a source of fibre or protein in conjunction with other high-energy supplements. Examples of such systems can be found in the USA and Eastern Mediterranean (Glenn et al., 1992; Alhadrami et al., 2005; Al-Shorepy et al., 2010). While the halophytes in these systems are generally only 30-50% of the diet (DM basis), it is likely that improving the digestibility or content of nutrients such as crude protein in these forages could still lead to increased profitability. The argument for doing this may be even more compelling if the high-energy supplements that are used in these systems are grains (rather than manufacturing by-products); in such cases the total profitability of the system might be maximised by selecting forages with increased NV, requiring the purchase of less grain on the market.

NV and VFI are inter-related. In this review we have attempted to separate the mechanisms with a consequence that factors such as digestibility, salt and toxins can be discussed in two sections – one with a focus on the impact on intake, the other with a focus on animal performance given that the animal has eaten the forage.

4. Nutritive value

NV refers to the responses in animal production per unit of VFI and is a function of the digestibility of the nutrients and the efficiency with which the nutrients are used for animal maintenance or production (SCA, 2007). There is a range of characteristics that collectively contribute to NV. For salt tolerant plants the most significant of these is metabolisable energy (ME), which is a function of the digestible organic matter in the dry matter (DOMD). The relationship between DOMD and ME for traditional roughage-type forages is generally regarded as linear, for example; ME per kg DM (MJ at the maintenance level of feeding) = 0.194 * %DOMD -2.577 (SCA, 2007). Concentrations of crude protein (CP), minerals, and secondary compounds also contribute to NV and are important considerations for halophytic forages (Masters et al., 2007).

. *4.1 Metabolisable energy*

In general the ME value of most halophytic forage species will be lower than in non-halophytic forages because the DOMD is low. Fig. 3 compares the nutritive value of a range of halophytic forages with two non-halophytic roughages, lucerne chaff (*Medicago sativa* and a clover/oaten hay (*Trifolium incarnatum/Avena sativa*; data from Bustan et al., 2005; Norman et al., 2009; 2010a). In this figure ‘edible’ DM (leaves and small stems < 3 mm in diameter) is divided into DOMD, indigestible OM organic matter (OM) (no energy value; generally indigestible fibre that is excreted in the faeces), insoluble ash and soluble ash. The amount of DOMD was lowest for *Acacia saligna* (35%). Chenopods, including *M. brevifolia* and three species of *Atriplex*, ranged from 43 to 62% and the halophytic grasses ranged from 48 to 58%. In contrast the DOMD of two non-halophytic fodders (lucerne chaff and clover/oaten hay) were 64% and 66% respectively. To put these values in perspective, Fig. 4 illustrates the predicted liveweight change of mature ewes (non-reproducing or lactating with twins at foot) offered unlimited quantities of roughage-only diets with various levels of DOMD (data are derived from the ruminant nutrition model Grazfeed; Freer et al., 1997). The non-reproducing ewes should maintain liveweight with forage of 57% DOMD (8.5 MJ/kg DM), but lactating ewes with twin lambs need a higher energy (concentrate) supplement to prevent weight loss. Some of the DOMD data from Fig. 3 have been superimposed on Fig. 4 to demonstrate how the energy value of these forages would impact on ruminants. It is important to note that any effects of high salt or negative secondary compounds are not accounted for in this analysis, so the actual value of the forages would be somewhat lower than indicated in Fig. 4. Lack of energy would be a major limitation for ewes grazing monocultures of the majority of these halophytes and this limitation would be compounded by the extra energy required for reproduction. Fig. 4 also shows the relative high value of small changes in DOMD to livestock production.

**Figs 3 and 4 near here, adjacent if possible

REPRODUCE FIG. 4 IN COLOR ON WEB, BLACK AND WHITE IN PRINT**

It is likely that the ME content of a range of halophytes could be increased but DOMD needs to be tested across a range of environments. There is apparent variation in DOMD both between and within halophytic species (e.g. for *A. nummularia* and *D. spicata* in Fig. 3). With only a few exceptions however, apportioning within species variation to genetic or environmental influences is not easily resolved within the current literature, although several recent studies indicate a genotype by environment interaction for ME content. In an assessment of 19 species from the salt-tolerant legume genus *Melilotus* grown at four levels of salinity (0 - 240 mM NaCl) there were differences in total energy value between species (dry matter digestibility adjusted for soluble salt) and differences in the energy response of species to increasing salt (Rogers et al., 2008). Within this study, the estimated energy value of *M. siculus* changed very little with increasing salinity, whereas, *M. speciosus* had an estimated decline in ME of 1.7 MJ/kg DM (from 10.5 MJ/kg at 0 mM NaCl to 8.8 MJ/kg DM at 240 mM NaCl). Put into production terms, a 50 kg wether would be expected to grow at a rate of approximately 165 g/day when grazing *M. speciosus* growing at zero salinity, but only 50 g/day when grazing *M. speciosus* growing at 240 mM NaCl (animal growth estimated using GrazFeed; Freer et al., 2007). In another study, there was significant variation in DOMD between 6 clones of *A. amnicola* and a significant genotype x salinity interaction for ME when these clones were irrigated with solutions containing 0–400 mM NaCl (Masters et al., 2010).

Halophytic grasses are characterised by high levels of indigestible fibre (Fig. 3). There are few publications where the digestibility of halophytic grasses has been determined *in vivo* as the total diet. This is not surprising as modern animal ethics protocols dictate that if feeds of poor NV cause rapid loss of animal liveweight, then experiments must be terminated.

Published results with ruminants usually focus on using such plants to provide forage in a mixed ration. Under such circumstances *D. spicata* and *S. virginicus* have been used to replace traditional, low quality, non saline forages in systems where diets are supplemented with high energy concentrates (Al-Shorepy et al., 2010; Alhadrami et al., 2003; 2005). Interactions between the salinity of the environment and the energy or fibre value of grasses are rarely large and not consistent. In one experiment, Robinson et al. (2004) irrigated various halophytic grass species with water with salinities of 15 or 25 dS/m and measured neutral detergent fibre (NDF) in the biomass. NDF increased by 5% with salinity for *C. dactylon* ($P < 0.05$), decreased by 3% for *T. ponticum* ($P < 0.05$) and did not differ significantly for *P. clandestinum* or *P. vaginatum* (Robinson et al., 2004). Pasternak et al. (1993) found no consistent relationship between fibre content of five halophytic grasses and soil salinity (EC_e 3.1 – 14 dS/m).

It is not possible to compare the energy value of many halophytic chenopods using published literature due to the use of inappropriate laboratory methods. Many *in vitro* methods of assessing NV that are designed for, and validated with, traditional forages such as cereal hays, are not appropriate for high salt accumulating plants (Masters et al., 2001; 2007). These methods subject DM to enzymatic or acid digestion and measure residual indigestible material (mostly fibre and insoluble ash) and therefore use indigestibility to predict digestibility. However, with halophytes the large soluble ash component of the DM may ‘appear’ to be digested with these common *in vitro* methods (Masters et al., 2001). Even if soluble salt is accounted for in the estimation of OMD, high soluble salt incurs a metabolic energy cost for an animal to process which can lower the efficiency of the conversion of digestible energy (energy consumed minus energy in faeces) to ME by up to 10% (Arieli et al., 1989; Masters et al., 2005). Even when the zero energy value and energy cost of soluble ash is taken into account, the energy value may still be significantly overestimated (Norman et al., 2010a). It is probable that halophytic chenopods contain antinutritional factors other than salt that change the composition and function of the rumen microbes (Weston et al., 1970; Mayberry et al., 2010). Published results for salt-accumulating plants where *in vitro* methods are used (e.g. El Shaer et al., 2010 amongst many others) should therefore be treated with extreme caution. Studies where authors have used standard equations to convert fibre content of chenopods to OMD or ME may also be seriously flawed. While *in vivo* studies are ideal, there are opportunities to create and use *in vivo* standards to correct *in vitro* predictions, and *in vitro* methods measuring gas production (product of digestion of OM rather than residual biomass after digestion) from fodder samples that are fermented in rumen fluid avoid some of the problems described above (for further discussion see Norman et al., 2010a).

4.2 Protein and non-protein nitrogen

Ruminants have a minimum protein requirement for maintenance, growth and reproduction. Minimum protein requirements for adult sheep or cattle that are not reproducing or growing are 7 to 9%, and this increases to approximately 14 to 18% for growing or lactating animals (SCA, 2007). It is difficult to define specific requirements as a proportion of protein consumed is degraded by microbes in the rumen (rumen degradable protein). Depending on the amount of energy supplied by the diet, some of this degraded protein is converted back to microbial protein by the rumen microbes and then passes down the digestive tract for absorption as amino acids. Any protein in the diet that is resistant to microbial breakdown (undegraded dietary protein) passes through the rumen and may be absorbed in the lower gastrointestinal tract. Therefore protein available for absorption is dependent on the type of protein, the energy available for microbial protein synthesis, as well as the protein content of the diet. Crude protein (CP) is an estimate of true protein and is based on the assumption (certainly untrue for halophytes) that all nitrogen in the biomass is or will become protein; i.e. CP (%) = nitrogen (%) * 6.25 (SCA, 2007).

Table 2 presents CP figures for a range of halophytic species growing on 7 saline sites across Australia (141 samples, data from Norman et al., 2003; 2004). The six chenopods (including four *Atriplex* spp., *M. brevifolia* and *T. pergranulata*) had CP figures between 10 and 15 % DM (Table 2), and these figures would have been 13–21% if presented on an OM basis. The chenopods had higher CP than halophytic grasses growing in the same environment, with four grass species having mean CP of 5 to 8 % DM. Others report higher CP figures for halophytic grasses, for example, Al-Shorepy et al. (2010) report CP of 8.7 and 9.8 % DM in *S. virginicus* and *D. spicata* respectively. Low CP in grass may be improved through agronomic means; for example, fertilising halophytic grasses prior to harvest with nitrogen fertilizers (Alhadraimi, 2003) or regular cutting (Bustan et al., 2005) have both increased CP in halophytic grasses. Salinity may also impact on CP; irrigation with increasingly saline water (12.5 % seawater to 50 % seawater) increased CP of *S. virginicus* from 6.8 to 9.0 % (Ashour et al., 1997). However, the effects of increasing salinity on CP in grasses is not consistent; CP concentrations in *C. gayana* and *C. dactylon* were 11.5 % and 16 %DM respectively and there was no relationship between soil salinity (EC_e 3.1 – 12 dS/m) and CP content (Pasternak et al., 1993). The only legume reported in Table 2, *Melilotus alba*, had 13 % CP and this high CP is typical of legumes as they are able to fix nitrogen using *Rhizobia* in root nodules.

Table 2 near here

In halophytes CP figures may be inflated by nitrate and soluble non-protein compounds that are synthesised for osmoregulation, including glycinebetaine and proline (Le Houérou, 1992; Briens and Larher, 1982; Masters et al., 2001; Flowers and Colmer, 2008).

The relative use of glycinebetaine and proline for osmotic adjustment varies between species. For example, with *Halimione portulacoides* (family Chenopodiaceae), the ratio of glycinebetaine to proline in leaves was ~85 : 1, whereas with *Puccinellia maritima* (family Poaceae), this ratio was ~1 : 48 (Storey et al., 1977). All halophytes would be expected to have increased concentrations of compatible solutes with salinity. Typical examples of such increases include 2- and 7-fold increases in glycinebetaine and proline respectively in leaves of *Atriplex spongiosa* as NaCl in the root-zone increased from 0 to 750 mM, and 1- and 7-fold increases in glycinebetaine and proline respectively in leaves of *Suaeda monoica* as NaCl in the root-zone increased from 0 to 1000 mM (Storey and Wyn-Jones, 1979). *Portulaca oleracea* is a widespread weed of saline systems and is considered a halophyte (Aronson, 1989; Yazici et al., 2007). Proline concentrations in leaves of this species increased by 73% and 100% with 70 and 140 mM NaCl respectively (compared to low salt controls) over 18 days. Leaves of *Atriplex* spp. have been reported to contain up to 30 g /kg DM glycinebetaine (Storey et al., 1977).

These non-protein N compounds may have positive, negative or relatively neutral effects on ruminants. Glycinebetaine can be involved in protein and energy metabolism as a methyl donor and assists in production of choline and recycling of amino acids that are essential for muscle growth (Ekland et al., 2005). Glycinebetaine therefore benefits meat production systems by increasing lean: fat ratio in meat thus improving carcase composition (Fernandez et al., 1998; Pearce et al., 2010). Unfortunately, more than 50% of glycinebetaine in the diet of ruminants is degraded in the rumen and this increases if the diet is energy deficient (Mitchell et al., 1979). Proline is a small amino acid that can be absorbed directly into the small intestine and is associated with collagen as hydroxy proline (McDonald et al., 2002). While important for growth and production, ruminants are generally able to synthesise enough to meet their requirements (McDonald et al., 2002). Proline concentration in biomass therefore does not have a negative effect or a largely positive effect on ruminant production. Nitrates can have toxic effects on ruminants at concentrations in excess of 5000 mg/kg DM (National Research Council, 1974) and concentrations over 8000 mg/kg DM have been shown to depress herbage intake by over 60% (Burritt and Provenza, 2000). For the 6 unfertilised chenopod species listed in Table 2, average nitrate concentrations in the leaves were in the range 130 – 1139 mg nitrate/kg DM, with the highest value being for *M. brevifolia*. Of the individual *M. brevifolia* plants tested, one had ~3000 mg nitrate/kg DM in a degraded and unfertilised pasture (Norman et al., 2002). Clearly, the case for nitrate toxicities in halophytes cannot yet be made based on these data, but care might need to be taken with heavily fertilised pastures.

Soluble non-protein N compounds are only converted to protein in the rumen if there is sufficient ME (SCA, 2007). If ME is limited, some of these compounds would be converted to ammonia in the rumen, which is absorbed by the animal, converted to urea and excreted in the urine (SCA, 2007). In *Atriplex barclayana* 42% of the nitrogen was non-protein in origin (Benjamin et al., 1992). Regardless of protein/non-protein ratios, the nitrogen content of chenopods is a valuable component to many ruminant feeding systems and may be sufficient to meet animal needs (Ben Salem et al., 2010). For example, in a full nitrogen balance study, sheep fed *A. nummularia* had a positive nitrogen status and achieved ~150% of their maintenance requirement (Abou El Zasr et al., 1996). Ben Salem et al. (2010) reviewed the amino acid composition of *Atriplex nummularia* and did not identify any notable deficiencies in the amino acids that ruminants cannot synthesise.

4.3 Sulphur

It is recommended that sulphur in the diet for sheep and cattle is 0.2 and 0.15 %DM respectively (SCA, 2007), and plants generally have concentrations of S between 0.05 and 0.5 %DM (Underwood and Suttle, 1999). S is used primarily in conjunction with N for the production of ruminal microbial protein and an N: S ratio of 12.5: 1 is considered optimal for sheep (SCA, 2007). S is essential for synthesis of structural proteins and is a component of three amino acids (cystine, cysteine and methionine), several vitamins, the hormone insulin and coenzyme A (McDonald et al., 2002). S deficiency limits liveweight gain, and as wool contains about 4% S, deficiency is especially problematic within wool production systems (McDonald, 2002; SCA, 2007). From the species listed in Table 2, grasses such as *T. ponticum* and *P. ciliata* (0.13–0.16 %DM) would be deficient in S for sheep.

S toxicity occurs when degradable S is not converted to ruminal protein but is converted to sulphide in the rumen. Sulphide reduces rumen motility, decreases VFI, causes damage to the central nervous system and induces Cu deficiency through reduced Cu absorption (Underwood and Suttle, 1999). Halophytic chenopods such as *A. amnicola* and *A. nummularia* typically exceed recommendations with concentrations of S ranging from 3.8 to 4.9 g/kg DM, with N: S ratios between 5.7: 1 and 3.7: 1 (Norman et al., 2004; 2008). Grasses may also accumulate S; the *P. vaginatum* in Table 2 had a mean S of 0.36 %DM (N:S ratio of 4:1).

4.4 Minerals

Halophytic grasses differ from chenopods in their method of osmotic adjustment, which impacts particularly on the mineral contents of the edible biomass. In the grasses, tolerance to salinity is based primarily on maintaining low salt concentrations in the leaves – achieved through a combination of Na^+ and Cl^- exclusion at the root surface, secretion of these ions from the leaves in some cases, and the use of ‘compatible’ organic solutes for osmotic adjustment. In contrast, with the chenopods tolerance to salinity is based more on the uptake of Na^+ and Cl^-, and the compartmentation of these ions in vacuoles where they play the major role in osmotic adjustment (reviewed by Flowers and Colmer, 2008).

Ash is the term used to describe the components of a tissue not combusted during exposure to high temperature (reaching 550^{o}C before cooling; Faichney and White, 1983), and DM minus ash is OM. A high ash concentration decreases the value of halophytes as forages because: (a) energy for the animal only comes from the digestion of the OM as ash has no energy value, and (b) the animal may need to spend more energy in excreting soluble components of the ash such as NaCl and KCl (Arieli et al., 1989). In addition, the concentrations of individual minerals within the ash may be deficient for animal needs, toxic or induce deficiencies (Masters et al., 2007, Norman et al., 2004; 2008). Manipulation of the relative proportions of Na^+ and K^+ in DM of plants with a high ash concentration is unlikely to provide benefits for animal production (Masters et al., 2005).

Chenopods have much higher levels of ash in DM than halophytic grasses or legumes. The data in Table 2 are typical; the grasses and legumes had mean ash levels less than 10% DM, values typical of non-saline forages (SCA, 2007). The highest ash content reported for a grass was 15.5 % for *P. vaginatum.* In comparison, with the chenopods the range of ash concentrations was 13 to 34 %DM, with means ranging from 20 to 27 %DM (Table 2). The highest level of ash reported for a chenopod was 42 % for *A. nummularia* (Pasternak et al., 1985; 1993). Most of the ash in chenopods is soluble with ~5 %DM as insoluble ash (Fig. 5). For halophytic grasses and legumes, less than 40% of the total ash is in the form of Na^+, K^+ or Cl, whereas for halophytic chenopods 63 to 81% of the ash is as these ions (Table 2). Halophytic grasses and chenopods also differ in the relative uptake of Na^+ and K^+ with grasses favouring K^+ uptake (Albert and Popp, 1977); in support of this, the ratio of K^+/Na^+ (molar basis) for the 6 chenopod species listed in Table 2 varied from 0.09 to 0.27, whereas for the grasses and legume this ratio was between 0.8 and 2.5.

In addition to having differing internal ion regulation, halophytes can vary in the development of leaf glands, which excrete Na^+ and Cl^-, decreasing salt in the biomass (Flowers and Colmer, 2008). This capability therefore also impacts strongly on the salt concentration in the biomass consumed by ruminants.

Figs 5A and 5B near here

Increasing salinity in the soil solution leads to changes in the composition of biomass and there are hundreds of published experiments that have shown relationships between internal and external concentrations of ions for a wide range of plants. Here, we cite two examples: the relationship between ash concentrations in 6 clones of *Atriplex amnicola* grown in the glasshouse with 0 to 400 mM NaCl in the irrigation solution (Masters et al., 2010; Fig. 5A) and the correlation between the concentration of chloride in leaves of 5 *Atriplex* species and the salinity of the soil solution at 20-40 cm 20 months earlier (calculated from the notes of the late C.V. Malcolm and Malcolm et al., 1988; Fig. 5B). In each of these cases, one from the glasshouse and the other from the field, the ash or chloride concentration in the leaves increased with the external salinity of the growth medium. The relationship may not be as well-defined in halophytic grasses. Pasternak et al. (1993) did not observe a consistent relationship between soil salinity (EC_e 3.1 – 14 dS/m) and ash content in the halophytic grasses *C. gayana, D. spicata, C. dactylon* and *P. vaginatum.*

Another consequence of salt accumulation is a change in leaf succulence (defined here as g water /g OM). The development of succulence is partly an environmental response: in many halophytes increases in external salinity cause an increase in leaf thickness (eg.

Aslam et al., 1986) or the degree of tissue hydration (e.g. water as %DM; Handley and Jennings, 1977; Glenn and O'Leary, 1985). Fig. 6A shows the relationship between water content and ash concentrations for the leaves of 10 dicotyledonous euhalophytic species from the study of Glenn and O'Leary (1985). *Atriplex lentiformis* had both the lowest water content (2.4 g/g OM) and ash concentration (15.9% DM), and *Salicornia europaea* had both the highest water content (23.7 g/g OM) and highest ash concentration (51.4% DM). A line of best fit between tissue water content and ash concentration compiled using the data for all 10 species was significant at $P < 0.001$. Succulence in itself is not of importance to ruminants; the concentration of OMD per unit of salt intake is the critical factor and the water content of the forage has little consequence. However measuring succulence (ratio of fresh matter/DM) offers an opportunity to rank genotypes for ash content without additional laboratory analyses. For example, in the *Atriplex amnicola* clone experiment previously mentioned (Masters et al., 2010), the lowest average ash concentrations (~23% DM) occurred with Clone 2 which had the least succulent tissues (tissue water 4.9 g water/g OM), the highest ash concentrations (29% DM) occurred in Clone 6 which had the most succulent tissues (tissue water 7.7 g water/g OM), and the line of best fit between rating ash concentrations to tissue water concentrations was significant at $P < 0.001$ (Fig. 6B).

Figs 6A and 6B near here

The consumption of salt accumulating shrubs can have other disadvantages as well as advantages for the mineral balance of ruminants. Potential toxicities in grazing ruminants can come from excess S (described in the previous section), B in *Atriplex* species (Norman et al., 2004; Grattan et al., 2004; Ben Salem et al., 2010) and Se in the halophytic genus *Leymus* (Suyama et al., 2007). On the other hand halophytes may also supplement ruminants with essential minerals that were otherwise deficient in the diet. Halophytes, both grasses and chenopods, easily exceed Na, K and Cl requirements for sheep and cattle (Table 2) and may provide a valuable source of these ions for grazing animals as part of a mixed ration. Na, K and Cl have an electrochemical function in ruminants and are associated with maintenance of acid-base balance, membrane permeability and the osmotic control of water in the body (McDonald, 2002). Fe, Mg, Zn and Mn also occur in halophytes in concentrations in excess of recommended requirements (Table 2). These are also essential to ruminants. Fe is associated with haemoglobin and enzymes, and deficiency leads to anaemia, Mg is in bone and has a role in enzymes relating to metabolism, Zn is in enzymes and deficiency leads to poor growth, and Mn is also associated with enzyme function, and deficiency leads to poor growth and skeletal abnormalities (McDonald et al., 2002). The Ca and P concentrations of halophytes in Table 2 appear to meet the requirements for maintenance but may not be sufficient for lactation (upper end of requirement figures). Both of these minerals are essential for bone and teeth, Ca has an additional role in transition of nerve impulses and P has a role in energy metabolism (McDonald et al., 2002).

Unfortunately, complex mineral interactions within plants and animals can make it difficult to assume that ruminant mineral requirements are met, even if there appears to be enough (or excess) of a particular mineral in plant biomass. In the *A. amnicola* experiment previously referred to (Fig. 5A) in which clones were grown at 0-400 mM NaCl, the concentrations of K, Ca, P, Cu and Zn were all inversely related to the concentration of Na in the plant tissue (Masters et al., 2010). Recent experiments have shown that the feeding of *A. nummularia* as the sole source of feed can cause mineral imbalances in sheep (Mayberry et al., 2010). Sheep were allowed to adapt to the feed for 3 weeks; over a subsequent week the animals had net losses (intake minus faeces, although further losses may have occurred in urine) of Mg (0.83 g/day), Ca (0.61 g/day) and P (0.46 g/day). This occurred despite the diet containing well above the minimum requirement for these minerals. In comparison, with animals fed cereal hay based diet with equivalent concentrations of added NaCl and KCl there was no effect on the apparent digestion or absorption of any of these elements. These results indicate that *Atriplex* forage as a sole source of feed may be unsuitable for ruminants with high nutritional demands, and further research is required to fully assess the mineral balance of animals consuming a wider range of chenopods. Others to note low Ca concentrations in blood or a net Ca loss when grazing saltbush include Franklin-McEvoy and Jolly (2006) and Aazzeh and Abu-Zanat (2004).

4.5 Organic acids

Halophytes use organic acids for osmotic adjustment and as anions to achieve cation-anion balance. From the point of view of NV, the most important of these is the divalent anion oxalate, although trivalent citrate can occur in some species, and malate also occurs widely at lower concentrations (Albert and Popp, 1977; Briens and Larher, 1982). In a survey of 21 halophyte species from the Neusiedler Lake Region in Austria, 5 species from the *Chenopodiaceae* and 1 species from the *Caryophyllaceae* had oxalate concentrations of more than 50 mM (plant water basis) accounting for 26-62% of total anionic charge; if these tissues had had a fresh matter to DM ratio of 12 (cf. Storey and Wyn-Jones, 1979) this would have been equivalent to at least 5 %DM. In the same survey, one species (from the *Brassicaceae*) had a citrate concentration of more than 70 mM (plant water basis), accounting for 21% of total anionic charge (Albert and Popp, 1977); with fresh matter/DM = 12, this concentration would have been equivalent to ~15 %DM.

Forage halophytes from within *Atriplex* and *Maireana* can produce substantial oxalate (Osmond, 1963; Albert and Popp, 1977; Davis, 1981). To illustrate oxalate's role in cation-anion balance in *Atriplex* species, we correlated the difference between total cation charge and total anion charge against oxalate concentration using some of our data for *A. amnicola* and *A. nummularia*. The data (Fig. 7) are significantly ($P = 0.012$) correlated, with divalent oxalate accounting for ~40% of the net difference in total charge between cations (Na^+, K^+, Mg^{2+} and Ca^{2+}) and anions (Cl^-, NO_3^- and $H_2PO_4^-$). The oxalate concentrations in Fig. 7 are equivalent to ~2–5 %DM, and these values are within the range reported for leaves of *Atriplex* spp. in other studies (e.g. 3.7 to 6.6 %DM; Malcolm et al., 1988). Osmond et al. (1967) found that 75% of excess cations in *Atriplex spongiosa* were balanced by oxalate.

Fig. 7 near here

Many chenopods have concentrations that approach toxic thresholds for oxalate (Masters et al., 2001). Oxalic acid inhibits several respiratory enzymes and reduces blood calcium concentrations by forming insoluble calcium oxalate in the body (Cheeke, 1998). Calcium deficiency leads to rickets, poor bone growth and milk fever (McDonald et al., 2002) and precipitation of calcium oxalate in the rumen and kidneys and this can lead to kidney damage, rumen stasis and gastroenteritis. Herbage with more than 7 % DM oxalate has been shown to cause acute poisoning in ruminants (Hungerford, 1990). Sheep however are able to detect oxalates in feed and if given a choice can adjust VFI; for example, lambs offered a diet containing 3 %DM oxalate ate half the amount of DM as lambs offered a similar diet without the oxalate (Burritt and Provenza, 2000). Oxalate could potentially bind to other minerals such as Mn, Fe, Cu and Zn. Our analysis of the data in Fig. 7 and the results of Osmond et al. (1967) suggest that the oxalate concentration in the leaves would have been sufficient to bind all the Ca^{2+} in 14 of the 15 genotypes sampled. Oxalate is the likely contributor to the loss of Ca in sheep grazing *A. nummularia* (reported by Mayberry et al., 2010) and discussed earlier. The provision of Ca feed supplements to animals is a tool that might substantially improve the utilisation of halophytes with high oxalate concentrations in the leaves. Villalba et al.

(2006) demonstrated that sheep fed oxalates learnt to eat calcium supplements to self-medicate.

4.6 Antioxidants

In plants, α-tocopherol is located in chloroplasts on thylakoid membranes, and its biosynthesis is thought to protect lipids from peroxidation by photosynthesis-derived reactive oxygen species (Munné-Bosch, 2005). Concentrations of α-tocopherol change significantly during plant growth and in response to environmental stress (Munné-Bosch, 2005). In ruminant nutrition α-tocopherol is commonly known as Vitamin E, and it is a powerful antioxidant associated with green (photosynthetic) plant material. Deficiency can cause nutritional myopathy and death (Gardiner, 1962). A recent survey has shown that 58% of recently weaned sheep flocks in the Mediterranean-type climate areas of Australia had Vitamin E deficiency when sampled in autumn, with 6% showing symptoms of severe muscle damage (White and Rewell, 2007). Vitamin E from *Atriplex* spp. slows the oxidation of lipids in meat and delays the oxidative change of oxymyoglobin to brown metmyoglobin, thus improving both the flavour and increasing the shelf-life of meat (Pearce et al., 2005; 2010). *Atriplex* species have been reported to contain α-tocopherol at concentrations of 116 to 139 mg/kg DM (Pearce et al., 2005).

Vitamin A is another antioxidant that has been reported at high concentration (e.g. 41 mg/kg DM in *A. nummularia*) in halophytic shrubs (Aguer, 1973; Ben Salem et al., 2010). For humans and ruminants, Vitamin A has a role as an antioxidant, inhibiting the development of heart disease and improving vision, bone growth, reproduction and immune response (SCA, 2007; Palace et al., 1999). Vitamin A is stored primarily as long chain fatty esters and as provitamin carotenoids in the liver, kidney and adipose tissue (Palace et al., 1999). As for Vitamin E, the risk of deficiency for ruminants is greatest in animals that do not have access to green feed during droughts, and this risk is exacerbated by feeding high concentrations of grain (SCA, 2007).

5. Voluntary feed intake

Variation in VFI accounts for at least 50% of the variation that is observed in the feeding value of forages (Ulyatt, 1973). Ruminants select a diet that is higher in digestible nutrients and lower in toxins than the average of available plant material on offer, indicating that feed selection is not random (Forbes and Mayes, 2002). The term palatability incorporates flavour, social learning and post-ingestive feedback cues from nutrients and toxins (Provenza and Pfister, 1991) and will vary according to choices on offer to the animal (relative palatability). Herbivores use flavour (sensory receptors in the mouth and nose) and vision to link information from chemo-receptors, osmo-receptors and mechano-receptors (Provenza et al., 2003). Intake is influenced primarily by hunger, which is distressing, and by satiety, which is pleasurable (Forbes, 1995). Nutrients and toxins both cause animals to satiate and excesses of nutrients, nutrient imbalance and toxins all limit food intake (Provenza et al., 2003).

5.1 Fibre and physical constraints

Weston (1996) proposed that VFI of forages is regulated by interplay between the rate of clearance of dry matter from the rumen and the amount of useful energy that is available to the animal, relative to the animal's capacity to use the energy. The resistance of forage organic matter pass from the rumen (i.e. the indigestibility of fibre) therefore limits intake. A reduction in indigestible fibre digestibility of poor quality forage will allow the potential rate of feed intake to increase. As discussed earlier, the halophytic grasses have high indigestible fibre so improving DOMD should lead to an increase in potential voluntary feed intake.

Potential intake is also a function of the quantity of herbage available, the spatial distribution of herbage, heterogeneity of species within the sward, bite rate, bite frequency and sward structure (SCA, 2007). For sheep grazing pasture it is estimated that when DM falls below 2 t/ha, the ability to meet potential intake declines (SCA, 2007). Compared to herbaceous annual pastures, fodder shrubs have a greater spatial distribution (or lower bulk density) of edible nutrients (Warren and Casson, 1993). Although data are scarce, it is reasonable to expect that intake of woody halophytic shrubs may be limited by the high spatial distribution of biomass on branches. Picking leaves from twigs while avoiding injury to eyes is likely to take a greater amount of time and effort compared to cropping a dense grass sward (Norman et al., 2008).

5.2 Salt

Salt in the diet is associated with positive and negative effects on VFI, depending on concentration. From a low salt diet, an increase in salt intake increases water intake, which flushes partially digested biomass through the gut more rapidly (Hemsley et al., 1975) and therefore has the potential to increase feed intake as clearance from the rumen is faster. On the other hand, ruminants have a limited capacity to ingest, absorb and excrete salt. High concentrations of sodium chloride or potassium chloride in feed or water have been shown to depress food intake (Peirce, 1957; Wilson, 1966; Masters et al., 2005), and alter the size and frequency of meals (Rossi et al., 1998). Even with unlimited quantities of edible plant material on halophytic shrubs and unlimited fresh water to drink, high salt levels (more than 5%

of the diet) can cause a depression in VFI and therefore in feeding value (Masters et al., 2005). Poor animal performance from *Atriplex* spp. has often been attributed to low digestibility (Norman et al., 2008); however, depressed feed intake due to salt may have greater significance (Masters et al., 2005).

5.3 Toxins

High fibre and salt are not the only factors influencing VFI. Using compounds that cause malaise, it has been clearly established that ruminants develop learned aversions to toxins in plants (du Toit et al., 1991), as long as the toxin does not lead to death before the aversion is learnt. Rate of toxin intake is mediated by rate of detoxification and elimination from the body; these processes require energy, protein and water (Provenza et al., 2003). Anti-nutritional factors that are likely to depress VFI of halophytes include: alkaloids, steroids, saponins, flavonoides (Gihad and El Shaer, 1994), excessive selenium in irrigated *Leymus* spp (Suyama et al., 2007), coumarins in *Melilotus* spp (Macias et al., 1999), excessive sulphur and oxalates in *Atriplex* and *Pennisetum* spp. (Norman et al., 2004; Reeves et al., 1996), high tannins in *Acacia* spp (Degen et al., 2010) and nitrate accumulation in *Maireana* spp. (Table 2). Animals can learn to self-medicate and mix diets to manage toxins (see review by Provenza et al., 2003).

5.4 The role of relative palatability in plant improvement

Differences in the relative palatability of plants may allow agronomists to select halophytes with improved feeding value. Halophytes vary in relative palatability both between and within species (Le Houeróu, 1992; Norman et al., 2004; Degen et al., 2010). In

Australia, scientists observed that sheep grazing mixed *Atriplex* stands preferred one species to another and also exhibited strong preferences between individual plants within species (Norman et al., 2004). In a subsequent experiment, Norman et al. (2011) compared relative palatability between ‘wild’ provenances of *A. nummularia* (representing two subspecies) collected from 27 locations across Australia. The provenances were grown in two geographical locations that differed in soil type, rainfall and soil salinity (18,000 plants in each) and relative preference was assessed from the rate of defoliation using young sheep that were also offered *ad libitum* hay. There was a significant relationship in the relative preferences of sheep amongst provenances at the two sites ($R^2 = 0.83$, $P < 0.001$). One subspecies was consistently preferred to the other, and within the preferred subspecies, the sheep had similar likes and dislikes across the range of provenances at each site (Fig. 8). Analysis of provenances and families within provenances suggests that differences in relative palatability are genetic in origin (Norman et al. unpublished) and that this is therefore a trait of value for plant improvement.

Fig. 8 near here

We conclude this section with the thought that although NV and VFI are often related, there are forage characteristics that may also influence each independently. From the perspective of improving feeding value and therefore production potential, improving NV will often also improve both the conversion of feed into animal product and the voluntary intake of forage. If more productive biosaline systems are to be developed, it is this aspect of plant improvement that should be a priority. Differences in relative palatability may offer valuable information about NV without the need for extensive and costly laboratory screening of plant genotypes. Animals may indicate the presence of negative compounds that scientists have not yet identified as a priority for laboratory measurement.

6. Strategies for improving the feeding value and productivity of halophytes

There are significant opportunities to improve the feeding value of halophytes and therefore the productivity and profitability of saline systems. In this review we have identified low ME, mineral imbalances and toxins as constraints to livestock production and have identified variation in these traits associated with plant species and genotype within species. Improvements in feeding value and thus profitability could easily occur without a reduction in biomass production. There are 3 approaches that could be used to improve the feeding value of salt tolerant plants within farming systems: (1) identify, domesticate and introduce 'new' naturally salt tolerant plant species that have a higher feeding value, (2) identify and select accessions within existing plant species that have higher feeding value, and (3) introduce genes (through molecular or traditional breeding techniques) for salt tolerance into traditional pasture plants that have higher feeding value.

An example of the first strategy is the domestication and proposed introduction of the annual legume *Melilotus siculus* to Australia (Rogers et al., 2008; 2011). The focus of this project was to find an herbaceous pasture legume that tolerates a saline environment. In a series of glasshouse experiments, this species had higher salt and waterlogging tolerance than other *Melilotus* spp., had exceptional root aeration characteristics and good dry matter production (Rogers et al., 2008; 2011; Teakle et al., 2010). Like many annual herbaceous legumes, *M. siculus* had reasonably good NV with ME of 10-10.5 MJ/kg DM and only moderate ash accumulation (approximately 12% DM; Rogers et al., 2008). This species also has the potential to improve soil fertility through nitrogen fixation, so in a systems context its growth should assist in improving the growth and feeding value of adjacent halophytic grasses. Work continues to select salt and waterlogging tolerant *Rhizobia* for *M. siculus.*

An example of the second strategy is efforts to improve the feeding value of the ecologically adapted and widespread species *Atriplex nummularia* (Norman et al., 2010b; 2011). In this case, the focus of the plant improvement activity has been in improving feeding value by screening natural variation. For *A. nummularia*, the key selection criteria have been ME and relative palatability, with biomass production, CP, S and recovery from grazing forming secondary criteria. This is perhaps one of the first times that animals have been used in the initial stages of plant improvement programmes to identify plants with higher nutritive value. This project is showing promising results with significant variation in NV, relative palatability and biomass production between genotypes within species (See Fig. 2; Norman et al., 2010b; 2011). Mean predicted *in vivo* ME of leaves from provenances ranged from 6.6 to 9.3 MJ/kg DM, and crude protein ranged from 12 to 19 % DM (Norman et al., 2010b). While the project has not been completed, 90 elite genotypes have been selected from an initial population of 80 000 plants and these should have substantially higher feeding value (*in vivo* confirmation is in progress). Given anticipated genotype x environment interactions, these clones will be tested in a range of production environments prior to commercial release.

The third strategy, molecular or traditional breeding, is a long term and potentially more expensive strategy to implement given the complex nature of salt tolerance mechanisms (Flowers et al., 1977). The simplest molecular methods may involve targeting genes that synthesise compatible solutes such as glycinebetaine (Flowers et al., 1997). It may be possible to improve ruminant production outcomes by encouraging genes associated with production of ‘positive’ or ‘neutral’ osmoregulators from an animal’s perspective (e.g. glycinebetaine, even if a proportion is degraded in the rumen or proline) in preference to tackling the ‘negative’ osmoregulators (e.g. oxalate).

The cost of screening for aspects of NV and determining relative palatability remains a significant limiting factor for plant improvement activities. Further development and use of the derived relationships between *in vitro* and *in vivo* NV provide an opportunity to select for both NV and biomass production in halophyte selection programs. In future, the use of near infrared reflectance spectroscopy (NIRS) to predict aspects of NV will allow inexpensive screening and selection of large numbers of candidate plants (Shenk and Westerhaus, 1994). NIRS is widely used to predict the chemical composition of a range of biological samples. Until recently this technique had not been validated for halophytic shrubs however, robust NIRS predictions of NV for halophytic chenopods are under development (Norman and Masters, 2010). NIR prediction of NV would enable the widespread screening of genotypes across a range of environments.

7. Concluding remarks

Improving the feeding value of halophytes requires multidisciplinary research focusing on the need to improve NV and VFI as well as biomass production. Halophytes offer a range of nutrients for ruminants, but these may not be balanced as a diet and plants may also contain toxins. Livestock managers need to take advantage of the benefits of halophytes while managing their negative consequences. For many saline systems, this may be as simple as changing the type of plant or species, altering the management system, growing/feeding plant mixtures or providing other feed supplements.

The interactions between genotypes and their environment should not be overlooked in efforts to select genotypes with higher feeding value. While glasshouse environments are a useful place to start plant screening, only field-testing in environments with differing combinations of abiotic stress (e.g. salinity, waterlogging, flooding, soil acidity, drought) can provide confidence in the resilience and value of the proposed solutions. The need for extensive genotype x environment screening is likely to be higher for saline systems than non-saline systems due to the diversity and heterogeneity of saline environments.

There is a significant opportunity to improve the feeding value of species already in commercial use and select new species for domestication. Improving ME is the key factor as this is the major limitation of the vast majority of halophytes described in this review.

We conclude with a final speculative thought. In addition to improving ruminant health and productivity, the use of halophytic forages may offer an opportunity to improve human health. Almost half of the world's population suffers from micronutrient undernourishment. Deficiencies in Fe, Vitamin A and/or iodine occur in 2.15 billion people, ~40% of the world's total population, including most women and children in the developing world, together with a surprisingly large number in developed countries (World Bank, 1994; Welch and Graham, 1999). Other target micronutrients include Zn, Se, Cu, B, Mn, Cr, Li, Vitamin E, folic acid and Vitamin C (Welch and Graham, 1999). In Turkey, NATO has improved Zn uptake in the human population by fertilising the soil with Zn, thus increasing Zn in plants and animals (Cakmak et al., 1999). Halophytes have a well-developed ability to accumulate a range of minerals and antioxidants; they may therefore offer an opportunity to provide enriched meat and milk. Further work is required to define this opportunity.

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Table 1. Halophytes commonly used for forage production in saline systems.

Group	Genus	*Species*	References
Grasses	*Chloris*	*gayana*	Pasternak et al., 1993; Semple et al., 2003
	Cynodon	*dactylon*	Pasternak et al., 1993; Qureshi and Barrett-Lennard, 1998
	Diplachne	*fusca* (syn. *Leptochloa fusca)*	Qureshi and Barrett-Lennard, 1998
	Distichlis	*spicata*	Pasternak et al., 1993; Leake et al., 2002
	Leymus	*angustus*	Rogers et al., 2005
		triticoides	Rogers et al., 2005
	Paspalum	*vaginatum*	Semple et al., 2003
	Pennisetum	*clandestinum*	Semple et al., 2003
	Puccinellia	*ciliata*	Le Houérou, 1986; Jenkins et al., 2010
	Sporobolus	*virginicus*	Aronsen, 1989; Barrett-Lennard et al., 2003;
		airoides	Aronsen, 1989; Alhadrami et al., 2005
	Thinopyrum	*ponticum* (syn. *T. elongatum)*	Le Houérou, 1986; Jenkins et al., 2010
Chenopods	*Atriplex*	*amnicola*	Malcom and Swaan, 1989; Masters et al., 2010
		barclayana	Benjamin et al., 1992; Swingle et al., 1996
		halimus	Valderrabano et al., 1996
		lentiformis	Watson et al., 1987
		nummularia	Wilson, 1966; Watson et al., 1987; Norman et al., 2004
	Maireana	*brevifolia*	Malcom and Swaan, 1989
	Salicornia	*bigelovii*	Swingle et al., 1996
	Suaeda	*esteroa*	Swingle et al., 1996
Legumes	*Acacia*	spp.	Le Houérou, 1986
	Melilotus	*siculus*	Rogers et al., 2008; 2011; Teakle et al., 2010

Table 2. Mineral composition of a range of halophytic plants growing on seven saline sites across southern Australia (data from Norman et al., 2002; 2004).

Family/species	n	Total ash (%DM)	Ash range (% DM)	Na, K & Cl as % of total ash	CP (% DM)	S (% DM)	P (% DM)	Ca (% DM)	Cl (% DM)	Na (% DM)	K (% DM)	Mg (% DM)	Zn (mg/kg DM)	Mn (mg/kg DM)	Fe (mg/kg DM)	Nitrate (mg/kg DM)
Chenopodiaceae																
Atriplex amnicola	26	24.4	15-29	81	10	0.42	0.14	0.82	10.8	6.5	2.5	1.03	19.5	186	188	130
Atriplex semibaccata	6	21.3	16-27	63	11	0.31	0.21	0.56	6.5	5.5	1.5	0.69	29.0	83	415	389
Atriplex nummularia	42	26.7	13-33	78	15	0.48	0.15	0.76	10.4	7.1	3.2	0.72	18.2	116	231	230
Atriplex undulata	5	19.8	16-26	77	15	0.35	0.22	0.59	7.4	6.3	1.6	0.65	32.6	182	183	335
Maireana brevifolia	9	23.5	19-29	68	15	0.28	0.21	0.53	6.2	7.8	2.0	0.49	23.1	187	391	1139
Tecticornia pergranulata	7	27.3	20-34	79	11	0.39	0.19	0.46	12.4	7.9	1.2	0.85	31.7	55	277	624
Poaceae																
Hordeum marinum	14	7.6	4-11.8	28	5	0.12	0.13	0.20	1.0	0.5	0.7	0.18	18.4	57	367	60
Paspalum vaginatum	3	10.0	9-11	22	8	0.36	0.16	0.46	1.1	0.4	0.7	0.33	42.5	105	252	81
Thinopyrum ponticum	14	8.4	5-11	41	8	0.16	0.17	0.19	1.6	0.4	1.4	0.21	25.9	85	188	79
Puccinellia ciliata	7	5.1	5-7	39	5	0.13	0.14	0.15	0.9	0.3	0.8	0.14	17.3	51	128	54
Fabaceae																
Melilotus alba	8	7.4	6-11	52	13	0.25	0.16	0.60	1.8	0.4	1.7	0.67	14.7	21	156	61
Dietary recomendations[1]																
Sheep					7 - 18	0.20	0.09 - 0.3	0.14 - 0.70	0.03 - 0.1	0.07 - 0.10	0.5	0.09- 0.12	9 - 20	20 - 25	40	
Cattle					7 - 18	0.15	0.1 - 0.38	0.2 - 1.1	0.07 - 0.24	0.08 - 0.12	0.5	0.13 - 0.22	9 - 20	20 - 25	40	

[1] From SCA, 2007. Note these recommendations are approximate and change according to the physiological state of the animal

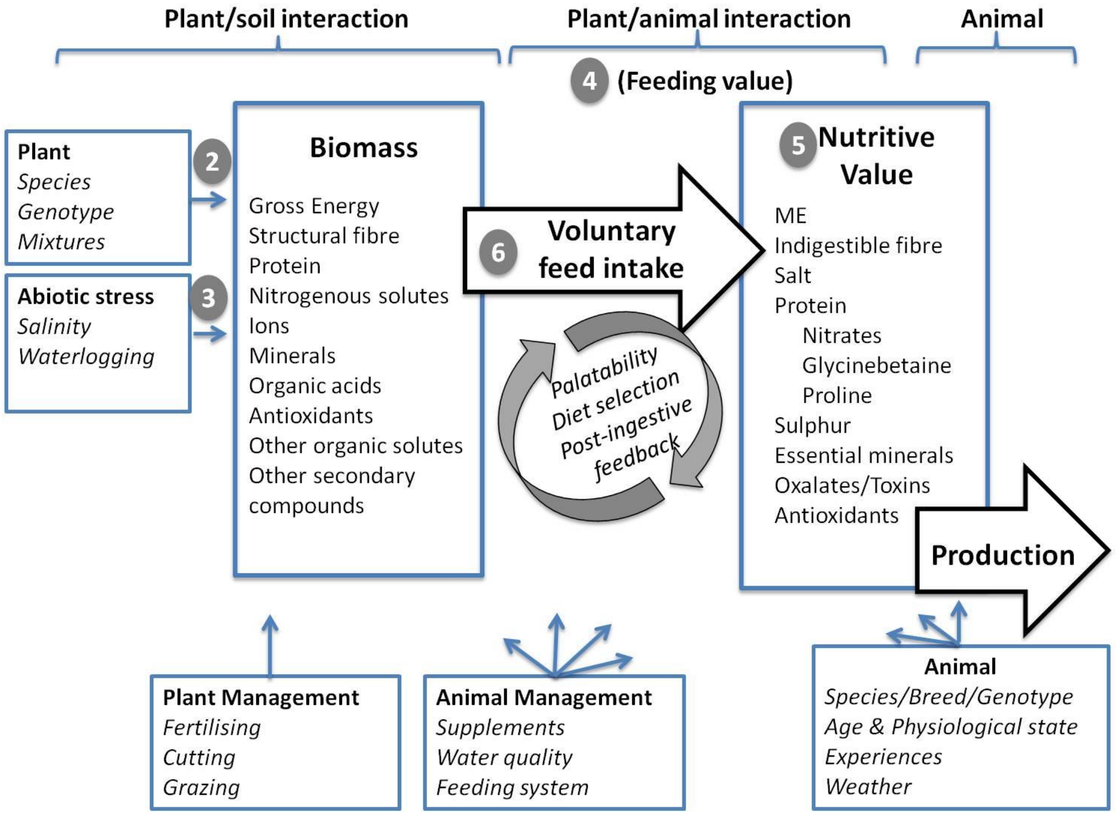


Fig. 1. Framework for thinking about the use of halophytes for livestock production. Livestock production depends on the utilisation of biomass. The quantity and chemical composition of biomass is a function of plant genotype, abiotic environment and management. Biomass has no value unless it is eaten and its chemical composition influences both voluntary feed intake and nutritive value. Feedback loops between the stomach and brain regulate diet selection and intake. Livestock production is also influenced by animal genotype and husbandry factors. This review focuses on the impact of salinity on chemical composition of biomass, intake and nutritive value; the numbered circles indicate the different section numbers of this review.

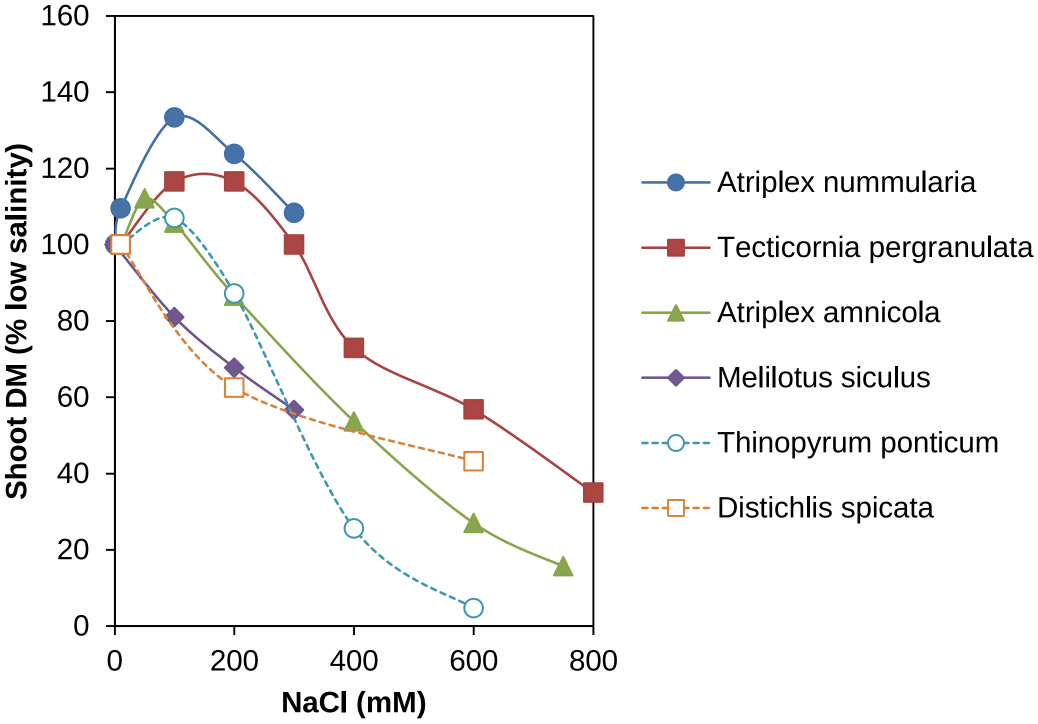


Fig. 2. Growth responses of halophytic forage species to salinity in nutrient solutions or irrigated sand cultures under glasshouse conditions. Dicotyledonous species (filled symbols, continuous lines) are: *Atriplex nummularia* (31 d; Greenway, 1968), *Tecticornia pergranulata* (83 d; Short and Colmer, 1999), *Atriplex amnicola* (21 d; Aslam et al., 1986) and *Melilotus siculus* (mean of 29 accessions; 21 d; Rogers et al., 2011). Moncotyledonous species (open symbols, dotted lines) are *Thinopyrum ponticum* (35 d; Jenkins et al., 2010) and *Distichlis spicata* (42 d; Leake et al., 2002).

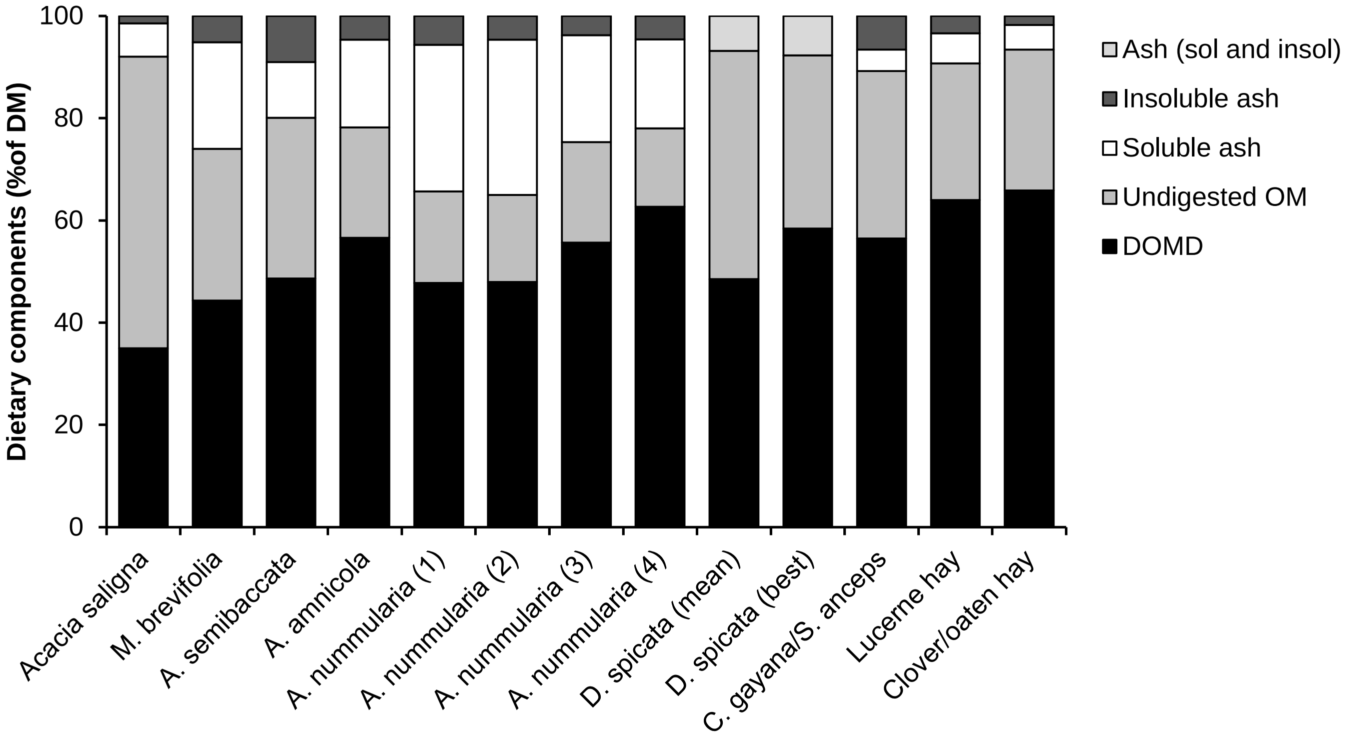


Fig. 3. Digestible organic matter in the dry matter (DOMD), indigestible OM and ash concentrations in a range of halophytic shrubs and grasses, and two non-halophytic feeds, lucerne chaff (*Medicago sativa)* and a clover/oaten hay chaff (*Trifolium incarnatum/Avena sativa*). Data for samples of *Acacia saligna, Maireana brevifolia, Atriplex semibaccata, Atriplex nummularia (4 provenances), Atriplex amnicola, Distichlis spicata* (mean of a group of genotypes and the best genotypes), a 50:50 mixture of *Chloris gayana*/*Setaria anceps* (Bustan et al., 2005; Norman et al., 2009; 2010). All data were derived through in vivo feeding experiments with sheep with the exception of *Distichlis spicata* which was derived by *in vitro* digestion using rumen fluid (Bustan et al., 2005).

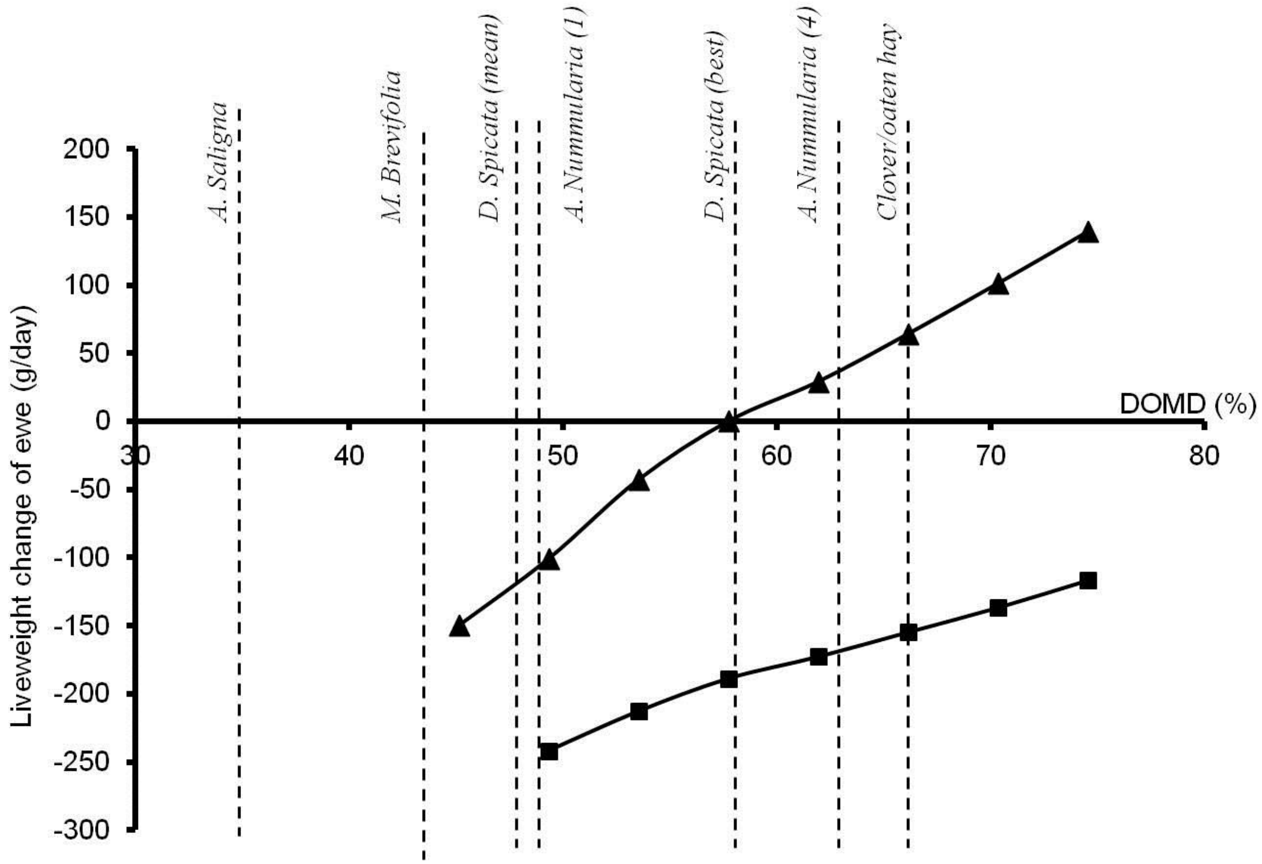
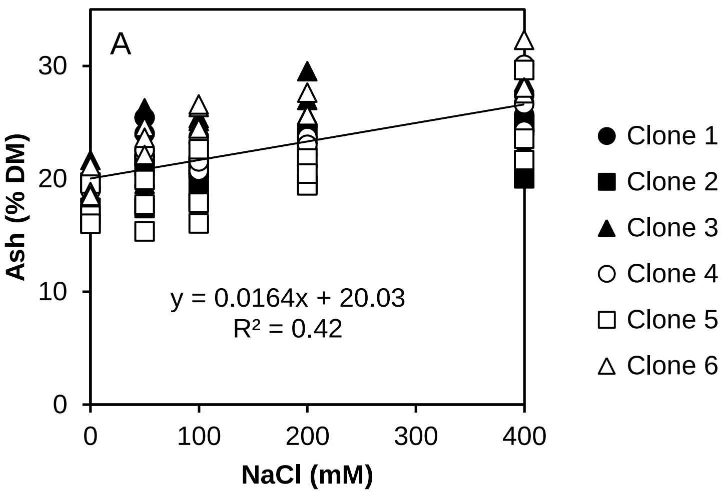


Fig. 4. Predicted relationship between DOMD of forage and liveweight changes for mature 60 kg Merino ewes that are either dry (▲) or lactating with twins 25 days after lambing (■). The data was generated using the ruminant nutrition model Grazfeed by 'offering' *ad libitum* hay supplements with DOMD values of between 45-85% and protein values of 15%.



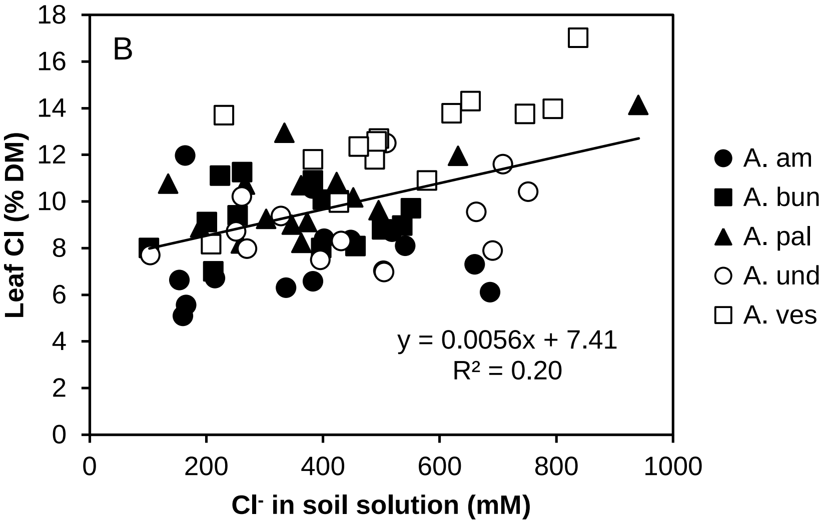


Fig. 5. Relationship between salinity of the external medium and leaf ash/leaf chloride. (A). Six clones of *Atriplex amnicola* with 3 replicates grown at 0-400 mM NaCl under glasshouse conditions (Masters et al., 2010). (B). Five *Atriplex* species with 3 replicates grown for 20 months in the field; chloride concentrations in leaves were related to concentration of Cl^- in soil solution (mM) 20 months earlier (calculated from data of the late C.V. Malcolm and Malcolm et al., 1988). Species are: A. am (*Atriplex amnicola*), A. bun (*Atriplex bunburyana*), A. pal (*Atriplex paludosa*), A. und (*Atriplex undulata*), and A. ves (*Atriplex vesicaria*). The lines of best fit (both significant at $P < 0.001$) are for composite data.

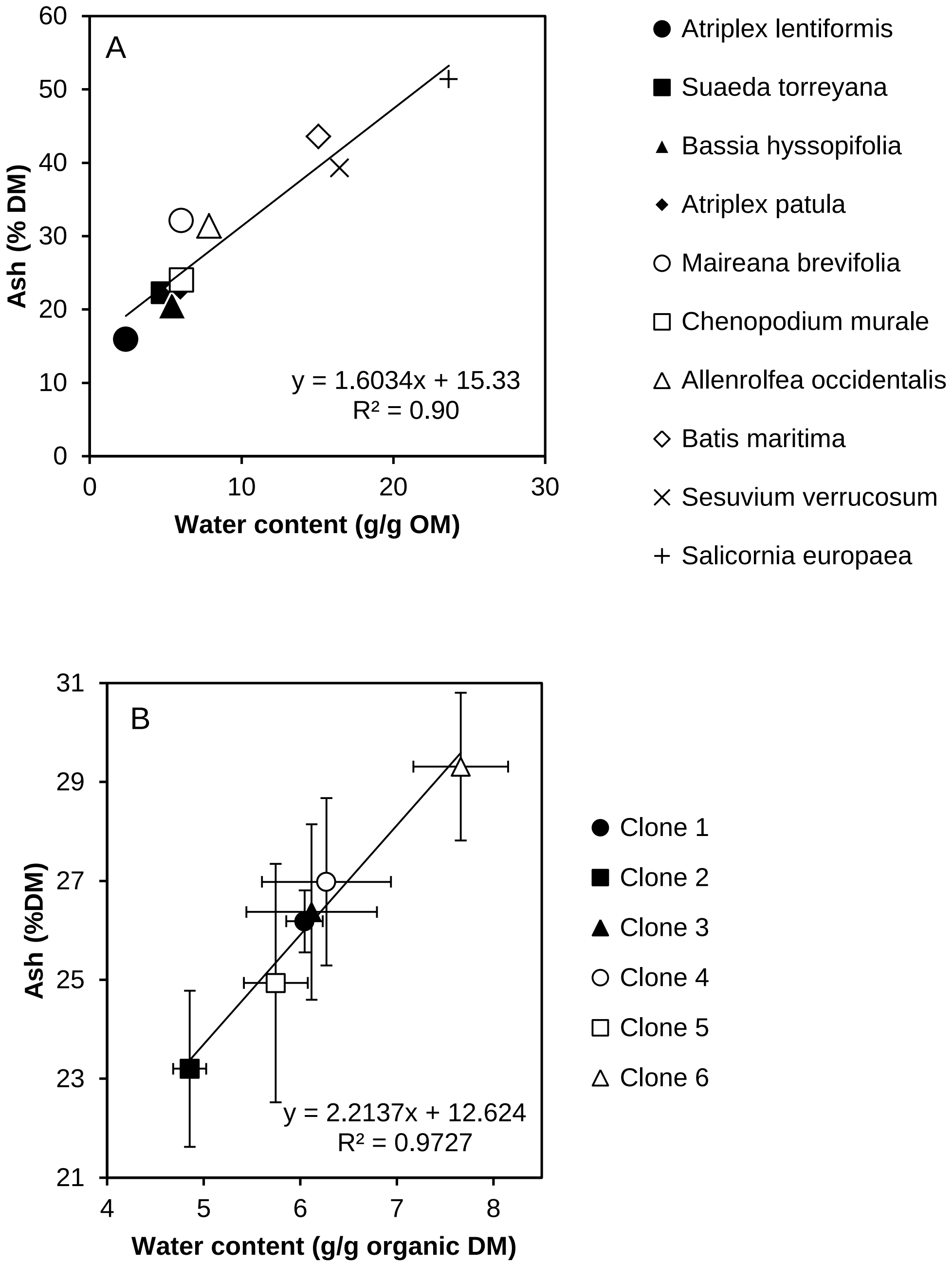


Fig. 6. Relationship between ash concentrations in the leaves of dicotyledenous halophytes and average tissue water. (A) Differences between euhalophyte species (Glenn and O'Leary, 1985). (B) Differences within a euhalophytic species – *Atriplex amnicola* (calculated from data of Masters et al., 2010). In the former study, plants were grown at 180 mM Na^+ (Cl^- + SO_4^{2-}) and each point is the mean of 10 to 20 values. In the latter study, plants were grown at 400 mM and each point is the mean of 3 values. Lines of best fit are for the averages of the composite data, and these were both significant at $P < 0.001$. Error bars denote the SEM.

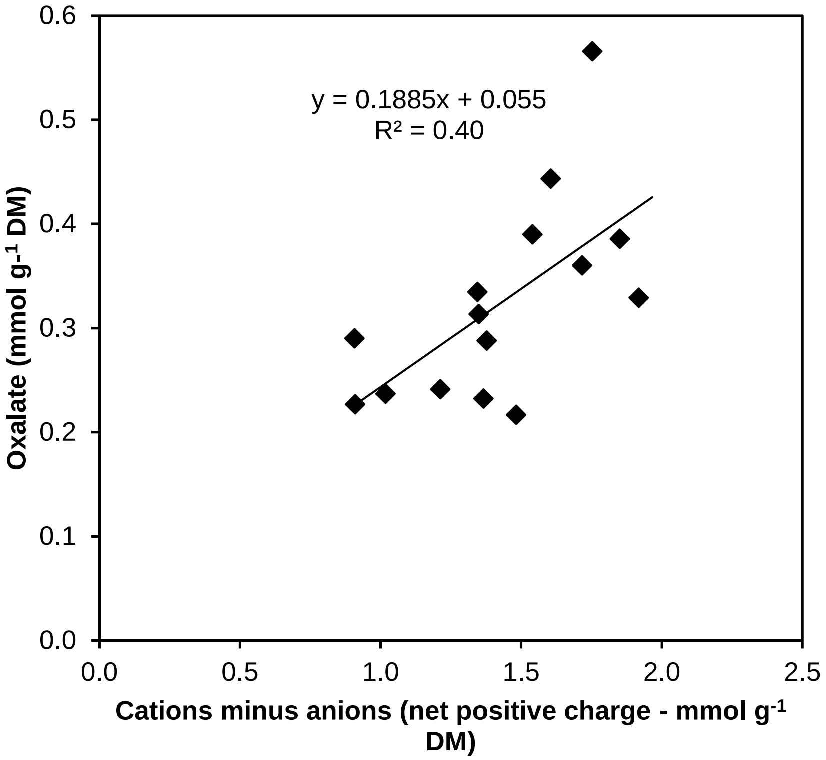


Fig. 7. Oxalate (mmol g^{-1} DM) plotted against the sum of cations (mmol charge g^{-1} DM as Na^+, K^+, Mg^{2+}, and Ca^{2+}) minus the sum of anions (mmol of charge g^{-1} DM as Cl^- and NO_3^-) in 15 individual bushes of *Atriplex nummularia* or *Atriplex amnicola* (calculated from data of Norman et al., 2004).

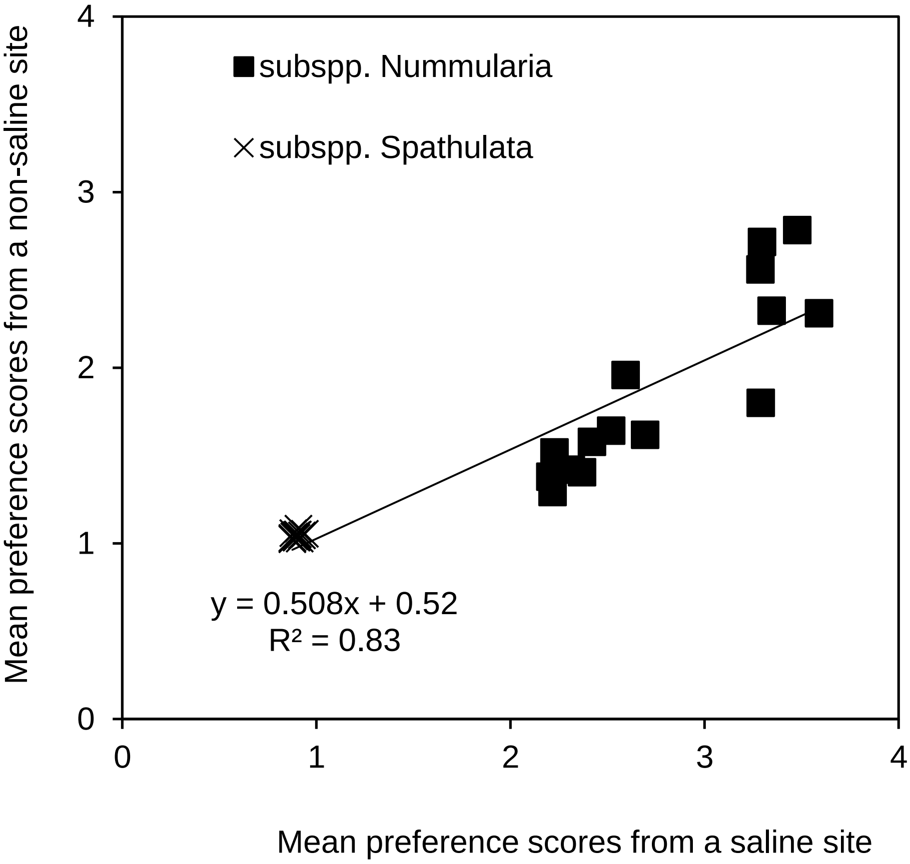


Fig. 8. Relative preferences of sheep amongst 27 provenances of *Atriplex nummularia* (from subsp. *nummularia* and subsp. *spathulata*) grazed with different flocks of Merino wethers at two separate sites (saline and non-saline). Oaten hay was offered *ad lib*. during grazing. Higher preference scores indicate greater defoliation of the provenance (data from Norman et al., 2010b).