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Plant-Herbivore Interactions in *Atriplex*: Current State of Knowledge

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Research Summary

The body of literature dealing with the biology of *Atriplex* is not only extensive and diverse, but is also scattered among a large variety of sources. The purpose of this review on plant-herbivore interactions in *Atriplex* (saltbushes) was to gain insight into the ecology of browsed *Atriplex* stands. Our emphasis was bringing together and synthesizing research related to the use of saltbushes as a browsing resource for ruminants. We took a broad view of the question and included most of the available literature relevant to the understanding of the complexities of saltbush-herbivore interactions.

This review is divided into five sections; the first four sections are divided into relatively self-contained subsections, allowing ready access to information of interest. At the end of each of these sections is a brief synthesis of common elements in the literature reviewed from an animal-plant interaction perspective.

The first section discusses aspects of the physiological ecology and life history of *Atriplex* that help to understand why saltbushes have been used so extensively as a browse resource and also why the ecology of browsed stands may not be simple. The second section addresses issues related to the effects of browsing on shrub fitness, and survival and reproductive behavior of saltbushes subject to herbivory and water stress are its central topics. How saltbushes defend themselves against herbivory is dealt with in the third section, with special emphasis on the literature related to saponins, a carbon-based defense compound, common in saltbushes and other chenopods. The fourth section discusses the effects that saltbushes have on the herbivores that consume them. Data both supporting and questioning the longstanding reputation that some saltbushes have enjoyed as excellent forage are reviewed in detail in this segment. In the fifth section we synthesize the information contained in the previous four sections, pointing out potential interactions between ploidy level, breeding system, defensive chemistry, and herbivory.

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Plant-Herbivore Interactions in *Atriplex*: Current State of Knowledge

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Introduction

Saltbushes (*Atriplex* spp.) exhibit a series of outstanding features—such as drought-hardiness, ability to grow in saline and disturbed environments, and tolerance to metal toxicity—that allow them to occupy a wide ecological range, spreading from approximately 20 to 50 degrees latitude in both hemispheres. Over 400 species of *Atriplex* have been identified on six continents, and even though they are formally considered to be absent from the tropics, a small number of species have been reported in Central America and the Caribbean (Le Houérou 1992; Osmond and others 1980).

The genus *Atriplex* is among the largest genera of the Chenopodiaceae. Only *Chenopodium* challenges *Atriplex* in number of taxa (McArthur and Sanderson 1984; Willis and Airy-Shaw 1973). The genus includes both herbaceous and woody forms. The shrubby taxa are thought to be more phylogenetically advanced. Evidence for this is threefold: (1) anomalous secondary thickening of woody stems and roots (Stebbins 1974); (2) C_4 photosynthesis is found in many shrubs but only in a few herbs (Osmond and others 1980); and (3) many of the shrubs have complicated derived sexual systems (Maywald 1996; McArthur 1977, 1989; Parr-Smith and Calder 1979). *Atriplex* and other chenopod genera have a high incidence of polyploidy based primarily on a base (x) number of 9 (McArthur and Sanderson 1984).

As with other members of Chenopodiaceae, the ability to succeed in ruderal environments makes saltbushes highly eligible for reclamation of areas where human activity has caused serious disturbances (Booth 1985; Goodall 1982; Graetz and Howes 1979; McArthur and Sanderson 1984; Sanderson and Stutz 1994b; Tiedemann and others 1984). In many parts of the world, several species of *Atriplex*—mostly *A. nummularia* Lindley, *A. canescens* (Pursh) Nutt., and *A. halimus* L.—have been cultivated extensively on rangelands degraded through overgrazing, on saline scalded areas, and on strip-mined lands. Such seeded stands of *Atriplex* are often used as a supplementary forage resource to feed small ruminants during periods of drought. Examples from the literature point to work carried out in some African countries (Egypt, Libya, Tunisia, Algeria, Morocco, Sudan, and South Africa), countries of the Middle East (Israel, Iraq, Syria, Iran, Yemen Arab Republic, and Saudi Arabia), Pakistan, Australia, and the United States (Abdul-Halim 1986; Atiq-ur-Rehman 1990 a,b; El Hamrouni 1986; Forti 1986; Gihad and El Saher 1992; Hobson and others 1986; Kessler 1990; Khair 1992; Khalil and others 1986; Nemati 1977; Runciman 1986; Sankary and Goodin 1986).

In the livestock industries of many arid and semiarid areas of the world, several species of *Atriplex* are considered a valuable browsing resource during periods of forage scarcity because their foliage is evergreen and exhibits a fairly high crude protein content. A large body of work dealing with nutritive value of *Atriplex* spp. (mainly *A. canescens*) and their potential use as browse for livestock has been published in recent decades (Atiq-ur-Rehman 1990a,b; Benjamin and others 1992; Benjamin and others 1995; Bhattacharya 1989; Chatterton and others 1971; Clarke 1981; Davis 1981; Garza and Fullbright 1988; Glenn and others 1992; Goodin 1979; Holecheck and others 1990; Kessler 1990; Khalil and others 1986; Le Houérou 1992; Leigh 1972; Leigh and Wilson 1970; McArthur and others 1984; McKell 1989; Nemati 1977; Northington and others 1979; Otsyina and others 1982; Rumbaugh and others 1982; Shoop and others 1985; Silva Colomer and Passera 1990; Sims and Taylor 1973; Ueckert and others 1990a,b; Warren and others 1990; Welch and Monsen 1981, 1984; Welch 1989; Weston and others 1969; Wilson 1966a,b, 1977).

The enthusiasm of some authors who have looked at chemical components of edible saltbush material, and reported its outstanding nutritional attributes, is not always shared by others who have carried out feeding-trial studies. Some of the latter suggested that under certain circumstances, animals fed on a diet composed entirely of saltbushes suffered detrimental metabolic alterations. These were probably caused by the presence of secondary compounds (such as saponins) or nonprotein nitrogenous compounds (glycinebetaine, for example) that cannot be readily utilized by ruminal microbes. Le Houérou (1992), arguing in favor of the nutritional attributes of *Atriplex,* stated that some of this controversy could be explained by the fact that feeding trials are generally too short to allow animals and microbes to adapt to saltbush diets.

A number of distinctive traits of *Atriplex*, including dioecy, female-biased sex ratios, sexual lability, polyploidy, and the presence of defense compounds, can confer a considerable degree of complexity to plant-herbivore dynamics in browsed populations. Browsing can affect male and female phenotypes differently. Preferential browsing and crown size reduction of female individuals can affect female reproductive fitness and alter sex ratios, in some cases to the extreme of impairing reproduction in local populations (Freeman and others 1993; Maywald, personal communication; Williams and others 1978). Secondary compounds could be responsible, in some cases, for the patterns of differential browsing among individuals of saltbush stands (Otsyina 1983; Sanderson and others 1987). Higher ploidy level is thought to reduce palatability to browsers (Stutz 1989), thus allowing for browsing selection in favor of higher ploidy level individuals in situations where shrubs of different ploidy levels coexist. Stress factors such as extremely cold winters, droughts, or prior heavy seed-set by females can induce changes in sex expression, generally toward maleness (Freeman and McArthur 1984; McArthur 1977; Van Epps 1975).

Aspects of the Physiological Ecology and Life History of *Atriplex*

Environmental Conditions

Most saltbush species prosper in areas with annual rainfall ranging from 200 to 400 mm. Where average precipitation is less than 200 mm, certain *Atriplex* must either behave as phreatophytes or receive irrigation in order to survive (Le Houérou 1992). Above 200 mm of yearly rainfall, this genus has adapted to a very broad range of temperatures—from cold coastal environments of northern Europe to very hot desert habitats such as Death Valley in California (Osmond and others 1980). According to Le Houérou (1992, p. 118), arid land saltbushes "…may be considered among the most heat-tolerant terrestrial dicotyledons." Cold temperature resistance, on the other hand, varies among and within species of this genus. Le Houérou (1992) divided *Atriplex* into three groups based on tolerance to cold temperatures:

1. A cold-resistant group, comprising several species that grow in the Great Basin of the United States, are known to withstand temperatures as low as –20 °C; some ecotypes of *A. canescens* are among them. Walser and others (1990) reported that in the Intermountain West, *A. canescens* did not reach lethal cold temperature until –80 °C in the winter, and that buds withstood temperatures of up to –35 °C in the spring.
2. Species such as *A. padulosa, A. barclayana,* and the Chilean *A. repanda* are known to be cold sensitive. Exposure to extended periods of –5 °C could be lethal to species of this group.
3. The Australian *A. vesicaria* Heward ex. Benth. and *A. nummularia*, together with the Argentinean *A. lampa* and some ecotypes of the North American *A. canescens*, are included in an intermediate group, withstanding moderately tolerant to cold temperatures.

There are some remarkable examples of drought resistance among *Atriplex*, such as *Atriplex hymenelytra*, that have survived 10 days at –6MPa of water potential in the root zone (Clark and others 1974). However, extensive shrub die-offs, especially of *A. confertifolia* (30 percent mortality in upland sites in western Utah due to a severe drought in 1931) (Stewart and others 1940), have been reported in the Great Basin as a consequence of environmental stresses such as drought, winter injury, or excessive rains (Nelson and others 1989). Le Houérou (1992) pointed to the fact that tolerance to drought and salinity was variable among species of *Atriplex.* He proposed a classification of species on the basis of salt and water stress resistance that ranges from the Xerohypohalophytes to the Hygro-hyperhalophites. The former included species such as *A. glauca*, *A. semibaccata*, and *A. leucoclada*, able to endure conditions of very low moisture and low salinity; and the latter comprised species such as *A. coriacea* and *A. barclayana*, unable to endure conditions of low moisture but successful in highly saline environments.

Low temperature is probably one of the few abiotic factors that limits the spread of this genus. However, the extraordinary range of environmental conditions in which members of *Atriplex* are successful points to their capability to respond to abiotic selective forces and to adapt to extremely dissimilar local conditions. Intraspecific variation, a characteristic of most members of the genus, is critical to their ability to adapt to contrasting environments.

Photosynthetic Pathways and Productivity

Contrary to what has been observed in most shrubs, the C_4 carboxylation pathway is present in the majority of *Atriplex* species. A few cases exhibiting the C_3 photosynthetic pathway, generally living in colder and more mesic environments and exhibiting herbaceous growth habit, have also been reported (Osmond and others 1980).

Laboratory experiments measuring gas exchange, photosynthesis, and water use efficiency of leaves and whole plants of C_3 and C_4 *Atriplex* found higher water use efficiency and productivity in the C_4 specimens (Slayter 1970). Transplant experiments with *A. patula* (C_3) and *A. rosea* (C_4) in northern California suggested that C_3 species were better adapted in moister coastal environments, while C_4 species seemed to be at a competitive advantage in dry desert habitats (Björkman and others 1969; Nobs and others 1972). Transpiration and uptake of a soil-applied insecticide ([^{14}C]phorate) in a greenhouse experiment showed higher transpiration and insecticide uptake rates in the C_3 *A. patula* compared with the C_4 *A. rosea* (Anderegg and Lichtenstein 1981). Greenhouse experiments conducted by Dwyer and DeGarmo (1970) in New Mexico, measuring root and shoot production, and water use efficiency of three native C_3 shrubs (*Larrea tridentata* [D.C.] Coville*, Prosopis juliflora* [Swartz] D.C.*,* and *Gutierrezia sarothrae* [Pursh] Britt. and Rusby), and the C_4 *A. canescens*, found the latter to be the most efficient in the use of water and on average the most productive. However, in cold, dry environments where C_3 and C_4 chenopod shrubs coexist, studies at the plant community level have not demonstrated clear advantages of one pathway over the other in terms of total (above and below ground) primary productivity measured throughout a growing season (Caldwell 1974; Caldwell and others 1977).

Results from research in Australia suggest that some *Atriplex* are able to perform as well or better than agronomic species exhibiting either the C_3 or C_4 photosynthetic pathway when water and nutrient supplies are not limiting (Osmond and others 1980). Jones and others (1970) grew two species of *Atriplex* (*A. nummularia and A. vesicaria*), a native cool season grass (*Danthonia caespitosa*), and common sunflower (*Helianthus annuus*) under controlled radiation and temperature conditions. Their data showed greater productivity performance in *A. vesicaria* compared to the other species, including the C_3 *H. annuus*. They also measured photosynthesis of field-grown *A. nummularia* (C_4) and *Zea mays* (C_4), and found that even though *Z. mays* exhibited greater maximum leaf photosynthetic rates, whole plant photosynthetic rates were higher in *A. nummularia.*

Many researchers have measured and reported primary productivity values for several *Atriplex* under different environmental conditions. Aboveground productivity values for both native and cultivated saltbush stands range from 12 to over 700 g per square m per year (Correal 1983; Gittens 1995; Goodin 1979; Liang and others 1989; Otsyina and others 1982; Passera 1983; Petersen and others 1987; Rumbaugh and others 1982). Productivity reported by these authors is in many cases hard to compare because of differences in the methods used and incomplete information on shrub densities and soils. Le Houérou (1992) stated that rain-use efficiency in well-managed, cultivated stands of *A. nummularia, A. halimus,* and *A. canescens* in the Mediterranean area ranged from 5 to 10 kg aboveground dry matter per ha per year per mm of rain.

Differences in photosynthate allocation within species exhibiting the C_4 pathway result in dissimilar root:shoot ratios and in potentially different aboveground productivity values (Osmond and others 1980). These authors quoted research carried out with *Atriplex vesicaria,* a warm-desert saltbush, and *A. confertifolia,* a cold-desert saltbush, that exhibited root:shoot ratios of 0.3 and 7.0, respectively. They pointed to the fact that cold desert *Atriplex* invested greater amounts of assimilates in root structure than warm desert C_4 plants of the same genus, in keeping with an empirical model proposed by Davidson (1969). This model predicted greater root:shoot ratios as soil temperatures depart from the optimum; its underlying assumption was that, within a certain range, increases in temperature triggered root activity increases, thus enabling a plant to invest less assimilate in root structure. The opposite was predicted to occur when temperatures were lower than the optimum. However, by the same token, an increase in temperature could promote root growth by favoring the conversion of assimilates and mineral nutrients into root structure (Wilson 1988). Probably, the striking differences in cold- and warm-desert C_4 *Atriplex* root:shoot ratios could be better explained by the interaction of several factors. Carbon and nitrogen uptake and translocation, together with moisture availability and both soil and air temperatures, might be some of the factors interacting to produce the observed patterns (Cannell and Dewar 1994; Thornley 1976; Wilson 1988). The idea of other factors, besides temperature, affecting root:shoot ratios is supported by research on *A. litoralis* (Steen 1984). He studied root and shoot growth of plants under different fertilization and irrigation treatments. He reported lower root:shoot ratios for *Atriplex* plants fertilized with K and NPK, compared with unfertilized plants. He also reported lower root:shoot ratios for plants irrigated with sea water, compared to those irrigated with fresh water.

Primary productivity of deserts and semideserts has been estimated to range from 10 to 250 g dry weight per square m per year (Whittaker 1975). Long-term data from the *Atriplex vesicaria* warm-desert communities of the Koonamore Vegetation Reserve in Australia showed productivity values that place these systems among the least productive (aboveground productivity = 26 g per square m per year) of arid land ecosystems (Noble 1977). Conversely, cold-desert *A. confertifolia* communities of the Desert Experimental Range in Ephraim, UT, USA, are among the most productive communities of dry systems (aboveground productivity = 195 g per square m per year) (Hutchings and Stewart 1953). These findings point to the fact that different species within the genus *Atriplex*, exhibiting the same photosynthetic pathway, have evolved the ability to succeed over a relatively broad environmental range.

Allocation patterns, photosynthetic pathways, and productivity of saltbushes are clear examples of both their enormous genetic variability and phenotypic plasticity. Many species of the genus are particularly attractive as a resource for forage production in agricultural systems of marginal areas because of the high productivity potential conferred by their C_4 photosynthetic pathway. The ability of *Atriplex* to produce as much or more biomass than traditional forage crops with irrigation, added to its stress-tolerance features, explains why *Atriplex* has been extensively used in revegetation projects for arid lands.

Lifespan, Age Structure, and Patterns of Survival and Recruitment

Anomalous secondary thickening, derived from several successive cambia, occurs in woody species of Chenopodiaceae, Amaranthaceae, and Nyctaginaceae (Fahn and Zimmermann 1982). Both woody and herbaceous genera of the Chenopodiaceae share this anatomical feature. Woody chenopods are believed to have arisen from the herbaceous members of the family, exhibiting an evolutionary trend opposite to what has usually been described for flowering plants in continental floras, such as herbaceous genera deriving from the woody genera of a family (McArthur and Sanderson 1984; Stebbins 1974).

As a member of the Chenopodiaceae, *Atriplex* exhibits included phloem, an anatomical peculiarity that is characterized by scattered groups of phloem cells included within secondary xylem bundles embedded in a conjunctive parenchyma tissue (Fahn 1974). While these anatomical modifications may confer resistance in harsh environments, secondary growth driven by successive cambial segments (with no real growth rings present) makes age assessment by means of vascular ring counts very difficult (Fahn and Zimmermann 1982). Schweingruber (1992), studying annual growth rings of native shrubs and trees of Australia, examined 16 woody species from the Chenopodiaceae. He reported that he was unable to determine their ages, partly due to his uncertainty as to whether the ring-like structures reflected yearly growth. In *A. halimus,* faint borders between increments in secondary body have been identified, yet methods involving labeled carbon might be the only way to tell if such increments correspond with annual growth cycles of the shrub (Abraham Fahn, personal communication).

Most authors who have looked at life spans in species of *Atriplex* agree in describing them as medium- to short-lived shrubs (but see Gulmon and Mooney 1977). Early research carried out in southwestern Utah reported counts of up to 40 vascular rings in *A. confertifolia* (Stewart and others 1940). Norton (1978) analyzed data from the Desert Experimental Range in southwestern Utah, on persistence of grazed and protected populations of *A. confertifolia*, for a 40 year period (1935 to 1975). He reported that in 1975, 67 and 77 percent of the grazed and ungrazed populations, respectively, were made up of plants that were less than 17 years old. West (1979) analyzed survival patterns of two cohorts of several cold-desert shrub species at the same site for a slightly shorter period (1935 to 1968). He found relatively high mortality in *A. confertifolia* in the first 2 years after establishment and in the last 10 years (1958 to 1968) of his analysis. He reported that in 1968, survival of the individuals of the 1935 cohort was 39 and 36 percent for grazed and ungrazed plots. Survival curves and tables (West 1979) suggest half-life "…time taken for a population to fall by 50 percent" (Harper 1977, p. 553) of approximately 27 years for this cohort of shadscale. Crisp (1978), working on demography and survival of *A. vesicaria* in the Koonamore Vegetation Reserve in South Australia, reported a half-life of 11 years for individuals of the population he studied. Yensen and Smith (1984) reported a mean age of 24 years (ranging from 3 to 61) for a sample of individuals from a population of *A. falcata* in southwestern Idaho. These authors used vascular ring counts to assess shrub ages, and pointed to the fact that anomalies in vascular growth patterns, typical of woody chenopods, could have rendered their results inaccurate.

Age structure assessment of *Atriplex* populations can be particularly meaningful to studies of structure of plant communities and population dynamics, and is by no means a trivial matter in studies of grazing and climate effects on saltbush populations. In an analysis of population pattern in chenopod communities of southern Australia, Anderson (1967, p. 456) found age-related alterations in the intensity of patterns in *A. vesicaria* "…expressed as the ratio observed/expected mean square for the appropriate block size." Revisited work carried out by Anderson (1967) found that pattern in *A. vesicaria* populations was in part due to "…an age-dependent phenomenon" (Malik and others 1976, p. 267). Malik and others (1976) stated that pattern was basically determined by the younger individuals; analysis of data subsets containing only older plants found an essentially random distribution.

To avoid problems associated with establishing ages of individuals, these authors divided the populations into four age categories (seedling, pioneer, building, and mature) on the basis of crown diameters.

Survival curve shapes for *Atriplex confertifolia* cohorts are not constant over time. The negative slope curve describing constant death rates in the two cohorts studied by West (1979) best characterized mortality of plants older than 2 to 3 years of age up to 34 years of age. Mortality rates for younger and older plants were considerably greater. This author reported no statistical differences in the shapes of mortality curves for grazed and ungrazed situations. However, Chambers and Norton (1993), studying the effects of grazing and drought on population dynamics of several grass and shrub species at the same site, reported higher adult mortality in the heavily grazed plots compared with the protected areas, irrespective of grazing season. They conducted their study between 1975 and 1978, a period that included several extremely dry years. They stated that "*A. confertifolia* is susceptible to the effects of below-average precipitation and that these effects are exacerbated by grazing" (p. 268). Recruitment of new individuals, on the other hand, was highest in the plots that had been most affected by grazing (the heavily grazed spring plots). These were the only plots to exhibit positive population turnover rates. Norton (1978) stated that in 1975 there were three times more shadscale individuals in the heavily grazed pastures, relative to the exclosures at this same site. Both Norton (1978) and Chambers and Norton (1993) attributed these differences to interspecific competition; the decrease of the more palatable species had allowed the less palatable (armed) shadscale to increase. Harper and others (1990), Kitchen and Hall (1996), and Whisenant and Wagstaff (1991) also studied shrub dynamics (including shadscale) at this site, using portions of the same data set analyzed by Chambers and Norton (1993), Norton (1978), and West (1979). These authors all concluded that season of grazing had important impacts on shrub dynamics. Shadscale densities were found to be independent of or even enhanced by grazing under the management practices at the Desert Experimental Range.

In *Atriplex vesicaria*, survivorship curves change over time. Heavy early mortality (type III survival curve) later changes to constant death rates (type II survival curve) (Crisp 1978). Crisp (1978) also described this shrub as exhibiting a fairly continuous recruitment strategy. In research on *A. vesicaria* on the Mundi Mundi Plain in New South Wales, Australia, Eldridge and Westoby (1991) reported 20 recruitment events out of the 21 periods they observed (between 1977 and 1987). They stated that recruitment occurred in all seasons, and survival of propagules was independent of the size of the recruitment event. Recruitment was also reported to occur irrespective of adult shrub density in the areas they sampled. The authors argued that their data suggested seed supply did not restrict recruitment in bladder saltbush stands with more than about 1,000 adult shrubs per ha. Contrary to what Crisp (1978) reported, survival patterns at this site were constant through time, and drought events affected both adults and young plants alike. Eldridge and Westoby (1991) attributed these disparities both to soil dissimilarity between the Koonamore site and their study area, and to differences in the length of time through which cohorts were followed at both sites.

Determining age structures in saltbush populations appears to be a challenge that has not received full attention in research dealing with the ecology of *Atriplex,* probably due to the considerable degree of complexity associated with the issue. Several authors have used age surrogates that have allowed reasonable approximations to the problem. However, questions about individual plant longevity of a number of *Atriplex* species remain unanswered. More accurate methods for establishing ages of saltbush shrubs (such as pantographic techniques) would undoubtedly advance the present understanding of population processes and patterns in browsed *Atriplex* stands.

Ecotypic Variation and Polyploidy

Speciation due to intraspecific differentiation and hybridization is a relatively common phenomenon in this genus (Le Houérou 1992; Osmond and others 1980; Stutz 1978; Stutz 1989). In fact, the concept of ecotype, as first developed at the beginning of the century by Turesson (1922), was in part a result of research on erect and decumbent growth forms of the annual *Atriplex litoralis*.

In North America, *Atriplex canescens* exhibits a remarkable dispersion area, occupying sites from Canada to Mexico, and from the Missouri River to the coast of the Pacific Ocean (Stutz and others 1975). Its ability to succeed over such a widespread area is explained by the degree of phenotypic plasticity it displays (associated with significant morphological variation) and by processes of hybridization and polyploidy that originate intraspecific heritable variation (Sanderson and Stutz 1994a; Stutz and Sanderson 1979).

Polyploidy, which is known to occur in numerous dryland shrubs (*Artemisia* spp., *Chrysothamnus* spp., *Larrea* sp.), is present in several species of *Atriplex* (McArthur 1989; Stutz 1989). Although only one third of the known saltbush species have been described as polyploids, North American saltbushes exhibit this feature fairly frequently. In populations of *A. canescens,* autopolyploids are far more abundant than diploids (Osmond and others 1980; Stutz 1989), and various authors have ascribed adaptive significance to this feature, occurring not only in *A. canescens* but also in *A. confertifolia* and *A. tridentata* (Dunford 1984, 1985; Sanderson and others 1990; Senock and others 1991; Stutz and Sanderson 1983; Stutz and others 1975; Stutz and others 1979).

Dunford (1984, 1985) studied distribution patterns of cytotypes of *Atriplex canescens* in southern New Mexico and northwestern Texas. He found that diploid (2n = 18) plants grew mainly on sandy soils of the mesas, while hexaploid individuals (2n = 54) could be found growing on the heavier alluvial soils of the floodplains. Tetraploids (2n = 36) were present on both soil types. He explained this distribution pattern as a plant adaptation to different soil textural types. This pattern confirmed research results of Stutz and his colleagues (Stutz 1989; Stutz and others 1975) who found a population of diploid plants of *A. canescens*, which they described as "…*a gigas* form of *A. canescens*," on the sandy soils of the Little Sahara Sand Dunes near Delta, UT. This diploid population grows three to four times taller than the normal *A. canescens* of the area. The area surrounding the sand dunes was inhabited by tetraploid plants, yet none of these were found growing on the dunes. Likewise, these authors were unable to find diploid individuals growing on the finer textured soils surrounding the dunes. In transplant gardens, the diploid *gigas* seedlings have far greater growth rates compared with "normal plants." Mature diploid plants exhibit unusual growth rates of new twigs, being able to put on as much as 100 cm of growth in a single growing season. McArthur and others (1983) found the *gigas* diploid to be among, yet not above, the leading producers in an 18-accession comparative study. This study was conducted on clay loam and stony loam soils. Senock and others (1991) studied differences in leaf morphology among cytotypes of *A. canescens* at a site near Las Cruces, NM. They found higher water use efficiency in hexaploids and tetraploids than in the diploid cytotype. Similar ecotypic differences have been reported for *A. confertifolia* by Stutz (1989), who stated that diploid shadscale could be found growing above the Pleistocene lake levels in the Great Basin, while tetraploids were presently found on the lakesides and various polyploids (4x, 8x, or 10x) in the ancient lake bottoms.

Contrary to what occurs in grasses and other herbaceous plants, increase in chromosome numbers in many shrub species decreases stature (Stutz 1989). Stutz observed this pattern among *Atriplex canescens* plants and argued that reduced size was of adaptive importance because it was associated with an increase in drought tolerance and a decrease in palatability to browsers. Studies of *Artemisia tridentata*, *A. confertifolia*, and *Chrysothamnus viscidiflorus* reviewed and augmented by Sanderson and others (1989) tend to confirm this relationship between ploidy level and plant size. However, in *A. confertifolia,* even though tetraploids are smaller than diploids, octoploids and hexaploids have similar statures, and decaploids are larger than both tetraploids and octoploids. These apparent deviations from the observed shrub-size:ploidy-level patterns were attributed to interspecific competition and adaptation to saline environments. Sanderson and others (1989) also pointed to findings of Solbrig (1977) in *Gutierrezia sarothrae,* and Stutz and others (1987) in *Grayia brandegei,* where shrub size increased with ploidy level.

Few authors have addressed questions related to the ways in which selective forces exerted by browsing may affect saltbush populations. Genetic processes that allow *Atriplex* to adapt to abiotic selective pressures should also confer browsed saltbush populations the ability to adapt to herbivory. The great variability and the active differentiation processes previously described suggest that the probabilities of occurrence of browsing-adapted saltbush genotypes should be high. The literature, however, reports more examples of local extinctions than adaptation to browsing by large herbivores. Nevertheless, moderately long-term browsed saltbush stands should offer unique opportunities to answer questions related to adaptations to browsing.

Breeding Systems and Sex Expression

Breeding systems regulate the flow of genes among plants. Shrubs, in particular, have evolved many of these systems that allow them to maintain genetic variability and succeed in patchy environments (McArthur 1989). Dioecy is a diclinous breeding system where each genet usually expresses one sex and, in angiosperms, is thought to have arisen from self-compatible inbreeders as a response to selective pressure for outbreeding or separation of male and female function (Richards 1986). Monoecy, on the other hand, is a monoclinous breeding system where sexual functions are separated in male and female flowers within the same plant. In this way, monoecious plants are hermaphroditic, but their flowers are not perfect, exhibiting either male or female functions (Richards 1986).

The dioecious condition is much less common than the perfect flower condition in flowering plants. Frequency of dioecy is higher than normal in some tropical forest woody species and island floras, in particular those from Hawaii and New Zealand (Bawa 1980). Both these cases and additional evidence from gymnosperms have been used to postulate models that explain evolution of dioecy, either as a response to selective pressure against inbreeding, such as the case of island floras, or as a result of selective forces acting through pollination and dispersal ecology of species, such as the case of tropical forests and gymnosperms (Bawa 1980; Bawa 1982; Givnish 1980; Givnish 1982; Thomson and Barrett 1981). Freeman and others (1980b) quantified the occurrence of dioecy in 40 different plant communities of the Intermountain West of the United States, ranging from the deserts in northwestern New Mexico to the alpine meadows of the Wasatch Mountains. They found the dioecious habit to be somewhat more frequent in this region than had been reported for angiosperms as a whole in the literature. They were also able to find a fairly strong positive association between dioeciousness and both anemophily and woody life-forms. These authors concluded that dioeciousness "…has arisen repeatedly through disruptive selection processes that are maximally effective in patchy environments dominated by anemophilous, woody species" (p. 416). In patchy environments, dioecy reduces intraspecific competition and enhances niche occupation through spatial segregation of male and female plants along moisture gradients (Freeman and others 1976, 1997; McArthur 1989).

Baker (1959) stated that most annual *Atriplex* were monoecious, while perennial individuals were commonly dioecious. Brown (1956) described dioecy as the most frequent breeding system in perennial species of North American *Atriplex*. Asexual reproduction has also been reported for *A. tridentata* (saltsage) and *A. canescens* (Nord and others 1969; Stutz 1989; Woodmansee and Potter 1970).

Breeding systems of tetraploid populations of *Atriplex canescens* studied by McArthur and Freeman (1982) were described as the "trioecious state of Darwin (1877)" (p. 481). These populations exhibited three floral phenotypes (males, females, and monecious or hermaphroditic individuals), with a fairly constant ratio of pistillate:staminate:hermaphroditic plants, clearly biased towards female sex expression. McArthur (1977) proposed a theoretical 55:35:10 ratio of sexual phenotypes, on the basis of a 7 year study he conducted on sex expression of a half-sib family of tetraploid *A. canescens* in a common garden in Ephraim, UT. Subsequent research conducted by McArthur and Freeman (1982), comparing 19 natural tetraploid populations from Utah, New Mexico, Arizona, Montana, Idaho, Oregon, and Colorado, showed that ratios of 11 out of the 19 populations did not differ significantly from the proposed ratio (55 pistillate:35 staminate:10 hermaphroditic). Similarly, the pooled ratio of all 19 populations was not significantly different from the theoretical ratio. In this paper, data from a diploid population were also reported; sex ratios were 1 pistillate: 1 staminate, with no presence of hermaphroditic plants. Barrow (1987) surveyed native populations of diploid, tetraploid, and hexaploid *A. canescens* in southern New Mexico and western Texas and found ratios similar to those described by McArthur and Freeman (1982). However, Barrow (1987) reported the presence of a few hermaphroditic individuals in the diploid populations. He found that numbers of hermaphrodite individuals increased with ploidy level. A study of four ecotypes of tetraploid *A. canescens* from western Texas showed sex ratios similar to those described above (Petersen and others 1987). Two ecotypes from more xeric environments exhibited less staminate plants and more shrubs with no sexual expression when grown in a common garden together with the other two ecotypes. Petersen and others (1987) attributed this to environmental controls of sex expression. Cibils and others (1997) found similar ratios in a winter-grazed stand of tetraploid *A. canescens* on the shortgrass steppe in northeastern Colorado. However these authors reported significantly different ratios (more female-biased) in long-term exclosures at the same site.

Stress conditions, defined by Charnov (1982) as those "…which reduce growth, reduce a plant's ability to allocate resources to reproduction, or lessen an individuals chances for survival" (p. 204), can induce sex change in some individuals of tetraploid *Atriplex canescens*. McArthur (1977) reported this phenomenon in the half-sib population he studied where 30 percent of the individuals changed their sexual phenotype after a mild autumn and extremely harsh winter sequence. Over a longer period, McArthur and Freeman (1982) reported that 59 percent of the individuals of this population showed constant sex expression, while 41 percent were sexually labile. They stated that sex changes were generally towards maleness and that greatest lability was found among the monoecious plants. All but one of these plants changed sex over the 6 year study period. Among females, 51 percent changed sexual expression, this occurred only in 15 percent of the males. Sex lability in tetraploid populations of *A. canescens* is thought to be genetically constrained (for example, environmental stress factors can induce sex change only in some individuals). McArthur (1977) proposed a model to account for this, whereby sexual genotypes would be either: XXXX, exhibiting a constant female phenotype; XXYY, showing a constant male phenotype; or XXXY, exhibiting a sexually labile phenotype. Both X and Y represented either loci or blocks of loci responsible for the genetic control of sexual expression. McArthur and others (1992) conducted a long-term (20 year) study using clonal material that demonstrated some individual plants are fixed in sex expression and others are labile, for example, they can respond to environmental cues by being male, female, and monecious on a temporal scale. Freeman and others (1993) and McArthur and others (1992) postulated that this trioecious system is an adaptation that allows fourwing saltbush individual plants and populations to more effectively occupy patchy heterogeneous habitats.

Freeman and others (1980a) stated that shifts in sexual expression in plants had been reported in 25 families and over 50 species of flowering plants. In some cases, changes imply year-to-year variation in sex expression of individuals, while in others, it occurs as sequential hermaphroditism driven by plant size. Moisture stress, severe winters, decreasing light intensity, and removal of reserve organs have all been reported to produce shifts towards maleness. The mechanisms responsible for these changes could include induced plant hormone imbalances (gibberellic acid:cytokinin ratios), especially in the case of water stress (Freeman and others 1984). Male and female individuals of some dioecious species are not equally fit in all environments. Because of this, it has been suggested that sexual lability could be of adaptive significance to species growing in patchy environments and a means to maximize population reproductive fitness (Charnov 1982; Freeman and others 1980a; Freeman and others 1984). In several species of *Atriplex*, females were found to be under greater internal water stress than males when fruit was in late stages of development or soils were dry (Freeman and McArthur 1982). This could explain in part the patterns of spatial segregation of sexes in *Atriplex* populations (Freeman and others 1976; Freeman and others 1993).

Sex ratios can be altered by environmentally induced sex switching. Freeman and McArthur (1984) studied the relative importance of mortality, nonflowering, and sex lability in biasing sex ratios of natural populations of *Atriplex canescens*, *A. confertifolia*, *A. corrugata*, and *A. cuneata*. They found sex change and nonflowering to be considerably more important than mortality, even though the relative importance of each factor changed from year to year. Strawbridge and others (1997) examined a population of *A. amnicola* over 5 years and reported sexual lability. Females and monoecious shrubs increased over the years, a process that the authors attributed to aging rather than environmental stimuli. Other factors, such as browsing, could also be responsible for biasing sex ratios. Williams and others (1978) reported they found male-biased sex ratios in a population of *A. vesicaria* due to preferential browsing of female shrubs by sheep. In this case, sheep browsing appeared to reduce survival of female shrubs. Even though browsing may be a factor inducing sex change, reports on this in the literature are not clear. Maywald (1996) reported that *A. vesicaria* includes labile plants in addition to males and females. Freeman and others (1980a) stated that examples from their literature search showed that leaf removal or crown-pruning produced shifts towards femaleness (contrary to the general stress-induced sex shift trend) in at least eight species of plants. Finally, competition was also hypothesized to alter sex ratios in *A. confertifolia* (Freeman and Harper 1980). At the site of their study, males were overrepresented inside protected areas, while females were more abundant outside in the grazed pastures. Freeman and Harper (1980) postulated that water stress due to competition was greater inside exclosures. This condition would affect females more negatively than males and, hence, the bias in ratios they observed. They also mentioned that, in this armored species, males exhibit fewer thorns than females of comparable size, yet surprisingly, they dismissed the possibility of biasing of sex ratios through preferential male browsing.

Experimental manipulation of sex ratios in *Atriplex amnicola* showed that maximum fruit fills were obtained when the population had 50 percent males (Strawbridge and others 1997). However, optimum seed productions were obtained within a relatively wide range of shrub sex ratios (from 11 to 50 percent males). These results are consistent with suggestions made for *A. canescens* by McArthur and others (1978).

The breeding system of *Atriplex* is perhaps the trait responsible for most of the complexities in plant-herbivore interaction patterns that will be described in subsequent sections. Most of the work on breeding systems of *Atriplex* has been carried out in *A. canescens*; however, surprisingly, almost no work relating breeding systems to intraspecific variations in plant defense levels and browsing patterns have been published for this species. The opposite situation exists with *A. vesicaria;* relatively little has been published about breeding systems and genetics of the species compared to the volume of browsing-related research results. Another unexpected fact is that questions related to the induction of sex change through browsing stress do not appear to have been addressed in either *A. canescens* or *A. vesicaria;* but see Maywald and others [in press].

Effects of Browsing on Shrub Fitness

Survival and Reproduction

Fitness of *Atriplex*, understood as the "genetic contribution by an individual's descendants to future generations of a population" (Ricklefs 1990), may be affected by browsing in a number of ways, ranging from reproductive alterations to death of an individual. Trlica and others (1977) conducted a clipping experiment to study the effects of rest following defoliation on the recovery of *A. canescens*—among other range species—on the shortgrass steppe. They stated that six heavy defoliations at different phenological stages, from fall through late summer, “would probably kill the plants” (p. 26). They also found that a single defoliation near maturity (= producing flowers) was most harmful to plants relative to defoliations of equal intensity carried out at the phenological stages of quiescence, early growth, or rapid growth. Multiple defoliation treatments in fourwing saltbush rendered smaller values of vigor (= subjective categories integrating measurements of live crown morphology with number and length of seedstalks), herbage yield, and basal stem total nonstructural carbohydrate levels, relative to undefoliated shrubs (Buwai and Trlica 1977). In this experiment, basal total nonstructural carbohydrates levels were less affected than herbage yield and plant vigor. No significant differences among sexes were found in the response variables these authors measured (Joe Trlica, personal communication). However, Tiedemann and others (1987) found seasonal differences in chlorophyll, total nonstructural carbohydrates levels, and other metabolites among ungrazed male, female, and labile bushes. Differences were found only in the spring when males had higher values than the other phenotypes. Buwai and Trlica (1977) suggested that fourwing saltbush at their research site might not be affected by either spring and fall, or spring and early summer utilization. They also reported that three moderate defoliations (removal of 60 percent of current year’s growth) during rapid growth, seedset, and quiescence stimulated twig growth. However, utilization at high intensity (defoliation of 90 percent of current year’s growth) and high frequency (four multiple defoliations) could kill the plants.

Pieper and Donart (1978) studied the effects of defoliation by moderate browsing in a population of *Atriplex canescens* in south-central New Mexico. They found significant differences in basal and aerial leader growth, and shrub mortality between browsing frequency treatments. Over a 4 year period, shrubs browsed for 3 years and protected during the last year exhibited somewhat greater aerial leader growth than those browsed continuously over the 4 years, and even slightly greater aerial leader growth than the protected plants. Basal leader production was approximately four times larger in plants that received a year’s rest compared with shrubs that were browsed throughout the period. Protected plants from the exclosure produced no basal leaders, apparently because basal buds were under apical dominance control. Mortality for a 7 year period of continuous browsing was nearly 25 percent, while less than 5 percent of plants browsed for 3 years and protected for 4 years were reported to have died. These authors concluded that fourwing saltbush at this site required periodic rest in order to survive and remain vigorous.

Price and others (1989) revisited and enlarged on work carried out by Pieper and Donart (1978) and stated that browsing with an adequate sequence of rest can stimulate growth in fourwing saltbush. These conclusions agree with results previously reported by Buwai and Trlica (1977). Price and others (1989) argued that grazing strategies, including a 60 day deferment of shrubs during the early growing season, would allow for adequate plant growth. They observed that greatest damage to axillary buds of secondary leaders (impairing adequate resprouting) occurred in both continuously browsed shrubs and in shrubs browsed after very lengthy rest periods, for different reasons in each case. Browsing secondary leaders when they were still tender and hae not become slightly woody at their bases generally resulted in damage to axillary buds. When more than 1 year of rest was allowed, secondary leaders became very long, woody, and brittle, and browsing caused the same effect as with tender leaders. Rest periods of more than 1 year promoted progressively larger number of flower stalks and less leader growth.

Eldridge and others (1990) conducted a study at a number of sites of the Riverine Plains in Australia to assess the effects of grazing by cattle and sheep on *Atriplex vesicaria* (a dominant species within these communities). The sites had been stocked at rates recommended by the Soil Conservation Service of New South Wales. They set up permanent transects at intermediate distances from watering points and followed individuals over a period of 7 years. They found no differences in the way either cattle or sheep browsing affected saltbush shrubs at the recommended (moderate) stocking rates. Moderate grazing was reported only to affect shrub size, while overall fluctuations in density did not differ between grazed and protected areas. Shrub population turnover was reported to be large (overall, about 50 percent per year) in both grazed and ungrazed situations. In the past, however, overgrazing of *A. vesicaria*-dominated rangelands is known to have caused large mortalities and replacement of this shrub by either grasses or shorter lived chenopods over extensive areas (Stanley 1983). Fatchen (1978) revisited transects that had been surveyed in 1932 in South Australia, and reported only four individuals of *A. vesicaria* compared with the original 946 reported by researchers in 1932. Fatchen (1978) was not able to establish the causes for this decrease but suggested cattle and sheep grazing as a possible driving factor. Severe defoliations in *A. vesicaria* led to shrub mortality in experiments on areas of the northwestern Riverine Plain (Leigh and Wilson 1970). In one experiment, paddocks stocked at 1, 0.5, and 0.25 sheep per acre suffered shrub mortalities of 100, 76, and 1 percent, respectively.

An experiment where remaining leaves were counted after each browsing event showed that bladder saltbush (*Atriplex vesicaria*) shrubs with less than 40 remnant leaves were unable to survive defoliation under dry conditions. Apparently, under conditions of severe defoliation, budded stems were removed by sheep, thus preventing subsequent resprouting and producing shrub death. According to Leigh and Wilson (1970), *A. nummularia* (the dominant saltbush species over most of the southeastern Riverine Plain) is more resistant to browsing than *A. vesicaria*, because it can produce leaves from buds on main stems and is capable of basal resprouting.

On mine reclamation lands grazed by cattle in Wyoming, numbers of individuals in seeded *Atriplex canescens* stands decreased dramatically throughout a 5 year period (Schuman and others 1990). Booth (1985) suggested that in such situations, *A. canescens* might act as a pioneer species, and that its progressive decrease could be explained by its inability to compete successfully with late seral species and by the effect of browsing and basal decay. In another 5 year experiment conducted on planted stands of *A. nummularia* and *A. canescens* in the northern Negev, Israel, Benjamin and others (1995) studied the effects of complete summer defoliation. Saltbush stands had been planted at different densities ranging from 625 to 10,000 shrubs per ha and were browsed by sheep and goats in some years, and by sheep alone in others. Animals were taken off the pastures when all shrubs had been completely defoliated. The authors measured shrub heights and widths and edible biomass (twigs and leaves) before and after each defoliation event. Neither *A. nummularia* nor *A. canescens* recovered their original crown sizes or biomass production level. Leaf biomass regrowth tended to decrease progressively throughout the experiment period. Differences in biomass production between stands planted at different densities, both on an individual and a surface-unit basis, also decreased with time. The browsing treatment imposed on the shrubs caused large mortality in *A. canescens* (at the end of the experiment most of the shrubs in the high density plantation were dead). Conversely, mortality was negligible in *A. nummularia* stands. *A. nummularia* actually out-yielded both *A. canescens* and *Cassia sturtii* R.Br., a third species included in the experiment. Malcolm and Pol (1986) reported results from grazing trials on seeded stands of *A. amnicola* (river saltbush), *A. undulata* (wavy leaf saltbush), and *A. padulosa* (marsh saltbush), among others, on areas of bare saltland soils in Western Australia. Browsing treatment imposed on the seeded plots was severe—defined by the authors as "…chewed back to sticks of about 5 millimeters thick" (p. 60)—and occurred in autumn and early winter for about 4 years. In one of the trials, marsh saltbush was extirpated by the treatment, while survival in wavy leaf saltbush and river saltbush was 54 and 94 percent. Recruitment of seedlings occurred in all cases.

Hodgkinson and Baas Becking (1977) looked at the effects of different defoliation treatments on root growth in *Atriplex vesicaria* and *A. nummularia*. Both interruption and resumption of root growth after defoliation was slower in the shrubs compared to the grass *Danthonia caespitosa* Gaudich (an abundant perennial grass of Southern Australia). The authors argued that reserve photosynthates in shrub stems, on one hand, and a slower resumption of shoot growth compared with the grass, on the other, could account for shrub root growth response to browsing in this experiment. According to these authors, the long period of root-growth depression in *A. vesicaria* could explain its inability to cope with severe defoliation. When both leaves and stems were removed, the situation became even more critical because reserves to resume root-growth, contained in small twigs, disappeared.

Examples from the previously mentioned literature point to the fact that even though there appear to be interspecific differences in response to browsing overall, important browse species of *Atriplex* are fairly sensitive to high levels of defoliation. This condition (browsing sensitivity) seems to be associated with the removal of buds and subsequent resprouting impairment. Of all species cited, *A. nummularia* and *A. padulosa* appear to be the most resistant.

Browsing intensity and frequency might affect reproductive function by producing a decrease in numbers of seedstalks. Conversely, protection from browsing tends to have the opposite effect (Buwai and Trlica 1977; Price and others 1989). In *A. canescens, s*hrub size, also altered by browsing, can affect male and female reproductive fitness differently. While smaller males may be more efficient in dispersing pollen, reduced size in females could lessen their ability to intercept pollen, thus affecting their fecundity (Freeman and others 1993).

Browsing and Drought Effects

Atriplex species exhibit a number of morphological and physiological traits that enable them to cope with drought. Some of these traits, reviewed by Newton and Goodin (1989), involve: (1) regulation of leaf inclination (in *A. hymenelytra*); (2) production of leaf trichomes and accumulation of salt crystals on the leaf surface to increase reflectance; (3) accumulation and synthesis of inorganic and organic solutes to maintain turgor; and (4) root association with endomycorrhizae that allows absorption of soil moisture at very low water potentials. Recently, molecular techniques have been used both to study drought induction of stress-protein synthesis and to identify specific genes responsible for the synthesis of drought-induced mRNA in *A. canescens* (Adair and others 1992). Such techniques, according to these authors, could help to understand the metabolism of drought tolerance mechanisms.

However, large scale shrub die-offs have occurred in saltbush stands due to what may have been mixed effects of browsing by large herbivores and drought. Such interactions are not always clearly understood, and have often been a source of controversy between livestock operators and researchers (Stewart and others 1940).

In a study reported in previous sections, Chambers and Norton (1993) concluded that *Atriplex confertifolia* was sensitive to below-average precipitation years and that browsing could aggravate stress in such situations. Stewart and others (1940) also reported extensive shadscale die-offs due to the combined effects of browsing and drought. However, timing and intensity of grazing might interact with drought, producing opposite effects on plant population survival. Heavy grazing or spring grazing of cold desert shrub communities in Utah were reported to have the most negative effects on members of the plant community during a period of drought. Conversely, winter grazing or light grazing had beneficial effects on plants of the community during below average precipitation conditions (Chambers and Norton 1993; Harper and others 1990; Whisenant and Wagstaff 1991). In an analysis of long-term data from the same site, Norton (1978) found that 40 years of heavy winter grazing by sheep did not produce any significant differences in density and percent cover trend of *A. confertifolia*, *Ceratoides lanata*, and *Artemisia spinesens* between grazed and protected plots, supporting Chambers and Norton's (1993) observations.

Turner (1971) studied vegetation cover for a number of soil types at a salt desert site close to Grand Junction, CO, for a period of 10 years (1953 to 1963). He compared trends in grazed and protected watersheds and found that, even though drought and grazing resulted in overall deterioration of cover, shadscale tended to increase its cover in the grazed watershed. Turner (1971) attributed this to larger recruitment of shadscale seedlings in the grazed pastures, which could have balanced the loss of adult plants killed by the drought. He also pointed to the fact that shadscale (an armed saltbush) is not a shrub preferred by sheep and cattle, and hence, grazing of competitors may have released resources and facilitated establishment of new plants.

In a study designed to determine the impact of degree of defoliation, time of defoliation, and soil moisture status on *Atriplex vesicaria*, Leigh and Mulham (1971) found that completely defoliated shrubs did not regenerate, irrespective of soil moisture status. They subjected shrubs to two treatments of defoliation by sheep (severe and complete), and to two conditions of soil water content (watered and nonwatered) in February and October. While previous research they cited had reported resprouting of shrubs completely defoliated by drought deciduousness, they were not able to produce the same results in watered shrubs completely defoliated by sheep. They reported high mortalities in severely defoliated shrubs that did not receive extra moisture by irrigation, especially when shrubs were left with less than 10 leaves and browsed in October. In moderately grazed pastures of *A. vesicaria,* Eldridge and others (1990) found greater rates of decrease in diameters and heights of grazed shrubs compared with protected shrubs during a drought period. Once conditions were again favorable, after the drought, differences disappeared. High mortality among old plants (over 30 years old) of *A. vesicaria* was reported to occur due to drought (Crisp 1978). Anderson (1967) also pointed to this fact, suggesting that larger "(and older?)" (p. 456) shrubs might be the first ones to suffer the effects of soil moisture deficit.

Work addressing the issue of drought-browsing interaction effects on saltbushes, relative to other aspects of saltbush biology, has seldom been reported in the literature. Work reviewed in this section suggests that factors such as intensity and timing of defoliation together with the status of *Atriplex* within the browsed community (whether it is dominant) may be crucial for predicting the effect of drought-browsing interaction on individuals.

Differential Browsing of Individuals Within Populations

Work carried out in *Atriplex vesicaria* and *A. canescens* point to the fact that saltbush stands are not a homogeneous browsing resource. There appears to be a considerable amount of spatial and temporal variation associated with actual forage quality and availability of browsed *Atriplex* populations.

Female-biased herbivory in a population of bladder saltbush in Australia was reported by Graetz (1978) and Williams and others (1978). Osborn and others (1932) were probably the first to report differential use of *Atriplex vesicaria* shrubs in heavily browsed areas around water points. Graetz (1978) and Williams and others (1978) recorded sex ratios for several sites and found that browsing by sheep promoted shifts towards male-biased ratios. They suggested that preferential browsing of female individuals produced reduction in plant vigor and a consequent increase in susceptibility to death, by either drought or trampling, as the sex-biasing mechanism. A greater acceptability of the female “green bladdery fruits” (p. 389), compared with male reproductive flowers, was offered as a likely cause for sex-based selectivity of sheep. Vegetative vigor of male adult plants was found to be greater than their female counterparts. This pattern was particularly significant because density of seedlings was more strongly influenced by vigor of female parents than by distance from pollen-producing male neighbors. Maywald [personal communication] is pursuing this topic and has reported that sheep discriminate bladder saltbush on the basis of sex, preferring to eat female plants and rejecting males.

Differential browsing in a heavily stocked population of fourwing saltbush in the Western United States was also described by Otsyina (1983). He did not report sex-related discrimination, yet stated that out of a total of 700 shrubs (all exposed to high stocking rates), one-third had been heavily browsed, one-third had been moderately browsed, and less than one-third had been lightly browsed. He suggested that variation in concentration of saponins—a common secondary compound in plants of the Chenopodiaceae—among individuals was responsible for the browsing pattern he observed. Differential grazing by rodents on a number of accessions of *Atriplex canescens* of different ploidy levels grown in a common garden was reported by Sanderson and others (1987). These authors found sharp differences in the content of saponins between accessions of *A. canescens* and postulated that this may have influenced herbivore preference.

Sex-biased herbivory has been described for several dioecious species, yet in the majority of cases plants with male sex expression were reported to suffer larger degrees of herbivory (Boecklen and others 1990). Examples of plant species where this is known to occur include willows (Alliende 1989; Boecklen and others 1990; Danell and others 1985), the dioecious herb *Rubus chamaemorus* (Agren 1987), and the tree *Acer negundo* (Jing and Coley 1990). A few authors have reported cases of female-biased herbivory occurring, however, in species (*Silene dioica* and *Rumex acetosella*) where male-biased herbivory also takes place at some phenological stage (Lee 1981; Lovett Doust and Lovett Doust 1985). Much of this research has looked at the impact of invertebrate herbivores, and cases reporting female-biased herbivory are based on studies of smuts and rusts. Browsed *Atriplex* stands are among the few cases in which sex-biased herbivory has been addressed using large herbivores. However, no clear pattern has yet emerged from such studies. While female-biased herbivory has been found in sheep browsing *A. vesicaria* (Maywald, personal communication) and in *A. canescens* browsed by heifers in winter (Cibils and others, unpublished data), in a study conducted on *A. canescens* during the growing season, sheep preferred male over female individuals (Maywald and others, in press). This same study reported no preference in a winter grazing trial. Further study of the causes and mechanisms of sex-biased herbivory in *Atriplex* would undoubtedly contribute to a deeper understanding of herbivory in dioecious plants, an area that according to Boecklen and others (1990) “…has been largely ignored in discussions of plant-animal interactions” (p. 586). These examples suggest that browsing patterns controlled by shrub gender-related differences in shrub palatability (perhaps as a consequence of defense chemicals) may be frequent in browsed *Atriplex* stands.

Defensive Chemistry of *Atriplex*

Defense Theory, Dioecious Plants, and *Atriplex*

Plant defenses vary among species and range from plant anatomical structures (thorns, for example) to chemically active metabolites (Fox 1981; Zangerl and Bazzaz 1992). Chemical plant defenses have been classified into “quantitative” dose-dependent compounds that reduce diet digestibility in herbivores, and “qualitative” compounds that are toxic to herbivores in relatively small doses (Feeney 1976; Rhoades 1979). Complexity of structures or metabolites and their turnover rates determine the inherent costs of synthesis and the maintenance of defense functions (Zangerl and Bazzaz 1992). The idea of costs and tradeoffs underlies most current theory on evolution of plant defenses (Coley 1988; Coley and others 1985; Feeney 1976; Herms and Mattson 1992; Rhoades 1979). A basic assumption of these models is that plant fitness is closely related to cost:benefit relationships of allocating resources to defense under varying conditions of resource availability, competition, and selective pressure by herbivores (but see Bryant and others 1985).

While plants living in different environments are known to have strikingly similar tissue concentrations of carbon, water, and minerals, the ways in which these resources are allocated to reproduction, growth, and defense differ considerably. The fact that these basic plant functions compete for limited resources has now been widely accepted (Bazzaz and others 1987; Chapin and others 1987). Allocation patterns vary both spatially (between parts of a plant and among individuals) and temporally (within a plant over time) (Bazzaz and others 1987; Zangerl and Bazzaz 1992).

Dioecious species offer interesting opportunities to study intraspecific allocation patterns because each individual has either male or female sexual expression. Harper (1977) stated that in certain dioecious species, females allocated a larger amount of assimilates to reproduction and less to vegetative growth than did males. Antos and Allen (1990, 1994) measured greater reproductive effort in female individuals relative to males in the dioecious shrub *Oemleria cerastiformis*. They reported that reproductive effort was twofold greater in terms of nitrogen and fourfold greater in terms of biomass in females compared with males.

Tradeoffs derived from different reproductive efforts between sexes can induce slower growth rates and smaller plant sizes in female individuals compared with males. Darwin (1877) demonstrated this in an experiment with strawberry plants (but see Gehring and Monson 1994). Intrinsic growth rate of a plant species could determine the degree to which it may allocate resources to defense (Coley and others 1985). In dioecious plants, this theory would predict selection for greater levels of defense in female plants because they have slower intrinsic growth rates relative to males. This could explain the fact that the great majority of sex-biased herbivory examples have been reported to be male-biased. An alternative hypothesis, which might explain female-biased herbivory, reported for *Atriplex* is that reproductive investment in females could constrain their ability to allocate photosynthates to defense. Another possible explanation might be that a strong investment in defense of reproductive structures could impair the ability of female saltbushes to defend vegetative structures.

Certain accessions of *Atriplex canescens* have been reported as containing relatively high levels of saponins, carbon-based plant defense compounds (Nord and Van Atta 1960; Otsyina 1983; Sanderson and others 1987). Nord and Van Atta (1960) examined utricle bracts of fourwing saltbush and isolated saponins that they identified as a triterpenoid derived from oleanolic acid. They reported very high contents of saponins (10 percent of weight of original bract chaff) and found this compound to have inhibitory effects on germination in an experiment they conducted on seeds of fourwing saltbush and antelope bitterbrush (*Purshia tridentata* [Pursh] DC). Recently, Siddiqui and others (1994) isolated atriplexinol, a triterpenoid sapogenin (the aglycone fraction of a saponin, see next section), from *A. stocksii* Bois, a saltbush that grows in marshes in subtropical and temperate climates.

Davis (1981) reported relatively high levels of oxalates (in some cases potentially toxic) in 6 week old greenhouse-grown plants of 14 species of *Atriplex*. Oxalates occur in plants as either oxalic acid (a simple dicarboxilic acid) or as calcium oxalate (an insoluble compound with a low calcium:oxalate ratio). Animals suffering acute poisoning by oxalic acid exhibit corrosion of digestive mucosas, nervous system alterations, low blood coagulability, and renal insufficiency. Animals consuming food with low levels of oxalates may suffer chronic calcium deficiencies (Koplík and others 1995). Anaerobic oxalate-degrading bacteria were isolated fairly recently from the rumen, from human feces, and from cecal contents of several animals. These bacteria use oxalates as a substrate. As content of oxalates in the diet increase so do bacterial populations and, therefore, toxic effects of these compounds are neutralized (Allison 1985). Allison argued, however, that adjustments of bacterial population size to level of oxalates require some time. Therefore, ingestion of high levels of oxalates by animals that have not undergone previous adaptation could cause poisoning. Davis (1981) reported that concentrations of oxalates varied among the 14 species of *Atriplex* he studied, and they decreased over time in all species. Seedlings of an Australian accession of *A. leptocarpa* exhibited the highest oxalate content (12.6 percent), while an accession of an unidentified species of *Atriplex* from Argentina yielded the lowest oxalate value (4.2 percent). Levels of 8.7 percent (dry matter basis inferred) of oxalate content were considered toxic according to Dye (1956). By the time field-grown plants were 6 months old, oxalate content had fallen below toxic levels, and at 1 year of age the content had dropped even lower. Oxalates have been reported in variable quantities in other annual and perennial chenopods of the United States (*Halogeton glomerulatus* and *Sarcobatus vermiculatus*) and Australia (*Maireana brevifolia, Chenopodium pumillo, Salsola kali*) (Jacob and others 1994; Morton and others 1959; Whitson 1994). Sporadic severe outbursts of sheep poisoning with halogeton (*Halogeton glomerulatus*) have been attributed to the presence of toxic levels of oxalates in this annual weedy chenopod (Morton and others 1959).

Davis (1981) also measured tannin content in the 14 species of *Atriplex* he studied, and reported it to be well below the levels required for animal rejection. Tannins exhibit powerful astringent flavor and have been defined as any polyphenolic compound with a molecular weight greater than 500 (Liener 1980). These substances have been classified as either hydrolyzable or condensed tannins, and are a relatively common secondary compound in shrubs. Close to 79 percent of deciduous shrubs and 87 percent of evergreen shrubs contain them. Tannins can form complexes with either plant protein or animal digestive enzymes, lowering protein availability to gut microbes in ruminants, and producing growth-rate depression in some monogastrics (Liener 1980; Rhoades and Cates 1976). Holecheck and others (1990) also reported low content of tannins and soluble phenolics in fourwing saltbush. In an analysis of 24 species from an *Atriplex-Artemisia* community, Cates and McElroy (1987) reported that terpenes, cyanide, and alkaloids were not detected in *A. canescens* specimens.

Other inorganic and organic compounds such as selenium (Se) and the nonprotein nitrogenous compound glycinebetaine could also render certain *Atriplex* species either toxic or of low nutritional value to browsers under certain environmental circumstances (Booth 1985; Davis 1972; LeHouérou 1992). Selenium toxicity occurs in most animal species when diets contain 5 ppm of this mineral. In livestock, a disease known as blind staggers that includes symptoms such as loss of hair, hoof sloughing, lameness, blindness, and paralysis followed by death is caused by an excess of Se in the diet (Pond and others 1995). A number of plants known as Se concentrators accumulate a considerable amount of this element when growing in selenium rich soils. Such plants take Se from the soil and concentrate it, mostly in the form of Se analog of sulfur amino acids (Koplík and others 1995). All 15 native North American and introduced accessions of *Atriplex* studied by Davis (1972) were found to concentrate Se when grown in selenium enriched soils. Three accessions of *A. canescens* exhibited the highest Se content.

Concentrations of glycinebetaine in water-stressed *Atriplex* were reported to have increased as a means of osmotic adjustment (Wynn Jones and Storey 1981). They reported the presence of glycinebetaine (the simplest of the N-methyl substituted amino acids, commonly known as betaines) in 60 species of the Chenopodiaceae, 14 belonging to the genus *Atriplex.* Rumen microbes require an adaptation period and energy supplementation to develop the ability to break down glycinebetaine (Le Houérou 1992). However, this compound is rapidly degraded by soil microbes (Wynn Jones and Storey 1981), probably under aerobic conditions. Experiments conducted in vivo where betaine-l-^{14}C and betaine-methyl-^{14}C were added to the rumen of sheep showed that one of the products of betaine metabolism, trimethylamine, was absorbed from the rumen but was probably not used by the animal. Addition of betaine-methyl-^{14}C to the rumen caused rapid increases of ^{14}C labeled trimethylamine, followed by the excretion of ^{14}C labeled trimethylamine oxide in the urine (Mitchell 1968).

Leaf surfaces exhibiting salt bladders are characteristic of some *Atriplex* species (*A. hymenelytra, A. confertifolia, A. lampa,* and others). Under conditions of drought, leaf bladders dry out allowing accumulations of salt crystals on the surface of the epidermis (Kenagy 1972; Mares and others 1997; Mooney and others 1977). While such salt accumulations are thought to be primarily a water-saving adaptation of desert halophytes (increasing leaf reflectance and thus reducing leaf temperature and transpiration), they can also act as a deterrent to herbivores. A few desert rodents from North and South America (the chisel-toothed kangaroo rat and the red vizcacha rat, respectively) and from Northern Africa (the fat sand rat) have evolved amazing adaptations to cope with salt crystal accumulations on saltbush leaves. Such adaptations include specialized lower incisors and bristle bundles (groups of stiff hairs on either side of the mouth), together with specialized kidneys that allow these herbivores to shave the hypersaline tissue off leaf surfaces before consuming them and to cope with diets containing large amounts of salts (Degen 1988; Kenagy 1972; Mares and others 1997; Schmidt-Nielsen 1964).

Among the secondary compounds found in *Atriplex,* saponins are probably the most important. They are the only plant defense metabolite in *Atriplex,* to our knowledge, that has been reported to alter herbivory patterns in both small and large browsers. While apparently no published research has addressed the issue of variation in content of saponins between sexual phenotypes, among different plant parts, or within individuals through time, the potential for alteration of browsing patterns in *Atriplex* populations driven by variation in saponin contents definitely exists.

Saponins: Chemical Characteristics and Mode of Action

Saponins are glycosides composed of a carbohydrate (L-arabinose, D-galactose, and D-glucose, for example) and a noncarbohydrate or aglycone portion. They are divided into two major groups on the basis of the nature of the aglycone fraction (also known as sapogenin or sapogenol) that can be either a triterpenoid or steroid derivative (Cheeke 1971; Price and others 1987; Velisek 1995). Saponins are widely spread among plants; nearly 100 plant families are known to contain them. A number of plants used in both human and animal feeding (some, such as spinach and sugar beets are chenopod relatives of *Atriplex*) exhibit different amounts and types of saponins (table 1) (Price and others 1987). Saponins present in legumes (such as alfalfa and soybean) have been extensively studied and belong to the triterpenoid type. Triterpenoids may occur either as saponins or as sapogenins in the plants that contain them. Steroid saponins, some of which are available commercially (Sarsaponins), are derived mainly from the yucca plant (*Yucca* spp.), and their steroid moiety never occurs in the free sapogenin form (Cheeke 1971; Valdez and others 1986). Identical sapogenin moieties attached to different sugar chains constitute a totally different saponin. The array and numbers of individual saponins isolated are enormous. Mahato and Nandy (1991) listed over 270 triterpenoid saponins, isolated between 1978 and 1989

Table 1—Some plant species containing saponins[a].

Species	Contents measured as percent of dry weight[b]	
Plants used as foods and foodstuffs		
Oats (*Avena sativa*)	0.1 to 0.13	(Rolled oats)
Sorghum (*Sorghum* sp.)	.007	(seeds)
Millet (*Pennnisteum* sp.)	.02	(seeds)
Spinach (*Spinaceae oleracea* L.)	.7 to 4.7	(roots)
Tea (*Thea sinensis* L.)	13	(seeds)
Peanut (*Arachis hypogaea*)	<0.001 to 1.6	(fruit)
Soya (*Glycine max*)	4.3	(beans)
Sugar beet (*Beta vulgaris*)	5.8	(leaves)
Asparagus (*Asparagus officinalis L.*)	1.5	(edible stalks)
Alfalfa (*Medicago sativa*) low saponin var.	.14 to 5.6	(ground leaves and stalks)
Alfalfa (*Medicago sativa*) high saponin var.	1.71	(ground leaves and stalks)
Alfalfa (*Medicago sativa*)	8.0 to 8.7	(sprouts)
Alfalfa (*Medicago sativa*)	.88	(roots)
Herbs and forbs		
Yarrow (*Achillea millefolium*)		
Tragacanth (*Astragalus gummifer* Labill.)		
Wormseed (*Chenopodium ambrosioides* L.)		
Pakistani ephedra (*Ephedra gerardiana* Wall. ex. Stapf)		
Canaigre (*Rumex hymenosepalus* Torr.)		
Dandelion (*Taraxacum officinale* Weber ex. wig)		

[a] Adapted from Price and others 1987, tables 2 , 5 , and 11, p. 33, 64, and 91.

[b] Where contents are not specified, presence but not levels of saponins were reported.

alone. Current chromatographic and spectroscopic techniques, they argued, allowed greater efficiency and accuracy in triterpenoid saponin isolation. Some of the results of early research on the effects of saponins in foodstuffs on either humans or animals were often contradictory, due in part to the inaccuracy of the techniques available at that time (Price and others 1987).

Plant materials containing saponins exhibit a bitter taste, and tend to produce foam subsequent to agitation in aqueous solutions due to their activity in lowering surface tension; hence, their name comes from the Latin *Sapo* that means soap. Saponins have also been described as able to hemolyze red blood cells, and early assays to determine presence of saponins were based on this property (Birk and Peri 1980). Hemolytical properties of saponins in alfalfa were probably one of the first aspects of their biological activity to be studied. However, a large number of biological effects (both negative and positive) have been ascribed to the presence of these compounds. Lysis of red blood cells is probably an example of the most negative effects, while at the other end of the spectrum are the ancient ginseng saponins from the Chinese plant *Panax* (from the Greek "pan" = all, and "axos" = cure) *ginseng*, with a great reputation as a natural medicine with alleged anti-aging effects (Price and others 1987; Velisek 1995).

Several authors have written extensive reviews on the biological effects of saponins (Birk and Peri 1980; Cheeke 1971; Mahato and Nandy 1991; Price and others 1987). Cheeke (1971) summarized biological effects attributed to saponins as "1) erythrocyte hemolysis; 2) effects on blood and liver cholesterol levels; 3) effects on growth; 4) bloating of ruminants; 5) inhibition of smooth muscle activity; 6) enzyme inhibition; 7) effects on nutrient absorption" (p. 622). Birk and Peri (1980) also mentioned fungicidal and bactericidal properties, together with insect-deterrent effects and inhibitory effects on seed germination. Ishaaya (1980) mentioned growth impairment in insects due to nonspecific association of saponins with proteins that inhibited digestive enzymes and food intake. Mahato and Nandy (1991) mentioned evidence of molluscicidal activity and both antitumor and antileukemic activity of certain triterpenoid saponins. Marston and Hostettmann (1991) also stressed the value of molluscicidal action of saponins, stating that their use could be valuable to control a number of snail populations that act as intermediate hosts for human intestinal parasites.

Most of the early work on effects of saponins in foodstuffs were related to legume saponins fed to monogastrics. Many of the effects enumerated by Cheeke (1971) were demonstrated either in experiments conducted in vitro or in feeding trials with monogastrics (mainly chicks and rats). According to Cheeke (1971), little attention had been given to ruminants where toxicity could only be demonstrated when saponins were introduced directly into the blood stream. He argued that biological activity was neutralized in the rumen where saponins were broken down into their sugar and aglycone moieties. In ruminants, there appeared to be a considerable amount of saponin breakdown by microbes in the gut, hence, the low record on negative effects of orally introduced saponins. Some in vitro experiments, where soybean saponins were incubated both with washed microorganism-free tissue from ceca and colons, and with cecal microflora alone, have shown that decomposition of saponins into sapogenin and sugar moieties occurred only in the presence of cecal microbes. No breakdown occurred in incubations with microbe-free ceca (Applebaum and Birk 1979). Negative effects of saponins in ruminants, according to the evidence examined by Cheeke (1971), appeared to be mostly restricted to the occurrence of bloat, a condition related to production of foam in the rumen and eructation impairment. Eventually, the accumulation of gases in the rumen can put pressure on the diaphragm muscle and cause heart failure or suffocation (Pond and others 1995).

Saponins are also known to increase the permeability of membranes, a property that could alter absorption in the mammalian digestive tract, and that is particularly dangerous for cold-blooded animals. Increased permeability of respiratory membranes in fish and tadpoles causes rapid loss of respiratory function and is, therefore, lethal (Price and others 1987). A considerable amount of research has focused on the hypocholesterolemic effects of saponins. Mechanisms that might account for this property are: (1) these compounds affect the absorptive capacity of intestinal mucosa by binding to membrane bound sterols, triggering greater cell exfoliations, and with them losses of cholesterol; and (2) saponins attach to bile salts thus not allowing them to be reabsorbed in the intestine, producing losses via feces of otherwise reabsorbed cholesterol (Cheeke 1971; Gee and Johnson 1988).

Sarsaponins, sterol-derived saponins from the yucca plant, have been reported to alter both protein metabolism by microorganisms in vitro, and ruminal digestion and flow (Price and others 1987). However, when these saponins were fed to dairy cows, no significant effect on rumen fermentation was found (Valdez and others 1986). In this experiment the authors reported that concentrations of ruminal ammonia, blood urea, and volatile fatty acids were not different between sarsaponin and control treatments. Another trial using lambs with a different steroidal saponin (smilagenin) reported improved growth rate of fattening lambs (Cheeke 1971). The structural similarity of this saponin to diethylstilbestrol (a growth promotor) was suggested as the probable explanation for the observed results.

The "bitter" or "astringent" taste ascribed to saponins is thought to act as a herbivore deterrent. Some feeding experiments with poultry, rats, and swine showed that these animals discriminated against diets with high-saponin alfalfa, while rabbits were found to preferentially select high-saponin diets (Price and others 1987). Other sensory related effects of saponins were reported in sheep consuming *Tribulus terrestris,* a South African plant containing steroidal saponins (Kellerman and others 1991). These authors were able to induce hepatogenous photosensitization, a disease locally known as geeldikkop, in an experiment in which water-suspended steroidal saponins extracted from *T. terrestris* were administered by stomach tube to Merino lambs.

Secondary compounds in plants, acting as potential antinutrients for herbivores, seldom occur in isolation. Interaction of saponins and tannins mixed in diets was found to have positive effects on both rats and ruminal microbia (Freeland and others 1985; Makkar and others 1995). Freeland and others (1985) conducted an experiment where mice were (1) allowed to choose between food containing tannin or saponin, (2) given diets with tannins or saponins alone, or (3) given diets with mixtures of predetermined amounts of saponins and tannins. Mice that were allowed to choose their own diets suffered none of the negative effects (food-intake depression, loss of weight, or high feces weight:food weight ratios) that were present when they were fed diets with either tannins or saponins alone, or diets with both antinutrients in predetermined amounts. The authors postulated that simultaneous consumption of tannins and saponins in the right proportions may have produced interactions that inhibited potential negative activity of either of them alone. Makkar and others (1995) conducted in vitro experiments with rumen liquor, adding different types of tannins and *Quillaja saponaria* bark saponins. They reported that efficiency of microbial protein synthesis was higher with both saponins and tannins added to the rumen liquor solution as compared to either tannic acid, quebracho tannins, or saponins added alone.

The fact that *Atriplex canescens* contains triterpenoid saponins that have been shown to have deterrent, hemolytic, and membrane altering effects in rats may imply that patterns of ruminant herbivory could be influenced by the presence of these chemicals. Capability of saponins to affect rumen bacteria and fungi should not be dismissed. However, because rumen microbes may break down saponins in the gut, potential negative effects on metabolism may be neutralized; therefore, deterrent effects of saponin's astringent taste may be the most important antiherbivore factor associated with these compounds.

Saponins in Other Chenopodiaceae

Recent studies have looked at saponin content of *Chenopodium quinoa* (quinoa), an ancient Andean crop known to be part of the diet of the Inca civilization. Renewed interest in its nutritional attributes, mainly due to the high protein content (14 to 18 percent) of its seeds, has promoted research on quinoa saponins regarding structure, content, and biological action (Gee and others 1993). Quinoa saponins have been divided, on the basis of their aglycon moiety, into those containing (1) oleanolic acid, (2) hederagenin, and (3) phytolaccageninc acid. Relatively little is known about the mode of action of this last group (Gee and others 1993; Price and others 1987). Differences in types of sapogenins have been established between lowland and highland varieties of quinoa in Peru (Cuadrado and others 1995). Gee and others (1993) performed in vitro and in vivo experiments with bitter, washed bitter (debittered), and sweet quinoa grains. They were able to show membranolytic activity of isolated saponins in vitro, which increased small intestine membrane permeability. Rats in the in vivo feeding studies showed marked aversion for the unwashed bitter flour and for grain diets containing a proportion of unwashed bitter flour. Both intake and conversion efficiency of the rats fed on bitter quinoa flour was significantly lower to that of the other groups. The authors postulated, on the basis of the results of their in vitro experiments, that this could be due to a significant decrease in intestinal function.

Other chenopods currently used in human and animal diets that have been reported to have saponins are spinach (*Spinacea olearacea)* and sugar beets (*Beta vulgaris*). Saponins from these chenopods are thought to be triterpenoid saponins derived from oleanolic acid, and in the case of the spinach plant, to have hemolytic properties (Price and others 1987). Saponins in these species, compared to other plant species (table 1), are found in relatively high concentrations.

Nutritive Value of *Atriplex* as a Forage for Ruminants

The work described below dealing with the nutritional attributes of *Atriplex* spp. can be divided into two main groups on the basis of the approaches followed. Authors from the first group, largely interested in scanning plant resources for range reclamation, have dealt mainly with the chemical composition of plant edible material (generally leaves and fine stems) and its variation between species, within a plant, and throughout the growing season. A second group of papers deals mainly with the effects of feeding saltbush diets to ruminants (mainly sheep and goats). Different degrees of detail were pursued among authors of this second group, ranging from live-weight monitoring in animals to measurements of digestibility of some key nutrients. Many of these trials have compared performance of ruminants feeding on *Atriplex*-based diets versus other conventional supplementation resources. Generally, feeding trials were conducted with animals subjected to different degrees of confinement, although at least two of the papers reporting diet composition of free-ranging ruminants are also included in this section. While there is a fair amount of agreement among authors in the first group, experiments conducted in the second group have sometimes yielded inconsistent results.

Chemical Characteristics and Palatability

Many saltbushes exhibit a number of desirable forage attributes that have stimulated research on their chemical and nutritional properties. High biomass production, crude protein levels comparable to those exhibited by alfalfa (table 2), evergreen foliage, resistance to drought, and high levels of salinity are some of the outstanding traits reported in the literature. However, low gross energy coupled with high mineral content (mainly NaCl) and a relatively high proportion of nonprotein nitrogen call for special management techniques when using saltbushes as a forage resource for ruminants (Glenn and others 1992).

Silva Colomer and Passera (1990) studied seasonal variation in the chemical composition of six species of *Atriplex* (*A. lampa, A. nummularia, A. cinerea, A. rhagodioides, A. bunburyana,* and *A. undulata*) from Tunisia, South Africa, and Spain. Most of the chemical composition data from their experiment fell within the ranges reported for North American saltbushes (table 2). They found levels of crude protein and energy of a mixture of dried leaves and fine stems to be remarkably constant across seasons and within species. Crude protein content for most of the species did not fall below 13 percent on any of their sampling dates. The authors remarked on the high content of phosphorous in the samples they analyzed. Monthly variation of chemical components in leaves and stems of *A. polycarpa* (Torr.) S. Wats., measured by Chatterton and others (1971), showed a general decrease in protein, fats, and total digestible nutrients during the summer months at a site in the San Joaquin Valley, CA. Absolute values of each component fell within the ranges reported (table 2). Winter protein content was higher in both leaves and stems at this winter-rainfall site, similar to that reported by Silva Colomer and Passera (1990), for the measurements

Table 2—Comparative chemical composition of *Atriplex* spp. and alfalfa[a].

		***Atriplex* spp. aerial parts**	**Alfalfa (*Medicago sativa*) hay**
Crude protein	range	5.6 to 24.2	9.3 to 33.0
(percent)	mean	17.7	21.3
Fiber	range	12.3 to 36.0	15.6 to 52.4
(percent)	mean	30.3	41.8
Cellulose	range	12.5 to 29.0	17.0 to 38.0
(percent)	mean	20.8	27.5
Lignin	range	9.5 to 16.0	5.0 to 18.0
(percent)	mean	17.5	14.0
Mineral content	range	4.2 to 29.0	4.4 to 17.6
(percent)	mean	16.6	11.0
Gross Energy	range	3.4 to 4.3	3.8 to 5.0
(Mcal per kg)	mean	3.9	4.4

[a]From National Research Council (composition of cereal grains and forages) (1958).

they conducted at sites with the same precipitation regime. On the whole, Chatterton and others (1971) reported that none of the nutrients they studied, except for phosphorous at the end of summer, fell below "nutritional requirements of a grazing animal" (p. 37).

In an effort to establish the winter crude protein content of *Atriplex canescens,* Welch and Monsen (1981) measured nitrogen content of 43 accessions grown in a common garden in Idaho. Accessions were collected at a number of sites in Utah, Idaho, Wyoming, Nevada, New Mexico, Arizona, and Montana. They reported winter crude protein content ranging from 6.0 to 14.2 percent, with a large degree of variation among accessions and between individuals within accessions. Variation of coefficients of up to 33.9 percent were reported for crude protein content of individuals belonging to the same accession. The authors pointed to the opportunities for artificial selection presented by such great variability among individual shrubs. Differences in crude protein, phosphorous, and digestible organic matter among four accessions of fourwing saltbush in western Texas were too small to be considered biologically or nutritionally significant to herbivores (Petersen and others 1987).

Crude protein content (among other chemical constituents) of armed saltbush (*Atriplex acanthocarpa* [Torr.] Wats) and fourwing saltbush were measured in each of the four seasons, at a site in southern Texas, where both of these shrubs grow together (Garza and Fullbright 1988). Values of crude protein for leaves and stems in armed saltbush were consistently higher than in fourwing saltbush at all sampling dates. Crude protein in leaves was remarkably high in armed saltbush (19 to 32 percent), and even though stem crude protein values (9 to 20 percent) would be expected to lower the overall value of edible biomass, this shrub exhibited larger leaf:stem biomass ratios than fourwing saltbush, enhancing interspecific crude protein differences. However, total standing crop per plant was 5.6 times larger in fourwing saltbush, exhibiting average crude protein values for leaves and stems that fell within the range of reported values (table 2). The lowest crude protein content values (11.6 percent leaves, 4.6 percent stems) in fourwing saltbush at this site were reported for the month of August, while the greatest values (23.7 percent leaves, 14.7 percent stems) were measured in February. Khalil and others (1986) performed chemical analyses on leaves of six *Atriplex* species (*A. nummularia*, *A. canescens*, *A. vesicaria*, *A. rhagodioides* F. Muell., *A. lentiformis* [Torr.] S. Wats, and *A. undulata* [moq.] Dietr.) grown in Saudi Arabia. They found somewhat higher crude protein content (16.7 to 25 percent) than those reported for North American *Atriplex* spp. (table 2). Sulfur amino acids were reported to be the most deficient essential amino acids in all species, while lysine content was close or above standard. Digestible energy content reported ranged from 3.2 to 3.4 Mcal per kg. While rumen microbes are able to synthesize all the amino acids classified as essential for monogastrics, a general sulfur deficiency could hinder microbial protein synthesis and could limit animal function (Van Soest 1994).

Gross energy and mineral content of annual growth in *Atriplex canescens* (measured as ash content and combustion heat of oven-dried material) reported for individuals from seven sites in Utah and Colorado was within the expected range of values (table 2). Average gross energy content (4.3 mcal per kg) was somewhat higher than the values reported for greasewood (*Sarcobatus vermiculatus*) (3.7 mcal per kg), yet lower than in *Artemisia tridentata* (4.7 mcal per kg), *Chrysothamnus nauseosus* (4.8 mcal per kg), and *Chrysothamnus linifolius* (4.5 mcal per kg). Relatively high content of essential oils and resins may account for energy content of *A. tridentata* and *C. nauseosus,* respectively (USDA 1937). Mineral content of fourwing saltbush (9.9 percent) was lower than in *S. vermiculatus* (20.2 percent), yet higher than in the other shrubs included in the study (Van Epps and others 1982).

Young greenhouse-grown plants of 14 species of *Atriplex* exhibited crude protein contents within the ranges reported for North American *Atriplex* species (table 2) in August and December measurements (Davis 1981). Another greenhouse experiment with young *A. lampa* designed to study the effects of water stress on growth and nitrogen content was conducted by Trione and Passera (1993). These authors reported that while low water supply gradually reduced growth, it did not affect nitrogen content of young saltbush plants. They also found that *A. lampa* stored a large amount of nitrogen (20 to 69 percent of total nitrogen) in the free form (nonprotein nitrogen inferred), and they related this to plant strategies of uptake and utilization of nitrogen not affected by the water-stress treatment.

Interplanting of fourwing saltbush into a seeded stand of crested wheatgrass at Nephi, UT, was reported to promote increases in grass forage yield and protein concentration, and to increase the total forage biomass as well (Rumbaugh and others 1982). Protein content of fourwing saltbush foliage in this experiment was twice the protein concentration of the grass at all sampling dates.

Sims and Taylor (1973) obtained rather surprising results in an in vivo digestibility trial with rumen fistulated steers on fourwing saltbush containing 5.6 to 11.5 percent crude protein (depending on phenological stage) from the shortgrass steppe in Colorado (table 3). They reported relatively low values of digestible crude protein in *Atriplex.* In fact, during dormancy of the four species they studied (*Bouteloua gracilis*, *Agropyron smithii*, *A. canescens*, and *Sphaeralcea coccinea*), fourwing saltbush was the species that exhibited lowest crude protein content. Cook and others (1977), in a table on average nutritive value of Colorado range plants, reported similar values of protein and digestible energy for both grasses and the forb, but reported almost twice the winter protein content for *A. canescens.*

Cattle diets, on sites with both sparse and abundant fourwing saltbush, on the shortgrass steppe (Central Plains Experimental Range) were composed of 23 percent (yearly average) fourwing saltbush (Shoop and others 1985). Microhystological analysis of feces showed that fourwing saltbush was the major component of winter diets on the Central Plains Experimental Range (table 4). These authors stated that 90 percent of the protein requirements and all the metabolizable energy requirements of a dry pregnant cow could be covered by a diet containing 33 percent fourwing saltbush and 67 percent blue grama (on the basis of the work by Cook and others 1977). Results from cattle diet analysis on the shortgrass steppe, reported by Shoop and others (1985), suggest that when fourwing saltbush is abundant, cattle tend to graze it preferentially. This strengthens apprehensions regarding the accuracy of Sims and Taylor's (1973) estimate of winter crude protein content for *A. canescens* on the shortgrass steppe in Colorado. However, cattle grazing a grass-fourwing saltbush mixture in Texas during the month of January took considerably fewer bites of fourwing saltbush compared to herbaceous forage (Petersen and others 1994). These authors

Table 3—Comparative chemical composition and average digestibility of two grasses, a forb and a shrub from the shortgrass steppe[a].

	Dry matter digestibility[b]		Crude protein	Digestible crude protein	Digestible energy	Ca	P
	Percent		Percent	Percent	*Mcal per kg*	*Percent*	*Percent*
Bouteloua gracilis	E	73	6.4	4.2	2.6	0.38	0.10
	D	48	6.2	3.9	1.8	.27	.12
Agropyron smithii	E	73	9.3	6.5	2.7	.20	.10
	D	48	5.3	3.2	2.2	.22	.14
Atriplex canescens	E	71	11.5	8.7	2.9	.89	.17
	D	50	5.6	2.3	2.3	.82	.10
Sphaerelcea coccinea	E	65	8.9	7.2	3.0	2.06	.15
	D	71	9.0	7.3	3.2	2.53	.15

[a] Adapted from Sims and Taylor (1973).
[b] E = early growth (early spring); D = dormant (midwinter).

Table 4—Winter and summer diets of cattle on sites dominated by fourwing saltbush on the shortgrass steppe[a].

Site	Winter Species frequency	Winter Diet composition	Summer Species frequency	Summer Diet composition
	Percent			
Sandy plains and overflow sites (abundant saltbush)				
Bouteloua gracilis	68.7	11	54.5	14
Agropyron smithii	21.3	19	24.8	15
Atriplex canescens	19.3	32	7.8	14
Sphaerelcea coccinea	21.8	2	64.8	5
Loamy plains site (sparse saltbush)				
Bouteloua gracilis	66.0	7	62.9	18
Agropyron smithii	5.2	7	0.8	7
Atriplex canescens	0.1	3	0.1	1
Sphaerelcea coccinea	40.8	3	51.7	11

[a] Adapted from Shoop and others (1985).

attributed this to the fact that cattle were able to use the herbaceous forage in a more efficient way. They estimated that it would take cattle about 3 minutes to consume as much shrub dry matter as they would consume by feeding approximately 1 minute on herbaceous forage.

A study on diets of sheep grazing in *Atriplex vesicaria*-dominated communities in Australia, however, revealed that animals discriminated against dominant shrubs, preferring associated herbaceous vegetation (Leigh and Mulham 1967). Palatability studies of *A. canescens* carried out by Nemati (1977) in Iran showed that *A. canescens* had intermediate palatability compared with the native browse species *Artemisia herba alba* and *Kochia prostrata.* The author gave sheep free access to two levels (1.8 and 2.0 kg) of availability of cuttings of each shrub and found that the amounts of *A. canescens* consumed were smaller than *K. prostrata* yet larger than *A. herba alba.*

Pearson and others (1990) conducted a browsing experiment with interplanted individuals of *A. vesicaria* from six different populations that had been historically submitted to either heavy or light grazing by sheep. Their objective was to study the influence of past grazing history on palatability of bladder saltbush to sheep. They suggested that plants with a long history of heavy grazing were less palatable than plants from the historically light-grazed populations. However, they were not able to distinguish differences in utilization of shrubs related solely to past history of grazing. When flowering or fruiting status and salinity were added to their model, they found significant differences in utilization (attributed to differential palatability) between individuals with different histories of grazing. Pearson and others (1990) also reported greater heterogeneity in palatability among plants with histories of heavy grazing than among those with histories of light grazing. They hypothesized that grazing by sheep may have selected in favor of less palatable phenotypes, thus increasing heterogeneity. While the authors postulated interesting questions, their results do not appear to be conclusive.

Overall, results from studies on chemical composition of edible biomass of *Atriplex* appear to coincide in describing it as a high crude protein-low gross energy forage. Palatability was generally described as intermediate to low, depending on species and season.

Performance of Ruminants Fed with *Atriplex* Diets

Trials with sheep fed on diets based on *Atriplex vesicaria*, *A. nummularia*, *A. angulata*, *A. pyramidata*, and *A. canescens* have, in general, reported animals to have maintained live weights (Atiq-ur-Rehman and others 1990a,b; Kessler 1990; Wilson 1966a). Live weight losses were reported for weanling Angora goat kids that lost 40 g per head per day in a 34 day trial on fourwing saltbush pastures (Ueckert and others 1990a). In this same experiment, however, animals grazing saltbush with either forb-grass mixtures or with 32 percent crude protein supplementation were reported to have gained weight. Live weight gains for yearling Angora does grazing fourwing saltbush-grass mixtures were also reported for both wet and dry winters (Ueckert and others 1992). Benjamin and others (1992) reported no live weight gains in sheep consuming 1200 g per day (dry matter) of 18 percent crude protein *A. barclayana* and up to 300 g of tapioca supplement. However, these authors also reported that live weight of sheep consuming a diet consisting of 900 g per day (dry matter) of *A. barclayana* and 500 g per day (dry matter) of tapioca increased 3 kg over a 30 day period (100 g per day). Trials conducted in Pakistan, comparing performance of sheep grazing seeded stands of fourwing saltbush or native mixed grassland-shrubland range, or native grazing range with barley or alfalfa supplementation, showed sheep gaining live weight in all treatments. However, the lowest absolute live weight gain values were recorded for the saltbush diet (Atiq-ur-Rehman and others 1990a). The author reported having found no statistical differences between saltbush diets and either range grazing or range grazing plus barley grain supplementation. This author argued strongly in favor of the use of *Atriplex,* not only for maintenance but also to produce weight gains in sheep. Kessler (1990) reported results from a trial in Saudi Arabia where even though sheep herds feeding on *A. nummularia* did not gain weight, they performed better than sheep grazing unimproved rangeland which lost weight over the trial period. Ueckert and others (1990b) found that yearling ewes grazing a grass-fourwing saltbush mixture during 60 days in winter gained 5.4 lb per head. Conversely, yearling ewes wintered on a dormant warm season grass or on a grass-saltbush rotation during the same period lost weight.

Wilson (1966a,b) was able to assess the importance of good quality drinking water (with low sodium chloride content) as a factor regulating levels of consumption of the *Atriplex* species he studied. Water with 0.9 to 1.2 percent NaCl depressed intake of *A. nummularia* in sheep to half the levels otherwise obtained with low-salt drinking water. The high content (3.2 to 8.2 percent) of sodium in the species of *Atriplex* used in this feeding trial required sheep to ingest larger amounts of drinking-water to be able to keep sodium dilution proportions in the body constant. MacFarlane and others (1967) reported a considerable amount of variation between two sheep breeds (Border Leiceseter and Merino) and among individuals of the same breed in water turnover time and, consequently, total volume consumed, to cope with high electrolyte concentrations in *Atriplex*. They reported some sheep using twice as much drinking water as others when browsing *A. nummularia* pastures.

Interplanting of *Atriplex nummularia* and *A. vesicaria* in natural grassland pastures had little effect on total production and on seasonal fluctuations of wool growth in another experiment conducted with Merino wethers in Australia (Leigh and others 1970). Hobson and others (1986) reported that a diet of *A. nummularia* alone was not sufficient to provide the energy required for pregnant Angora goat nannies. Supplementation with a maize-based ration was required to avoid abortions and guarantee optimal fetal growth.

Several experiments cited by Glenn and others (1992) were conducted with cattle, sheep, and goats to test the ability of several *Atriplex* species to replace traditional feeds, such as alfalfa hay. The results of these studies suggested that some *Atriplex* species could act as a substitute for alfalfa, provided they were fed together with energy-rich foodstuff. An interesting feed lot experiment with crossbreed heifers showed that *A. undulata* was as readily accepted as alfalfa by animals that had not been preconditioned to its use when it composed 20 percent of the ration.

Most feeding-trial studies have shown that ruminants fed with *Atriplex* diets tend to maintain body weights. Claims regarding the possibility of body weight gains in animals fed on saltbush diets do not appear to be substantiated by most of the research results reviewed. However, the value of *Atriplex* as a forage resource may increase considerably when it is fed to ruminants together with adequate energy supplementation (but see table 5).

Metabolic Alterations in Ruminants Consuming Atriplex

Weston and others (1969) conducted a 21-day digestibility trial with mature Merino wethers that were kept in metabolism cages and fitted with ruminal and abomasal cannulae. Several digestion parameters (including flow of digesta and digestibility of organic matter and protein) were measured for animals consuming leaves of *Atriplex nummularia*. The authors had previously performed a similar experiment with 23 common pasture plants. They reported that values

Table 5—Nitrogen status of ruminants fed on *Atriplex*-based diets.

Species	Diet	N Intake	Fecal N	Urinary N	N balance	Reference
		- - - - - - - - - - - - - *g per day*			- - - - - - - - - - - - -	
Sheep	(*A. nummularia*)	16.3	3.5	14.9	–1.97	Hassan and others 1979
Goats	(*A. canescens*)	8.0	2.0	7.0	–1.0	Ueckert and others 1990a
Goats	(*A. canescens*) + concentrate	23.0	5.0	13.0	5.0	Ueckert and others 1990a
Sheep	(*A. barclayana*)	16.6	4.5	9.1	3.0	Benjamin and others 1992
Sheep	(*A. barclayana*) +100 g per day tapioca	17.8	5.3	9.4	3.1	Benjamin and others 1992
Sheep	(*A. barclayana*) +200 g per day tapioca	18.3	5.7	9.7	2.9	Benjamin and others 1992
Sheep	(*A. barclayana*) +300 g per day tapioca	18.9	5.9	7.8	5.2	Benjamin and others 1992

of measured parameters for *Atriplex* fell within the ranges observed in previous experiments, except for two aspects of digestion. Saltbush "…deviated markedly from the others" (p. 520) in extent of digestion of organic matter in the "stomach" (rumen?) and rate of absorption of volatile fatty acids in the rumen. Because residence time for *Atriplex* in the rumen was comparable to other forages, Weston and others (1969) suggested that ruminal microbes could have suffered metabolic alterations that prevented them from digesting fiber. A very low percentage of volatile fatty acids was reported to be absorbed from the rumen, as compared with other forages. A slight increase in rumen pH was measured (+0.3 to 0.9), but according to the authors, this could not account, by itself, for the degree of absorption impairment. Finally, Weston and others (1969) stated that the protein value of these diets could be appreciably lower than what might have been inferred from chemical analyses of the crude protein. A large amount of the ingested crude protein was degraded to ammonia in the rumen; the crude protein in forms other than ammonia was stated to be equivalent to 60 percent of the total content of forage crude protein.

Questions related to the metabolism of nitrogen in ruminants fed with the apparently protein-rich saltbushes have arisen repeatedly in a number of trials with sheep and goats. A common element in trials that have measured nitrogen inputs and outputs is a surprisingly high level of urinary nitrogen, which sometimes causes a negative nitrogen balance in animals. Several authors have related this phenomenon to the low content of gross energy in saltbushes. However, experiments in which animals that were fed on saltbush diets received energy supplementation did not appear to confirm this hypothesis completely (table 5).

Hassan and others (1979) reported negative nitrogen balances in crossbred sheep consuming an average of 801 g dry matter per day of hand-harvested leaves and succulent stems of *Atriplex nummularia*. Six 43 kg animals were housed individually for 21 days in metabolic cages. Urinary nitrogen losses measured by the authors were more than 10 times higher (table 5) than the predicted values of 1.4 g N per day for 43 kg sheep, according to calculations made by Swanson (1982). Fecal nitrogen losses were similar to those predicted by NRC (1985) for 43 kg sheep (4 to 6.4 g N per kg of dry matter consumed).

Ueckert and others (1990a) studied nitrogen balance of yearling Angora nannies fed ad libitum spring-growth leaves and twigs of fourwing saltbush, with 16 percent crude protein and 62 percent dry matter digestibility, for a period of 20 days. Half the animals received a diet of saltbush alone, while the other half were fed a diet of saltbush leaves and supplement. The supplement consisted of 300 g of 32 percent crude protein concentrate for each animal per day. Goats eating saltbush alone lost 88 percent of their daily nitrogen intake in the urine, while goats fed on saltbush and concentrate lost only 57 percent of the ingested nitrogen in the urine. An estimate of expected daily urinary nitrogen loss for the goats in this experiment, under average conditions, would have been approximately 1.27 g N per day (assuming a live weight of 35 kg, and following Swanson's (1982) estimate for sheep). Expected losses of fecal nitrogen, on the other hand, can be estimated to range from 4 to 6.4 g of N per kg of dry matter consumed (NRC 1985). Although animals were able to feed ad libitum, it seems reasonable to assume consumption to have been close to 1.1 kg of dry matter per day (close to 3 percent of the animal's live weight on a dry-matter basis). While values of fecal nitrogen content were approximately within expected ranges (table 5), urinary nitrogen contents were consistently much higher than what would otherwise have been expected.

Benjamin and others 1992 fed four 40 kg crossbred male lambs a mixture of leaves and twigs of *Atriplex barclayana*, either alone or mixed with different amounts of tapioca (table 5). Each animal was randomly assigned one of the diets for a period of 9 days (having been previously adjusted to the diet for 10 days); all animals were submitted to all diets. Even though Benjamin and others (1992) did not find negative nitrogen balances, the values for urinary nitrogen were very high compared with expected value (1.37 g N per day for 40 kg live weight, following Swanson's (1982) estimate for sheep). Again, fecal nitrogen losses were within the expected range for animals consuming 1,200 g of *Atriplex* and up to 300 g of tapioca daily.

In both cases supplementation improved nitrogen retention status but, overall, it was unable to bring urinary nitrogen values down to normal ranges. Ueckert and others (1990a) suggested, as possible explanations for what they observed, that either plant secondary compounds were interfering with nitrogen retention, or plant crude protein was being hydrolyzed in the rumen and rapidly absorbed as ammonia and excreted in the urine. Benjamin and others (1992) related the greater losses of urinary nitrogen, partly to greater volumes of urine excreted in sheep consuming *Atriplex*. They also stated that, as with other halophytes, *Atriplex* exhibited high mineral content and high levels of nonprotein nitrogen, including quaternary ammonium compounds associated with salt tolerance mechanisms. Both of these characteristics, they argued, would represent drawbacks in the energy and nitrogen balances of ruminants consuming *Atriplex* diets.

Le Houérou (1992) argued that results showing *Atriplex* as having little forage potential production resulted from overly short feeding trials (2 to 5 weeks) with unadapted animals. This author stated that in a 9 month trial conducted in Libya, sheep doubled their initial intake of saltbush (*A. nummularia* and *A. canescens*) over a period of 3 to 5 months (from 0.8-1.2 to 1.5-2.5 kg digestible matter per head per day). He reported that, with the levels of saltbush intake he obtained in this trial, body weight of mature animals could be maintained indefinitely, and that when saltbush was used as supplementation to grazing, live weight gains could be expected.

Even if Le Houérou's (1992) assertion about the negative effect of short feeding trials on the assessment of forage attributes of *Atriplex* is accurate, the fact that saltbush stands are often used to bridge relatively short periods of forage scarcity still poses interesting questions about its alleged qualities. If livestock are fed on saltbush over a drought or winter season (3 to 5 months average), they probably spend most of the time adapting to *Atriplex* and are unable to assimilate a large amount of its crude protein content. Further research on gut microbe adaptation times and processes is necessary.

Possible Management Implications of Herbivore-*Atriplex* Interactions

Research on aspects of the ecology of *Atriplex* reviewed in previous sections deals with three scenarios that are not always explicitly addressed by the authors. The first one comprises situations in which *Atriplex* is a dominant within the community; two examples of this are the *A. confertifolia*- and *A. vesicaria*-dominated communities. A second scenario occurs with species from this genus that grow as local populations within a community where *Atriplex* is clearly neither a dominant species nor a strong competitor; *A. canescens* is a good example. Finally, there are situations in which *Atriplex* has been seeded on rangelands that have undergone some type of major disturbance and that are subjected to fairly intense management (irrigation, fertilization, rotation grazing); many species of *Atriplex* have been used in these situations, but *A. canescens* and *A. nummularia* are probably the most important. Generalizations and comparisons across scenarios may not always be pertinent. Responses to browsing may differ in each case, depending on the status of *Atriplex* within the community. *A. confertifolia* appears to be a clear example of a saltbush species that under certain circumstances is favored by grazing while the general trend is opposite. Even when it may seem contradictory, it is not surprising that many of the saltbush species that are considered a valuable browsing resource are the most browsing-sensitive. They are, perhaps, the species within the genus that have evolved less efficient defense mechanisms, and are thus unable to cope with herbivory and competition successfully.

Variability, plasticity, and active population turnover are important characteristics of the genus that have probably helped a number of *Atriplex* species cope with herbivory. Half-lives of approximately 20 years (such as short generation times) can be expected to favor perceptible heritable changes over relatively short periods of time. History of browsing could potentially have strong effects on local populations by selecting for better defended, less palatable, and more resistant genotypes. Clipping experiments and some browsing research suggest that a number of saltbushes should be managed within very narrow boundaries of defoliation and rest to guarantee survival and adequate reproduction. However, aspects of plant defense that may be able to control browsing patterns under situations of reasonable use by browsers may have been underestimated.

Spatial and temporal heterogeneity of the effective browsing resource is probably a crucial issue in browsed *Atriplex* populations. Such heterogeneity stems from the interactions between breeding system, defense ecology, age structure, soil patchiness, climate, and other factors. Differential defense of males and females at different phenological stages can alter seasonal availability of forage to browsers. The extent to which a shrub is able to withstand defoliation and still allocate carbon to defense could control the ability of plants to influence browsing patterns through time. The ability of some individuals to switch sexes and potentially alter carbon allocation priorities could change their defense capabilities, thus altering forage availability to herbivores. Segregation of sexes across the landscape (controlled by soil texture and moisture), coupled with differential levels of defensive compounds in males and females may control distribution of browsers over small areas.

Results from feeding trials with *Atriplex* suggest that chemical analyses of nutritional attributes of saltbushes need to be interpreted with care, lest the actual nutritional value in vivo be overestimated. Further understanding of the interactions between soil salinity and drought, with the relative amount of nonprotein nitrogen compounds and minerals contained in edible tissues, may be an important key to predicting the relative nutritive value of saltbushes. Questions related to the metabolic pathways of nonprotein nitrogen compounds from *Atriplex* in ruminants, and their interaction with the digestible energy content of the forage, may also be crucial to fairly assess the amount of nitrogen from edible shrub biomass that is effectively available for secondary production. Ways in which secondary compounds from *Atriplex* might alter nitrogen metabolism in ruminants also appear to require further research.

If sustainable browsing of saltbush stands is to be attained, managers must take into account interactions occurring between herbivory and both interspecific and intraspecific competition in the plant community. Unlike other shrub species, where recruitment events are rare and individuals are long-lived, saltbushes are relatively short-lived and recruitment events are fairly common. These processes, which affect population turnover rates, appear to be far more dynamic and sensitive to both biotic and abiotic factors in saltbushes as compared to other shrubs. The success of management strategies for browsed saltbush stands may depend, to a great extent, on the ability of such strategies to balance rates of recruitment and mortality of individuals.

Factors affecting recruitment appear to be more closely related to competitive interactions (altered by herbivores) than to the direct effects of browsing on seed production or propagule survival. Competitive interactions with other members of the plant community could limit recruitment success in many circumstances. Research reviewed in previous sections indicates that in communities with *A. confertifolia* increase in density of shadscale plants in grazed pastures, as compared to protected areas, could have been a result of decreased competitive ability of the more heavily browsed members of the community. Furthermore, different degrees of browsing on saltbushes, affecting crown sizes and shrub density, could alter the shrub interspace environment and indirectly affect conditions for recruitment by either facilitating or hindering the establishment of potential competitors. Further research is required to understand these interactions.

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Appendix: Index of Scientific and Common Plant Names (some species have no established common names)

Scientific name	Common name
Acer negundo	Boxelder
Achillea millefolium	Yarrow
Agropyron smithii	Western wheatgrass
Arachis hypogaea	Peanut
Artemisia herba alba	White sage
Artemisia spinesens	Budsage
Artemisia tridentata	Big sagebrush
Asparagus officinalis	Asparagus
Astragalus gummifer	Tragacanth
Atriplex barclayana	
Atriplex acanthocarpa	Armed saltbush
Atriplex amnicola	River saltbush
Atriplex angulata	
Atriplex bunburyana	
Atriplex canescens	Fourwing saltbush
Atriplex cinerea	
Atriplex confertifolia	Shadscale
Atriplex coriacea	
Atriplex corrugata	Mat saltbush
Atriplex cuneata	Castle Valley clover saltbush
Atriplex falcata	Falcate saltbush
Atriplex glauca	
Atriplex halimus	
Atriplex hymenelytra	Desert holley saltbush
Atriplex lampa	Zampa
Atriplex lentiformis	Big saltbush
Atriplex leptocarpa	
Atriplex leucolada	
Atriplex litoralis	Shore orache
Atriplex nummularia	Oldman saltbush
Atriplex padulosa	Marsh saltbush
Atriplex patula	Spearscale
Atriplex polycarpa	Allscale
Atriplex pyramidata	
Atriplex repanda	
Atriplex rhagodioides	
Atriplex rosea	Redscale
Atriplex semibaccata	Fleshscale
Atriplex stocksii	
Atriplex tridentata	Saltsage
Atriplex undulata	Wavy leaf saltbush
Atriplex vesicaria	Bladder saltbush
Avena sativa	Oats
Beta vulgaris	Sugar beet
Bouteloua gracilis	Blue grama
Cassia sturtii	Senna
Ceratoides lanata	Winterfat
Chenopodium ambrosioides	Wormseed
Chenopodium pumillo	

(con.)

Appendix (Con.)

Scientific name	**Common name**
Chenopodium quinoa	Quinoa
Chrysothamnus viscidiflorus	Douglas rabbitbrush
Chrysothamnus linifolius	Spreading rabbitbrush
Chrysothamnus nauseosus	Rubber rabbitbrush
Danthonia caespitosa	Wallaby grass
Ephedra gerardiana	Pakistani ephedra
Glycine max	Soya
Grayia brandegei	Spineless hopsage
Gutierrezia sarothrae	Broom snakeweed
Halogeton glomerulatus	Halogeton
Helianthus annuus	Common sunflower
Kochia prostrata	Forage kochia
Larrea tridentata	Creosote bush
Maireana brevifolia	Bluebush
Medicago sativa	Alfalfa
Oemleria cerastiformis	Indian plum
Panax ginseng	Ginseng
Prosopis jubiflora	Mesquite
Purshia tridentata	Antelope bitterbrush
Quillaja saponaria	Soap-bark tree
Rubus chamaemorus	Cloudberry
Rumex acetosella	Sour weed
Rumex hymenosepalus	Canaigre
Salsola kali	Russian thistle
Sarcobatus vermiculatus	Greasewood
Silene dioica	Red campion
Sphaerelcea coccinea	Scarlet globemallow
Spineacea olearacea	Spinach
Taraxacum officinale	Dandelion
Thea sinensis	Tea
Tribulus terrestris	Puncture vine
Zea mays	Corn

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Atriplex is a widespread genus with species dispersed over almost all continents. Many taxa within this genus perform outstandingly under a variety of stress conditions and are often an important source of forage for herbivores. Such attributes have drawn the attention of many researchers who have conducted extensive studies on *Atriplex* across a wide variety of environments and management scenarios. This report reviews much of the literature dealing with aspects of the biology of *Atriplex* from an animal-plant interaction perspective.

Keywords: saltbushes, shrub ecology, animal-plant interactions

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