

Chenopodiaceae—Goosefoot family

***Atriplex* L.**
saltbush

Susan E. Meyer

Dr. Meyer is a research plant ecologist at the USDA Forest Service's Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, Utah

Growth habit, occurrence, and use. The genus *Atriplex* L.—saltbush—is cosmopolitan in distribution and comprises about 250 species of annual and perennial herbs, subshrubs, and shrubs (McArthur and Sanderson 1984). Most species are halophytic (at least to some degree) and occupy salt desert, coastal strand, or saltmarsh habitats. Shrubby species are important in arid and semiarid regions throughout the world, with centers of diversity in south central Asia, Australia, temperate South America, and western North America. Western North America is an area of particularly high genetic diversity, with more than 20 principal species of shrubs and subshrubs as well as countless hybrids and variants; 12 of these species are described here (table 1). The genus is in a state of active evolution in the Intermountain region (Stutz 1978, 1984). The drying up of Pleistocene lakes 10,000 or so years ago opened up vast areas of unexploited salt-desert habitat. Shrubby saltbush species migrated in rapidly from several directions and hybridized freely, giving rise to the rich complex of forms in the region today.

In terms of areal extent, the most important species are probably shadscale and Gardner saltbushes (Blauer and others 1976). These species are regional dominants over millions of hectares in the Intermountain and northwestern Great Plains regions, respectively. Shadscale saltbush mostly occurs with winterfat (*Krascheninnikovia lanata* (Pursh) Guldenstaedt.); budsage (*Artemisia spinescens* D.C. Eaton); and other salt-desert shrubs, whereas Gardner saltbush is able to maintain codominance with perennial grasses (Stutz 1978). In the Mojave Desert, desert-holly is an upland landscape dominant, particularly in the Death Valley region, whereas allscale saltbush is a dominant species on playa fringes. Fourwing saltbush is the most widely distributed shrubby saltbush in North America and is often an important component of grassland communities, especially in the Chihuahuan Desert and western Great Plains. Sickie and basin saltbushes are inconspicuous but common components of northern Intermountain salt-desert vegetation.

Shrubby saltbush species are extremely important as forage plants for livestock and wildlife in arid and semiarid regions worldwide (Goodall 1982). They provide palatable and nutritious feed on a year-round basis and are especially important on winter ranges. As a consequence, they have been studied and used in range rehabilitation far more extensively than most other shrubs (Jones 1970; McArthur and Monsen in press; Osmond and others 1980; Tiedemann and others 1984). There is also considerable interest in utilizing saltbush species as irrigated forage crops on marginal, salinized agricultural land (Glenn and others 1992; Watson and O'Leary 1993). Some shrubby saltbush species are also used extensively for the stabilization of drastically disturbed land because of their ability to establish and grow on harsh sites.

Geographic races and hybrids. An important feature of infraspecific variation in many saltbush species is the presence of series of races at different ploidy levels (Sanderson and others 1990; Stutz 1978; Stutz and Sanderson 1979). Polyploid races often show dwarfing and adaptation to extremely harsh environments. The tendency to evolve polyploid races has also been important in facilitating the formation and stabilization of interspecific hybrids. Saltbush species possess a wealth of genetic variability, both within and among ploidy levels for numerous traits that may be important for survival both of local populations in nature and of the products of artificial seedings. Hybrid forms, even those that have not yet formed stabilized populations in nature, may possess attributes that make them useful in specific disturbed land rehabilitation applications (Stutz 1995).

Common garden studies with fourwing saltbush have demonstrated ecotypic variation in growth form, growth rate, winter-greenness, drought and cold hardiness, palatability, nutrient status, seed size, and seed germination and establishment traits (McArthur and others 1983; Springfield 1970; Van Epps 1975; Welch and Monsen 1981, 1984). It is

Table 1—Atriplex, saltbush: ecology and distribution			
Scientific name	Common name(s)	Geographic distribution	Ecology
<i>A. canescens</i> (Pursh) Nutt.	fourwing saltbush, chamisa	Widely distributed in W North America	Wide ecological amplitude; mostly in sandy uplands & gravelly washes
<i>A. confertifolia</i> (Torr. & Frem.) S. Wats.	shadscale saltbush, spiny saltbush, sheepfat	Widely distributed in W North America	Wide ecological amplitude; mostly on silt or clay soils of low to moderate salinity
<i>A. corrugata</i> S. Wats.	mat saltbush	Colorado Plateau N to Red Desert of Wyoming	Restricted to heavy saline clays on shale outcrops
<i>A. cuneata</i> A. Nels.	Castle Valley saltbush	Colorado Plateau	Restricted to heavy saline clays on shale outcrops
<i>A. falcata</i> (M.E. Jones) Standl.	sickle saltbush, falcate saltbush, Nuttall saltbush	N Great Basin	Subsaline soils of benches & alluvial fans
<i>A. gardneri</i> (Moq.) D. Dietr.	Gardner saltbush	NW Great Plains, Wyoming, & Montana	Mostly on saline or subsaline clay soils
<i>A. hymenelytra</i> (Torr.) S. Wats.	desert-holly	Mojave Desert	Clay flats & gravelly fans under extreme aridity
<i>A. lentiformis</i> (Torr.) S. Wats.	big saltbush, quailbush, lensscale	Mojave Desert; cismontane & coastal California	Mostly around saline springs & seeps
<i>A. obovata</i> Moq.	mound saltbush, broadscale saltbush	Chihuahuan Desert	Saline flats
<i>A. polycarpa</i> (Torr.) S. Wats.	allscale saltbush, cattle saltbush, desert saltbush	Mojave Desert; Central Valley of California	Saline & subsaline slopes & flats
<i>A. semibaccata</i> R. Br.	Australian saltbush, trailing saltbush	Introduced from Australia	Along roadsides & in saline disturbances
<i>A. tridentata</i> Kuntze	basin saltbush, trident saltbush	NE Great Basin, & Uinta Basin of Utah	Saline flats
Sources: Ansley and Abernathy (1985), Meyer (1996), Mikhail and others (1992), Young and others (1980).			

likely that other widely distributed saltbush species possess similar ecotypic differentiation. Many researchers who have studied saltbush establishment from artificial seedlings emphasize the importance of using not just adapted species, but locally adapted ecotypes of these species (Bleak and others 1965; McArthur and others 2004; Nord and others 1971; Plummer and others 1968; Springfield 1970).

Cultivar development for saltbush has also emphasized ecotypic adaptation. The 3 released cultivars of fourwing saltbush were developed for warm winter ('Marana'), intermountain cold desert ('Rincon'), and northwestern Great Plains ('Wytana') planting applications (Carlson 1984). 'Wytana' was developed from a fourwing saltbush × Gardner saltbush hybrid entity known as *Atriplex aptera* A. Nels.

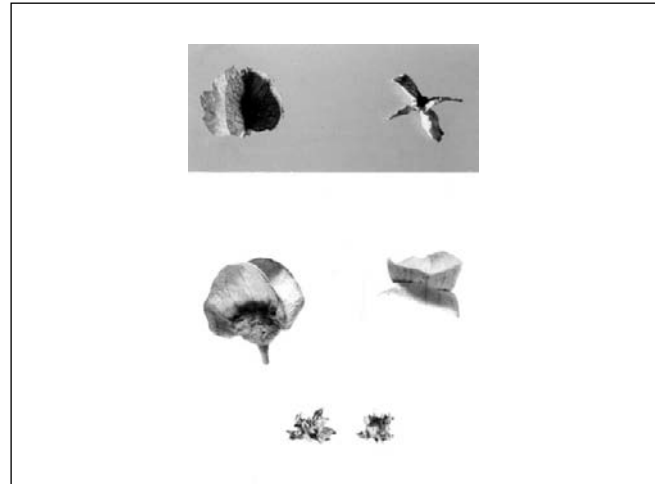
Flowering and fruiting. The flowers of saltbush are yellowish or brownish, inconspicuous, and unisexual, and are borne in the axils of the upper leaves or in terminal spikes. The male flowers consist of groups of stamens within a shallow 5-toothed calyx; petals are absent. Both petals and calyx are absent in the female flowers. The naked 1-seeded ovary is borne instead between 2 leaflike bracteoles.

Most native shrubby saltbush species are dioecious, that is, the sexes are borne on separate plants. Fourwing saltbush possesses a unique gender system known as trioecy, with genetically male plants, genetically female plants, and a third category that can switch sexes depending on environmental conditions (McArthur and others 1992). Australian saltbush is monoecious, that is, the flowers are unisexual and both sexes are present on the same plant.

Saltbush species flower in early to late summer, and fruits ripen from early fall to winter. The flowers are wind-pollinated. The leaflike bracteoles stay green and photosynthetically active until quite late in the ripening process and probably provide resources directly to the ripening ovule within. The fruits often persist on the bushes at least until spring, and it is not uncommon to find 2 generations of fruits on a plant simultaneously. Harvestable seedcrops of fourwing saltbush are produced on average 3 of every 5 years, whereas some of the more xerophytic species, such as mat saltbush, produce good seedcrops only occasionally.

The terminology describing the fruits of saltbush has been a source of confusion. The family Chenopodiaceae as a whole is characterized by a fruit type known as a utricle, which is defined as a small, bladdery 1-seeded fruit with a thin, membranous pericarp (Munz 1974). The utricle in saltbush is contained within the bracteoles, which enlarge in size and become more or less sealed, forming a false-fruit, which will hereafter be referred to simply as "the fruit"

Figure 1—*Atriplex*, saltbush: bract-enclosed utricles ("fruits") of; *A. canescens*, fourwing saltbush (**top**), *A. confertifolia*, shadscale saltbush (**middle**); and *A. falcata*, sickle saltbush (**bottom**).



(figure 1). The bracteoles are not fused to the utricle, but in native species they usually enclose it so completely that threshing is not possible. In Australian saltbush, the bracteoles are not fused across the top and the utricles may be threshed free (figure 2) (Foiles 1974).

The saltbush seed itself is contained within the utricle and is generally not separable from it (figure 3). The disk-shaped seed has a curved embryo on its outer perimeter and a scanty provision of storage tissue (in this case perisperm) in the center. In most native species, the ovule (and thus the seed) is inverted within the fruit, meaning that the radicle end points upward. This facilitates radicle emergence from between the bracteoles, which often have their only opening or weakest point at the tip. The degree of woody thickening of the bracteole walls varies among and within species and may be linked to the persistent seed dormancy often encountered.

Seed collection, cleaning and storage. Saltbush seeds are harvested by stripping or beating the ripe fruits into shoulder hoppers, boxes, or bags, or onto tarps spread under the bushes. Vacuum or reel-type harvesters may also be used (McArthur and others 2004). In field cultivation, 'Wytana' fourwing and Gardner saltbushes have been cut and wind-rowed with a hay-swather and then combine-harvested. Seeds shattered during combining were salvaged using a vacuum harvester (Carlson and others 1984).

Seed collections of fourwing and shadscale saltbushes are commonly hammermilled to remove the bracteole wings (McArthur and others 2004). This reduces bulk by half and facilitates cleaning, handling, and seeding through conventional drills. Hammermilling has little effect on dormancy of

Figure 2—*Atriplex semibaccata*, Australian saltbush: bract-enclosed utricle

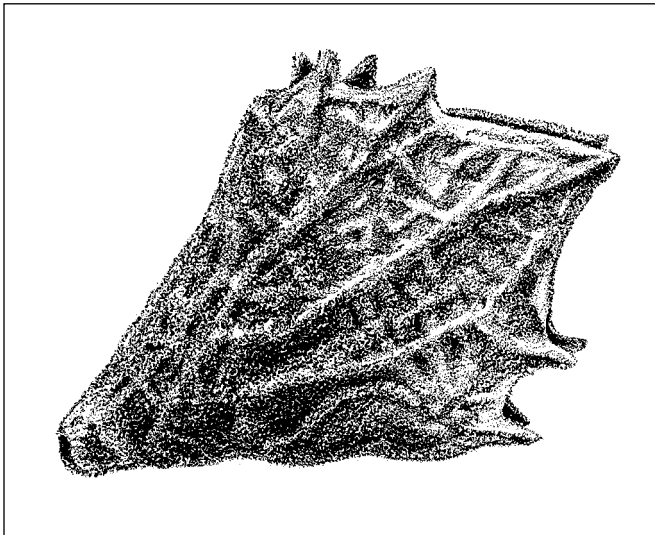
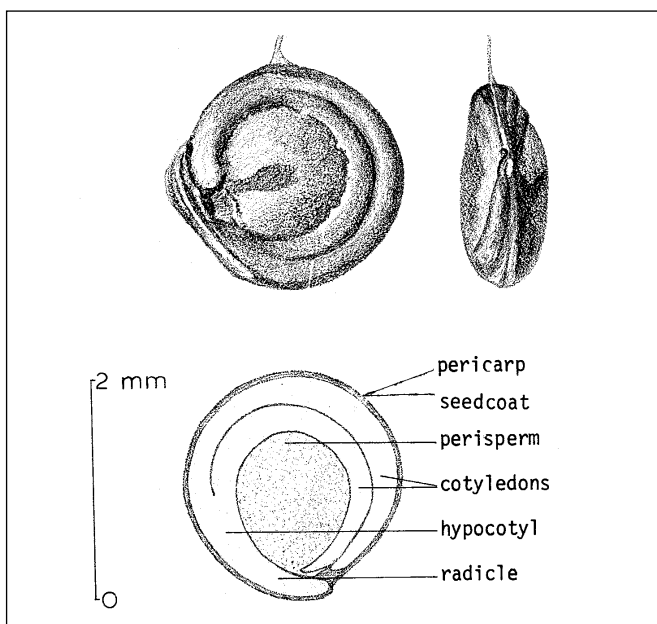


Figure 3—*Atriplex semibaccata*, Australian saltbush: exterior views in 2 planes of utricles removed from their bracts and a longitudinal section through a utricle.



fourwing saltbush but may speed the germination of nondormant seeds somewhat (Gerard 1978; Springfield 1970). Collections of wingless small-fruited species such as Gardner, sickle, and mat saltbushes do not require hammer-milling. Seed collections of all species may be cleaned by screening and blowing in a fanning mill (McArthur and others 2004).

Even relatively high-quality seedlots of saltbush may average only 50% fill. A cut test to determine fill is often

carried out before harvest. Fills of 40% or less are usually considered substandard. Such a seedlot would not normally be worth the expense of harvesting, cleaning, and transporting. Field-grown saltbush seedlots often have higher fill than wild-collected lots (Briggs 1984; Carlson and others 1984; McArthur and others 1978; Stroh and Thornberg 1969). Most of the weight of a saltbush fruit is in the bracteole walls, even after de-winging. Filled and unfilled fruits thus have similar density, making it impossible to remove unfilled fruits by fanning. Also, the variation in fruit size within a lot is not highly correlated with fill, so that screening to improve fill is not feasible.

Fruit size varies considerably among and within lots, especially for fourwing and shadscale saltbushes (table 2). Polyploid races often have smaller fruits. This variation in fruit size makes it essential to explicitly consider number of fruits per unit weight as well as fill percentage when planning seeding rates.

Seeds of most saltbush species are long-lived in dry storage and can be stored in an open warehouse for at least 5 to 10 years with little or no loss of viability (Springfield 1970; Stevens and others 1981). Controlled storage presents little advantage over open warehouse storage for these species. Attack by seed-destroying insects such as dermestid beetles (*Dermestes* spp.) during storage has been reported (Haws and others 1984).

Germination. Seeds of saltbush species as a group are characterized by high levels of dormancy and complex multiple dormancy mechanisms. The most universal characteristic seems to be the tendency to lose dormancy, or after-ripen, under dry conditions. For less-dormant species and lots this is manifested as an increase through time in the fraction of seeds germinable without pretreatment, or in the fraction of seeds able to germinate under non-optimum conditions, for example, osmotic stress. For more dormant species, after-ripening is manifested as an increase through time in storage in the response to dormancy-breaking treatments such as chilling (table 3).

In general, species and populations from warm desert and California cis-montane habitats produce seeds that are relatively nondormant, after-ripen quickly, and do not require chilling (Cornelius and Hylton 1969; Edgar and Springfield 1977; Kay and others 1977a&b; Mikhiel and others 1992; Springfield 1970; Warren and Kay 1984; Young and others 1980) (tables 1 and 3). Seeds of species and populations from cold desert, foothill, and northern plains habitats often require chilling for germination even after an after-ripening period (Ansley and Abernethy 1985; Meyer and others 1998) (tables 1 and 3). Shadscale saltbush seeds

Table 2— <i>Atriplex</i> , saltbush: fruit yield data				
Species	Fruit (x1,000) /weight			
	Range		Average	
	/kg	/lb	/kg	/lb
<i>A. canescens</i>				
intact	17–120	8–55	68	31
de-winged	29–326	13–148	118	54
<i>A. confertifolia</i>	65–277	30–126	142	65
<i>A. corrugata</i>	—	—	174	79
<i>A. cuneata</i>	—	—	180	82
<i>A. falcata</i>	—	—	434	197
<i>A. gardneri</i>	210–262	95–119	233	106
<i>A. hymenelytra</i>	—	—	477	217
<i>A. lentiformis</i>	900–2,000	409–909	1,957	890
<i>A. obovata</i>	—	—	457	208
<i>A. polycarpa</i>	785–1,370	357–623	1,078	490
<i>A. semibaccata</i>	165–317	75–144	—	—
<i>A. tridentata</i>	120–370	55–168	280	128
Sources: Belcher (1985), Foiles (1974), McArthur and others 2004).				

Table 3— <i>Atriplex</i> , saltbush: germination data					
Species	Storage (months)	Incubation treatment	Germination (%)		Samples
			Mean	Range	
<i>A. canescens</i>	3	15 °C	32	4–96	23
	24	15 °C	54	10–100	23
	3	4 wk @ 1–15 °C	41	4–93	23
	24	4 wk @ 1–15 °C	69	21–100	23
<i>A. confertifolia</i>	3	5/15 °C	0	0–1	15
	36	5/15 °C	2	0–6	15
	3	16 wk @ 1–5/15 °C	16	0–47	15
	36	16 wk @ 1–5/15 °C	46	4–83	15
<i>A. gardneri</i>	3	Mean multiple treatments	26	—	1
	15	Mean multiple treatments	48	—	1
<i>A. hymenelytra</i>	8	5/15 °C	33	—	1
<i>A. lentiformis</i>	8	10/20 °C	56	29–71	3
	24	Mean multiple treatments	39	39–40	2
	24	Best treatment 10/25 %C	68	—	1
<i>A. obovata</i>	8	10/20 °C & 0.05 M NaCl	42	—	1
<i>A. polycarpa</i>	8	10/20 °C	53	11–94	2
	8	20/30 °C	50	21–79	2
<i>A. semibaccata</i>	24	Mean multiple treatments	41	37–46	3
	24	Best treatment 10/25 °C	69	—	1
Sources: Ansley and Abernathy (1985), Meyer (unpublished data), Mikhail and others (1992), Young and others (1980).					
Note: Germination period is 28 days and germination is expressed as percentage of filled fruits, except for <i>A. gardneri</i> data, where germination is 14 days, and for <i>A. lentiformis</i> and <i>A. semibaccata</i> data, where germination is expressed as percentage of total fruits.					

rarely become germinable without chilling, regardless of their habitat of origin (Mikhiel and others 1992) (table 3).

Other treatments that have sometimes been found to remove dormancy include scarification and leaching (Ansley and Abernethy 1985; Graves and others 1975; Nord and Whitacre 1957; Sabo and others 1979; Twitchell 1955; Young and others 1980). Scarification apparently acts by

weakening the bracteole walls. Actual rupture of the membranous utricule wall is usually damaging to the seed (Sabo and others 1979). After-ripening may also act on the bracteole walls, as evidenced by work with a seedlot of the South American species *A. repanda* Phil., for which optimum time for sulfuric acid scarification decreased from 7 to 2 hours during 5 years in dry storage (Fernandez 1978). The bracte-

ole walls may also be weakened by the action of saprophytic fungi under field conditions (Vest 1952). Hand-removal of the bracteoles promotes increased germination in many species but does not necessarily remove dormancy completely, suggesting that either the utricle wall or the testa interacts with the embryo to impose dormancy even in excised fruits. The failure of excised fruits to germinate suggests a chilling requirement. Sanderson and others (1990) found that excised fruits of warm-winter populations of shadscale saltbush were more likely to germinate without chilling than those of cold winter populations.

Leaching probably promotes germination by removing some inhibitor from the fruit, either inorganic salts such as sodium chloride (Beadle 1952) or an organic inhibitor such as saponin (Nord and Van Atta 1960). It is important to remove excess water after soaking, as germination can be inhibited by inadequate aeration (Beadle 1952; Young and others 1980). Rates of leaching under field conditions are probably controlled by the osmotic potential of the seedbed. In the highly saline litter underneath bushes of many species, the salts in the bracteole walls would make only a minor contribution.

The complex dormancy mechanisms shown by many saltbush species function both to time germination appropriately within a given year and to ensure carryover of a persistent seedbank between years (Garvin and others 1996). Seed pretreatments to circumvent these mechanisms have limited application in field plantings but may be useful in seed quality evaluation and in nursery propagation.

Seed quality evaluation in saltbush is complicated by dormancy problems. Seedlots are usually cleaned to high purity, making the purity analysis quite simple. For fourwing saltbush, we proposed a 21-day germination test at 15 °C, a recommendation that was subsequently accepted as the official testing procedure (Meyer and others 1986). The most important determinant of viability is the fill percentage, that is, the proportion of fruits that contain an undamaged seed with a well-developed embryo. Post-test viability determination is essential in fourwing saltbush. Germination percentage may vary as a function of after-ripening status, or the test temperature may not be optimum for a particular lot. Post-test evaluation is even more essential for species of saltbush with less-known germination requirements.

In practice, few seedlots of saltbush are evaluated using a germination test. Because of dormancy problems, the tetrazolium test has become the standard method. The general method is to soak the intact (bracteoled) fruit for several hours or overnight and extract the utricle by either prying open the bracts, clipping at the stem end, or off-center longi-

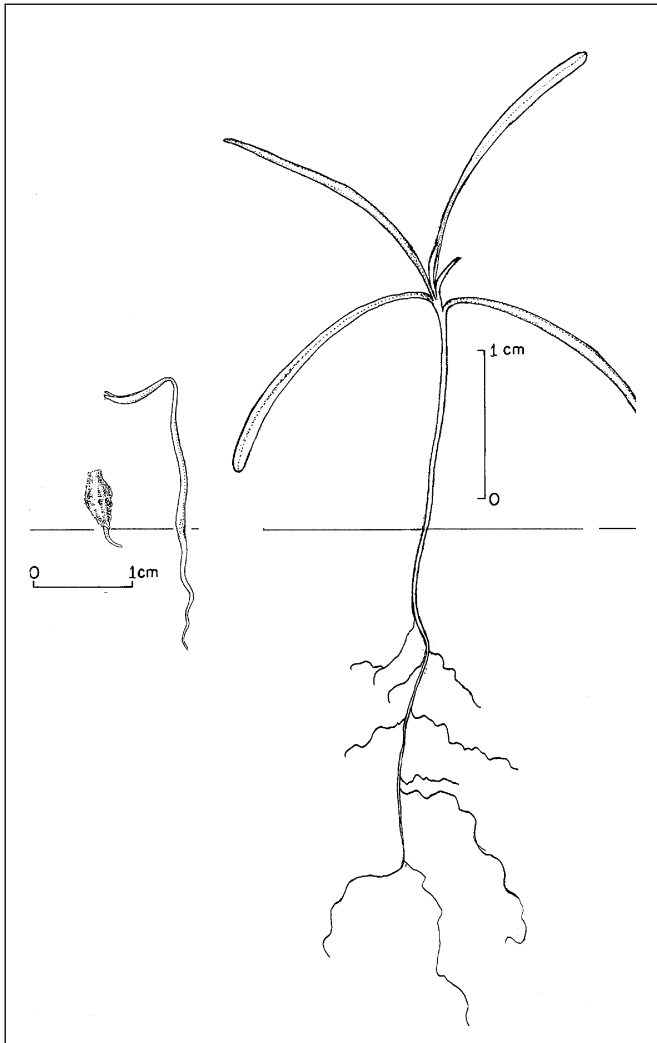
tudinal bisection (Belcher 1985). The utricles are then pierced in the center and placed in 1% tetrazolium solution for several hours, and the staining patterns on the linear embryos are evaluated. Saltbush seed quality is somewhat difficult to evaluate using tetrazolium. Staining is often weak and incomplete for embryos that are germinable, resulting in viability estimates that tend to be low (Ansley and Abernethy 1984; Springfield 1970).

Nursery and field practice. Saltbush species have been successfully propagated in the nursery, both as container stock (Ferguson 1980) and as bareroot stock (Shaw and Monsen 1984). Most of the information available is for fourwing saltbush, but it is probably broadly applicable to other species. Propagation may be from seeds or from stem cuttings (McArthur and others 1984; Richardson and others 1979). The latter are advantageous for obtaining clonal material of known sex for the establishment of seed orchards with optimal sex ratios (McArthur and others 1978). When high-quality seedlings of an adapted ecotype are outplanted during periods of optimal moisture, survival can be high (Foiles 1974; McArthur and others 2004). Wildlings of fourwing saltbush have also been used as transplant stock.

Saltbush species may also be direct-seeded successfully, although results have been inconsistent (McArthur and others 2004). Pitfalls include poor choice of species or ecotypes; using poor-quality seeds (low fill); planting too deep; planting at the wrong season; excessive competition from weeds or seeded grasses; interactions with pathogenic fungi such as damping-off diseases; and seedling predation by grasshoppers, rabbits, or other animals. Fourwing saltbush fruits are apparently not particularly attractive to granivorous rodents (Everett and others 1978), possibly because of the saponin content of the bracts (Sanderson and others 1986), so pre-emergence seeds predation is rarely a problem. Seeding rates of 4 to 8 kg/ha (3.5 to 7 lb/ac) have been recommended for de-winged lots of fourwing saltbush. This corresponds to about 200 to 530 live seeds/m² (25 to 50/ft²) for a seedlot of average fruit size (122,000/kg) and fill (50%). In regions of low and unpredictable precipitation, saltbush seedlings may fail to emerge or survive in dry years even when all planting guidelines are followed. As annual recruitment is not necessary for the perpetuation of natural stands, this poses a problem only in artificial revegetation. Once seedlings establish, however, young plants grow rapidly (figure 4) and may become reproductively mature in their second growing season.

The large fruits may create the impression that saltbush should be drill-seeded at considerable depth, but seed reserves are small, as bracteole tissue is not nutritive. Most

Figure 4—*Atriplex canescens*, fourwing saltbush: seedling development at 1 and 2 days after germination, and at a later time.



authors recommend drilling at depths of 0.5 to 1 cm. Broadcast seeding followed by chaining has produced good stands of fourwing saltbush (Plummer and others 1966). Most species probably need shallow coverage. Young and others (1980) reported that surface seeding prevented emergence of quailbush and reduced that of Australian saltbush by half, even under conditions of unlimited moisture.

Optimal season for planting varies according to precipitation patterns. In winter precipitation zones such as the Intermountain area and the Mojave Desert, fall or early winter planting has been most successful (Kay and others 1977a&b; McArthur and others 2004; Plummer and others 1968). In summer precipitation zones such as the southern Great Plains and Chihuahuan Desert, spring and midsummer plantings are more likely to succeed (Springfield 1970). Northern Great Plains species with a chill requirement, such as Gardner saltbush, are probably best fall-seeded, whereas

fourwing saltbush could be fall- or spring-seeded in the northern Great Plains area.

The expectation that highly dormant seedlots will emerge during the first year after planting is possibly the major source of disappointment in saltbush seedlings. Knowledge of after-ripening patterns in the genus suggests that the best way to circumvent this problem is to use seedlots that have been given ample opportunity to after-ripen in dry storage prior to planting.

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