Chromosome Races of Fourwing Saltbush (*Atriplex canescens*), Chenopodiaceae

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Abstract—*Atriplex canescens* (Pursh.) Nutt. is the most widespread species of perennial *Atriplex* in North America, distributed from southern San Luis Potosi, Mexico, to southern Alberta and Saskatchewan, Canada, and from the Pacific Coast of California and Baja California to Texas, Oklahoma, Nebraska, Kansas, and the Dakotas. Throughout its distributional range, *A. canescens* shows considerable between-population variation. Some of this variation may be due to phenotypic plasticity, but most of it appears to be genetic. Mutations, polyploidy, introgressive hybridization, and segregation from interspecific hybrids all appear to have contributed to its extensive heritable variation. Polyploidy is unusually common with numerous chromosome races (2x, 4x, 6x, 8x, 10x, 12x, 14x, 20x).

Proper identification is important to the utilization of fourwing saltbush in reclamation. While many of the races have been named as varieties, others have not. Even though differentiated by ploidy, chemical constituents, geographic distribution, and morphological characters, they may lack sufficient diagnostic differences to allow facile identification, at least in the herbarium. Rather than combining unnamed races under those that do have a taxonomic name, it seems better at present not to use the formal infraspecific categories in treating the fourwing saltbushes, but to consider them all as races. One new variety, ***Atriplex canescens*** **var.** ***obtusifolia*** **var. nov.,** is described, and the combination ***Atriplex canescens*** **var.** ***prosopidium*** **(I. M. Johnston) comb. nov.** is made.

Introduction

Atriplex canescens forms a polyploid complex based on x = 9, with chromosome numbers of 2x, 4x, 6x, 8x, 10x, 12x, 14x, and 20x (Sanderson and Stutz 1994; Stutz and Sanderson 1979). The most widespread and economically important of these are the 4x (tetraploid) and 6x (hexaploid), while diploids and higher polyploids are less widespread or local endemics.

Atriplex belongs to the order Caryophyllales, in which many of the taxa differ from other dicots in having perisperm as a nutritive tissue, rather than endosperm. It seems likely that lack of endosperm (Cronquist 1988; Cronquist and Thorne 1994), and therefore of endosperm-based barriers against polyploidization (Ramsey and Schemske 1998), may be a factor in the abundance of polyploidy within these taxa (Sanderson and others 1999). Another somewhat distinguishing factor of *Atriplex* may be the ability for multisomic segregation in polyploids with little meiotic irregularity, probably both for genic reasons (Jackson and Casey 1979) as well as small chromosome size (Ruas and others 1998; Stebbins 1971). An apparent intolerance of taxa in the Chenopodiaceae to aneuploidy is worth noting. Practically the entire family has a base number of x = 9 (exceptions are *Spinacia* and *Camphorosma*, x = 12, and a few species with x = 8 and 7 in *Chenopodium*) (McArthur and Sanderson 1984), and it can also be inferred that the frequency of chromosomal reorganization is low. Because of these and possibly other characteristics, the cytogenetic behavior of chenopods is somewhat different than that of dicots in general. Examination of meiotic behavior in numerous species hybrids in *Atriplex* suggests that little chromosomal differentiation exists between North American perennial species (Stutz and Sanderson, unpublished data on file at Brigham Young University). As a result, hybrids tend to be fertile and meiotic behavior in polyploids is, therefore, probably of an autoploid type, even when hybridization between species is involved.

This paper presents a key and descriptions for fourwing saltbush chromosomal races, along with commentary upon their nature and possible origins.

Methods and Materials

Chromosome counts were made by acetocarmine squash methods (Sanderson and Stutz 1994). More than 1,800 individuals from 800 populations were counted over a number of years. Flavonoids were identified as aglycones by paper chromatography using aluminum chloride as a color reagent (Sanderson and Stutz 1994), and more than 1,200 determinations for fourwing saltbush taxa were made (table 1). Populations were examined in the field, and representative specimens deposited at BRY and other herbaria.

Results and Discussion

Establishment of Polyploidy

Because of different probabilities of cytological events at successive ploidy levels, distinct pathways of polyploidization appear to predominate at the diploid, tetraploid, and hexaploid levels in North American *Atriplex*. At the diploid level,

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
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Table 1—Discriminative flavonoid characters of fourwing saltbush. All taxa also produce the common flavonols kaempferol, quercetin, and isorhamnetin (not listed). Besides the universally present unsubstituted flavonols, derivatives modified at the 3 or 6 positions may be observed, as shown below, and tricin, a flavone, is also present in certain taxa.

	Number of samples examined	6-methoxy-substituted flavonols	3-0-methyl-substituted flavonols	Tricin
2x				
Angustifolia (Mexico)	15	–	+	–
Angustifolia (USA)	60	–	–	–
Brevis	48	–	+	–
Garrettii	21	–	+	–
Gigantea	31	–	–	–
Linearis	61	+/–(very weak)	–	+
Piochensis	12	–	–	–
Stewartii	2	–	–	–
4x				
Angustifolia–4x	24	+	–	–
Aptera	42	+	–	–
Bonnevillensis	44	+	–	–
Canescens	17	+	–	–
Cunescens	6	+	–	–
Mexicana	8	–	+	–
Navajoensis	41	+/–(polymorphic)	–	–
Occidentalis	330	+	–	–
6x				
Diegensis	10	+	–	–
Nana	65	+/–(polymorphic)	–	+
Nevadensis	119	–	–	+
Occidentalis–6x	28	+	–	–
Prostrata	9	–	+	–
Rachelensis–6x	17	+	–	–
Tooelensis	6	+	–	–
Vallis	69	+	–	–
8x				
Cuyamaensis (Laciniata–8x)	9	–	–	+
Obtusifolia	24	+	–	–
Prosopidium–8x	2	–	–	+
Rachelensis	11	+	–	–
10x				
Prosopidium	5	–	–	+
12x				
Laciniata	51	–	–	+
Macilenta	28	–	–	+
14x				
Laciniata–14x	24	–	–	+
20x				
Grandidentatum	33	–[a]	–	+

[a]Traces are occasionally seen, apparently due to hybridization with *Atriplex polycarpa*.

an interesting type of chromosome number increase seems to prevail, which we term polyploidization by introgression. When it happens that a diploid population comes into sympatry with a tetraploid, possibly genetically dissimilar or even a separate species, unidirectional introgression from the diploid into the tetraploid may result (Lowe and Abbott 2000; Petit and others 1999; Qu and others 1998; Stebbins 1971; Zohary and Nur 1959). If this occurs, and providing that the diploid enjoys sufficient numerical dominance, the tetraploid may be significantly altered by the introgression, eventually to the point that its original racial or taxonomic identity may no longer be obvious. At that point, if the population were examined, it would of necessity be categorized as belonging to the race or species of the diploid, although having a tetraploid chromosomal level.

Unidirectional introgression may be the result of either of the two more probable cytological mechanisms in this situation, the formation of triploid hybrids, followed by fertilization of their unreduced 3x gametes with x gametes ($x + 2x = 3x$, $3x + x = 4x$), or more directly, the combination of unreduced gametes from the diploid with normal gametes from the tetraploid (2x + 2x = 4x) (Lowe and Abbott 2000; Zohary and Nur 1959). However, since observed introgression between diploids and tetraploids seems exclusively unidirectional (Stutz and Sanderson, unpublished data on file at Brigham Young University), a third pathway involving generation of progeny out of the segregation of euploid gametes in triploids, which might result in bi-directional introgression, does not appear common.

The relative frequencies of polyploidization by unidirectional introgression versus that for within-population autoploidy, besides depending on ease of hybridization, would in addition depend on the relative opportunities for establishment of the polyploidized products from each pathway (both mechanisms are dependent upon the formation of unreduced gametes). Establishment of within-population autoploidy would require a relatively unlikely isolation of the tetraploid products, which could otherwise be swamped by pollen flow from the diploid parent, leading to sterile products. In contrast, an established population already exists by definition for tetraploids in the introgressive pathway, once introgression has begun, enabling the polyploidization process to proceed smoothly and rapidly and to succeed more frequently. Also, as a practical matter, diploids are weak competitors and easily limited to special habitats or isolated locations (Sanderson and Stutz, unpublished data on file at Brigham Young University; this paper), with tetraploids expanding and eventually taking over. Because of adaptive characteristics that appear to commonly be passed from older tetraploids to the newly formed ones, fertility and vigor of tetraploid introgressants tend to be high. One trace of the founding original tetraploid's genetic influence that seems to persist in introgressed populations is the enzymatic capacity for flavonol 6-oxygenation, a trait that is generally absent from diploid perennials (Sanderson and Stutz 1984) but present in most tetraploid North American *Atriplex*. Because of this distribution, flavonol 6-oxygenation is often a useful marker in documenting the introgressive process.

From the tetraploid level, further polyploidization differs somewhat from polyploidization out of the diploid level. Because numerical combinations with unreduced gametes produced by tetraploids do not readily yield a match for gametes produced by hexaploids (2x + 3x = 5x; 4x + 3x = 7x; 2x + 6x = 8x; 4x + 6x = 10x), hybridization between tetraploid and hexaploid populations would not serve directly as a route for unidirectional introgression. However, an even-ploid product can be formed directly from unreduced gametes in tetraploids (2x + 4x = 6x, as opposed to x + 2x = 3x in diploids) to yield hexaploid offspring. Unreduced gametes can be inferred to be relatively common at the tetraploid and higher ploidy levels (Stutz and Sanderson, unpublished data on file at Brigham Young University). The probability of spontaneous within-population polyploidization to a higher level, observed to be rare at the diploid level, might, therefore, be expected to be higher within tetraploid populations. In fact, hexaploid individuals are observed occasionally in populations of tetraploid *Atriplex canescens* (Stutz and Sanderson, unpublished data on file at Brigham Young University). These individuals might either become isolated to begin a hexaploid population, or could hybridize with existing hexaploid taxa to bring about, indirectly, introgression from tetraploids into hexaploids. Such introgression seems to be much less widespread, however. While hybridization appears a factor in formation and development of *Atriplex* hexaploids, it does not reach the level of importance inferred for the origin of tetraploidy.

At higher ploidy levels, there are an increasing number of possible pathways involving unreduced gametes, hybridization, or backcrossing for producing even-ploid offspring at various ploidy levels. However, these tend to conflict with each other to prevent easy resolution. The chromosome number progressions that are observed in the two higher polyploid series in *Atriplex canescens,* from the Chihuahuan and the Sonoran Deserts (Sanderson and Stutz 1994; this paper), seem to suggest chance isolation of relatively rare products.

Identification of the Races

Our studies (Sanderson and Stutz 1994; Stutz and Sanderson 1979, this paper) and those of Dunford (1984, 1985) show that the chromosomal races of *Atriplex canescens* are usually identifiable on morphological grounds, as well as by cytological and geographical criteria. The most generally useful characters in distinguishing fourwing saltbush races are the leaf dimensions, notwithstanding the tremendous seasonal variations exhibited by leaves. Seasonal variation exists because larger leaves are produced during times of vigorous growth, while clustered smaller leaves appear in leaf axils during slower growth on unelongated or partially elongated shoots. As explained in an earlier report (Sanderson and Stutz 1994), in seasons of aridity, first the larger and then successively smaller leaves are shed to reduce water loss. Some races also produce distinctive winter leaves that are small, involute, and curled against the stem. As has been noted in previous studies (Dunford 1985; Sanderson and Stutz 1994; Stutz and Sanderson 1979), with the exception of race Garrettii (Garrettii and Stewartii may be considered separate species from *A. canescens* proper—see below for racial description and discussion), diploids have leaf length-to-width ratios generally above 10:1. This ratio decreases from diploid to tetraploid chromosome levels, and also somewhat more from tetraploid to hexaploid levels. Foliage color is generally more yellowish in diploids, apparently because of reabsorption of a portion of the chlorophyll during arid, relatively dormant seasons (Munné-Bosch and Alegre 2000), a response that is absent or less noticeable in polyploids. While leaves of all *Atriplex* species have a covering of bladder hairs, the Diegensis (6x) race is greener and less pubescent, while the Rachelensis (8x) race is more gray-canescent than most species. Prosopidium (8x, 10x), Grandidentatum, and others have very abundant hairs, giving the foliage a whitish or bluish appearance.

Races sometimes also differ in chemical constituents, for instance, in presence or absence of 6-methoxylated flavonols, as already mentioned. While fourwing saltbushes as a group produce abundant, bitter triterpene saponins, these are usually reduced in quantity in races Vallis and Diegensis. The key to races in this report is somewhat a work in progress, and it seems likely that with further observation, characteristics will be identified (for example, winter leaves, or anther size) that can strengthen racial descriptions.

Use of Racial and Taxonomic Designations

As sometimes suggested by molecular phylogenetic studies (Bolger and Simpson 1995; Hardig and others 2000; Setoguchi and others 1998), and as seen in the evolutionary behavior of island taxa (Ganders and others 2000; Soltis and others 1996), speciation may frequently proceed in bursts, yielding groups of taxa with approximately equal relationships to a common ancestor. Where this type of situation exists, it would be phylogenetically misleading to lump arbitrary subsets of the related taxa. Burst-type of speciation has been suggested for North American *Atriplex* (Stutz 1978) generally, and may be suggested in the present study by the surprising number of fourwing saltbush races in lower ploidy levels. Because in fourwing saltbush many of the races recognized here have not been designated as varieties or subspecies, it would seem inappropriate to apply the existing infraspecific categories because the taxonomically unnamed races would then have to be combined with some of the named taxa. This situation requires that all of the evolutionary units of fourwing saltbush be granted taxonomic status, or that formal infraspecific categories be ignored in favor of racial designations, which is what we have chosen to do here. It is our opinion, however, that for utilitarian reasons every evolutionary unit that can be proven to exist ought to be able to have a taxonomic name, although it might not then be desirable to include all infraspecific taxa in a flora designed, for example, for field use. This is an issue that will eventually be dealt with by the plant taxonomic community, as the number of known instances of cryptic speciation is multiplied and as more and more plants are studied in detail. Like some other taxonomic problems, it appears to arise because of fundamental differences in speciation and evolutionary behavior between plants and animals (Cronquist 1988; Grant 1971), especially regarding their propensities for hybridization and polyploidization, and the resulting hazard for systematists of applying inappropriate zoological constructs to plants.

Description of Fourwing Saltbush Races

Fourwing saltbush races are listed alphabetically within ploidy levels, and their taxonomic designations, if any, are listed.

Race Angustifolia (2x)

Taxonomic nomenclature: *Atriplex canescens* var. *angustifolia* (Torrey) S. Watson, Proceedings of the American Academy of Arts, Sciences and Letters 9: 121. 1874.

Type: Valley of the Rio Grande from El Paso to 40 miles below San Elceario, *Wright 1742* (lectotype NY).

Robust shrub 1–3 m in height, leaves narrowly linear, well developed leaves during drier parts of the summer only 1–2 (3) mm wide in most populations, flat or slightly folded. Some growing season leaves usually retained during winter, often with dwarf, down-curved leaves present on short shoots. Fruiting wings usually large, 1–2 cm in width, 6-methoxy flavonols absent.

Angustifolia occurs in New Mexico, westernmost Texas, some localities in Arizona, and in the Mexican States of Chihuahua, Coahuila, and southern Nuevo Leon, often on sand. During warm arid periods, the foliage becomes somewhat yellowish-green, in contrast to the relatively gray-green foliage of Occidentalis (4x) and most other polyploids of *A. canescens*. Mexican plants differ from those in the United States by the production (abundant) of flavonol 3-methyl ethers (table 1). A form of Angustifolia with more robust summer and winter leaves occurs in the vicinity of San Ysidro and Zia Pueblo in New Mexico, and possibly elsewhere.

In spite of an earlier start of anthesis and only partial flowering overlap with Occidentalis, Angustifolia gives rise to numerous intermediate populations at the tetraploid level that may be called "Angustifolia-4x" (see racial description below). These probably arise through production by diploid plants of unreduced gametes that unite with the 2x gametes of tetraploids (2x + 2x = 4x), resulting in rapid one-way introgression, believed to be a common phenomenon in *Atriplex* (see above in Results and Discussion). Although affected tetraploids more or less resemble Angustifolia, conversion of flavonoid pattern has not been observed, the synthetic ability for 6-methoxy flavonols being consistently retained. Leaf length-width ratio and other characters are seldom also precisely those of diploids. Most tetraploids are strongly competitive, and have probably replaced diploids over wide areas.

Race Brevis (2x)

Taxonomic name: none.

Small shrubs to about 0.5 (1) m, growing season leaves small, narrowly linear. Early growing season leaves reaching about 5 mm in width, dry season leaves only 1–2 (3) mm in width. Winter foliage of small, folded, down-curved leaves on short shoots, more or less appressed against the stem, the summer foliage leaves being shed (sometimes even in the greenhouse). Fruit including wings usually less than 1 cm in width, 6-methoxy flavonols absent.

Race Brevis is endemic to the west side of the Rio Grande Gorge, in northern Taos County, New Mexico, and southernmost Conejos County, Colorado, on basaltic substrates. It looks like a miniature Angustifolia, short in stature, with small leaves and relatively small fruits. It is distinguished at most seasons from Occidentalis and from introgressed tetraploids in the same area by somewhat narrower leaves and a more yellowish foliage color. Foliage color has been observed to be especially useful at a time in the spring when 4x introgressants are actively growing, but Brevis is still in dormancy. Both of them flower at approximately the same time.

Like Angustifolia, Brevis appears to cause modification of adjacent tetraploid populations by one-way introgression, and numerous dwarf tetraploids are found in northern Taos County and in San Luis Valley, Colorado. More study is needed on individual and seasonal variation occurring in zones of introgression to better distinguish tetraploid variations from diploids at all times of year.

Brevis differs markedly from Angustifolia in climatic tolerance. San Luis Valley, the habitat of Brevis, is altitudinally high, about 2,100 to 2,400 m (7,000–8,000 ft) and, therefore, exceptionally cold in the winter. Brevis has distinctive winter foliage, while Angustifolia usually does not seem to, although more years of observation are needed. Angustifolia is sufficiently cold sensitive that plants from several sources all winter killed at Provo, Utah, at an elevation of less than 1,500 m (5,000 ft).

Race Garrettii (2x)

Taxonomic names: *Atriplex garrettii* Rydberg, Bulletin of the Torrey Botany Club 39: 312. 1912. *Atriplex canescens* ssp. *garrettii* (Rydb.) Hall & Clements, Carnegie Institute of Washington, Publ. 326: 344. 1923. *Atriplex canescens* var. *garrettii* (Rydb.) Benson, American Journal of Botany 30: 326. 1943.

Type: USA, Utah, Grand County: vicinity of Moab, *Rydberg & Garrett 8465* (holotype NY, isotypes US, UT, photograph POM).

Small bushes, usually about 0.3 m or less in height, leaves oval to obovate, fruiting wings well developed, 6-methoxy flavonols absent.

Race Garrettii is found on slopes on saline shale and mixed sandstone-shale, stratigraphically below the Navajo Sandstone, in canyons of the Colorado River drainage in southeastern Utah. After the spring growing season, the foliage normally becomes a rather bright yellowish-green. Garrettii is closely related to the tetraploid race Navajoensis (*A. garrettii* var. *navajoensis*), of similar foliage color, but taller and with longer and slightly narrower leaves, evidently a derivative of hybridization and one-way introgression involving races Garrettii (2x) and Occidentalis (4x).

Race Gigantea (2x)

Taxonomic name: *Atriplex canescens* var. *gigantea* Welsh & Stutz, Great Basin Naturalist 44: 189. 1984.

Type: Utah, Juab County: Lynndyl sand dunes T35S R4W, *Welsh & Moore 5126* (holotype BRY).

Large bushes, length-width ratio of summer leaves greater than 10:1, leaf width occasionally reaching 1 cm. Some smaller leaves of the summer foliage retained in winter (although more observation is needed), with small short-shoot leaves of winter morphology also present. Fruits large, to about 2 cm in width including wings, 6-methoxy flavonols absent.

Endemic to the Little Sahara Dunes, Juab County, Utah. Tetraploid plants of race Occidentalis grow on shallower, more stabilized sand at this location, with plants of Gigantea occurring only on the active dunes (Stutz and others 1975). The yellowish-green cast often seen in diploids is weaker but still slightly visible, outside of the spring season of active growth. Little or no hybridization occurs between Gigantea and Occidentalis because of a disjunction in flowering time, Gigantea flowering much later than sympatric Occidentalis.

Race Linearis (2x)

Taxonomic names: *Atriplex linearis* S. Watson, Proceedings of the American Academy of Arts, Sciences and Letters 24: 72. 1889. *Atriplex canescens* ssp. *linearis* (S. Watson) Hall & Clements, Carnegie Institute of Washington, publ. 326: 344. 1923. *Atriplex canescens* var. *linearis* (S. Watson) Munz, Manual of Southern California Botany 141: 598. 1935.

Type: Mexico, Sonora: in alkaline soil about Guaymas, *Palmer 235* (lectotype GH).

Bushes low except in unusually favorable sites, commonly about 0.3 m in height, foliage slightly bluish compared to other *Atriplex* (fruits and foliage sometimes blackish in dried specimens), leaves linear, mostly 3 (7) mm wide or less. Fruiting wings deeply toothed or lobed, very small and reduced to wing-ridges, or larger and irregular. Fruit body sometimes hardened and swollen. Fruits, including wings usually 5–7 (10) mm wide or less, mostly sessile but varying within a plant from sessile to short pedicellate, or rarely long pedicellate. Fruiting beaks more or less prominent (the end of the paired fruiting bracts that extend beyond the winged part of the fruit), entire, or occasionally 3-toothed, 6-methoxy flavonols weak or absent.

Plants of this race grow in alkaline or low-lying areas of the Sonoran Desert of California, Baja California, Arizona, and Sonora. Linearis bears a strong superficial resemblance to the 12x race Macilenta (they are combined in Brown 1956), but can be distinguished by foliage color, and the short or absent fruiting pedicels, and relatively prominent beak of Linearis. The sometimes spongiform fruit body may suggest a phylogenetic connection of Linearis to *Atriplex acanthocarpa* of the Chihuahuan Desert.

Race Piochensis (2x)

Taxonomic name: none.

Moderate sized shrub, 1 to 1.5 m high, and as in Race Angustifolia, leaves during the drier growing season narrowly linear. Leaves of winter foliage on short shoots, small, often folded, but mostly not reflexed, 6-methoxy flavonols absent.

Piochensis occurs in southern Lake Valley in eastern Lincoln County, Nevada, at elevations of 1,500 m (5,000 ft) or greater, with Wyoming big sagebrush or pinyon-juniper. It shows little of the yellowish color often seen in diploids. Introgressed tetraploids are widely distributed in the same area.

Tetraploids with very long and narrow leaves are found at Overton and Valley of Fire State Park, Clark County, Nevada, 195 km to the south, and may be evidence of a wider distribution for Piochensis in the past. In addition, a small population of diploids fairly similar to Piochensis in leaf color and winter foliage have been found on a sandy reclamation site near Tuba City, northern Arizona (Glenn and others 1998). Although the seed sources (which included *A. canescens*) for the reclamation are unknown, morphological variation suggestive of fairly widespread introgression into Occidentalis in the area indicates that the Piochensis-like plants are native and not just a recent introduction.

Tetraploid populations or individuals having longer and narrower leaves are also occasionally encountered in northwestern New Mexico. However, Angustifolia occurs along roadsides in that region, and so either it or Piochensis could be responsible. In any case, it seems possible there are other populations of Piochensis not discovered yet. Their location might be revealed by the occurrence of Piochensis-like variation among plants of Occidentalis in the locality.

Race Stewartii (2x)

Taxonomic names: *Atriplex stewartii* I.M. Johnston, Journal of the Arnold Arboretum 22: 110. 1940. *Atriplex acanthocarpa* ssp. *stewartii* (I.M. Johnston) Henrickson, Southwestern Naturalist 33: 457. 1988.

Type: Coahuila, Llano de Guaje: margin of playa at base of Lomas del Aparejo, abundant, erect globose bush 10–16 in. tall, August 28, 1940, *Johnston & Muller 777* (holotype GH).

Suffrutescent plant, leaves narrowly linear to oblong, margins of larger leaves often broadly and shallowly toothed and wavy. Fruit four-winged, wings well developed, 6-methoxy flavonols absent.

Stewartii occurs in el Bolson de Mapimí (Mapimi Basin) in western Coahuila, Mexico. Vegetatively this plant resembles *Atriplex acanthocarpa,* but the four-winged fruits suggest relationship to *A. canescens*. Winged fruits might have come about either by hybridization of *A. acanthocarpa* and *A. canescens*, giving rise to Stewartii as a hybrid derivative, or alternatively, four wings may have been a plesiomorphic character within ancestors of a group consisting of *A. canescens* and most of the North American suffrutescent species, for example *A. acanthocarpa*, *A. gardneri*, and *A. falcata*. Observation of breakdown of the four-winged character in *A. canescens* hybrids suggests that the winged character is multigenic, with individual loci producing wing fragments or tubercles by themselves. Tubercles on fruiting bracts are common in all of the suffrutescent members of this group, although they are unusually elongated and spine-like when present in *A. acanthocarpa*.

Race Angustifolia-4x (4x)

Taxonomic names: none.

Plants more or less resembling Angustifolia (2x), at least at some times of year, but also somewhat intermediate between that and Occidentalis (4x), 6-methoxy flavonols present.

Angustifolia-4x is common in New Mexico, apparently because of active or previously occurring 2x–4x hybridization. Plants referable to this race are also found in the Sonoran Desert and occasionally in northern Arizona and southern Nevada, suggesting a wider distribution of Angustifolia (2x) or the closely related Piochensis (2x) in former times. However, they seem to be rare or absent in Mexican portions of the Chihuahuan Desert, apparently the ancestral home for Angustifolia (2x).

Race Aptera (4x)

Taxonomic names: *Atriplex aptera* Nelson, Botanical Gazette 34:356. 1902. *Atriplex canescens* ssp. *aptera* (Nelson) Hall & Clements, Carnegie Inst. of Washington, publication 326: 343, pl. 58. 1923. *Atriplex canescens* var. *aptera* (Nelson) C. L. Hitchcock, Vascular Plants of the Pacific Northwest 2: 186. 1964.

Type: Wyoming: Laramie, September, 1901, *Elias Nelson 738* (holotype PH).

Plants mostly low growing, leaves shorter and wider than in races Occidentalis or Canescens. Fruits usually small, 5–7 (10) mm in width, fruiting wings lacerate or lobed, wings often irregular in the sense that some of the wings may be only partial, and that wing fragments may sometimes grow between normal wing positions, 6-methoxy flavonols present.

Aptera occurs in Alberta, Saskatchewan, Montana, the Dakotas, eastern Wyoming, and northwestern Nebraska of the western Great Plains. The frequently irregular wings of Aptera are similar to those seen in the hybrids of wingless species with fourwing saltbush, both as observed in nature and as produced synthetically. Aptera is believed to have the parentage of race Occidentalis x *Atriplex gardneri*. There is a more or less clinal variation from robust in the south to slender in the north in Aptera that seems to reflect a series of separate origins or hybridizations, involving in the south *A. gardneri* var. *gardneri*, and in the north (mostly Canada) *A. nuttallii* in the sense of Bassett and others (1983). The latter might best also be considered a variety of *A. gardneri*.

Race Bonnevillensis (4x)

Taxonomic names: *Atriplex bonnevillensis* C. A. Hanson, Studies in Systematic Botany 1:1. 1962. *Atriplex canescens* var. *bonnevillensis* (C. A. Hanson) Welsh, Great Basin Naturalist 44: 190. 1984.

Type: Utah: Millard County, Desert Range Experiment Station, dry lake bed 1.5 miles northeast of headquarters, *Hanson 356* (holotype BRY, isotypes K, GH, POM, UC, US).

Plants low growing, fruiting wings lobed or laciniate, often irregular. Fruits small, usually about 5–7 mm or less in width, highly variable within and between plants, occasionally wingless, then often resembling those of *Atriplex tridentata*, with the paired fruiting bracts having three or more teeth*,* 6-methoxy flavonols present.

Bonnevillensis is found in a few isolated locations in the eastern Great Basin desert. The known populations are in bottomlands or near populations of *Atriplex tridentata*. It is of evident hybrid origin, by race Occidentalis crossing with a suffrutescent species. Hanson (1962), the descriptor, suggested *A. falcata* (2x except for one known 4x population in central Nevada), a relatively uncommon taxon of valley bottoms and slopes with fruiting bracts fusiform and untoothed, but usually tuberculate, as the second parent. However, as is the case with some other diploid suffrutescent species that rarely hybridize, natural hybrids involving diploid *A. falcata* are seldom observed. A species more often hybridizing, and more acceptable on the basis of bract dentition, is *A. tridentata* (mostly 6x), a bottomland species with bracts having side teeth or at least "shoulders." Origin from the latter would most likely have required the difficult derivation of tetraploid individuals by segregation of euploid gametes (2x) from 5-ploid hybrids (2x + 3x = 5x), while euploid gametes (3x) appropriate for derivation of hexaploid individuals should be equally frequent, as confirmed by Stutz and others (1979). Furthermore, since the presence of occasional hexaploid individuals in tetraploid Occidentalis, as commonly observed, should allow facile introgression at the hexaploid level, a hexaploid overall outcome should be strongly favored for hybridization and introgression between race Occidentalis and *A. tridentata*. The tetraploid chromosome number of Bonnevillensis is, therefore, surprising. Perhaps, however, the circumstance of an overwhelming preponderance of plants of Occidentalis compared to those of *A. tridentata* would be sufficient to tip the balance towards tetraploidy in spite of these factors. A possible scenario is as follows: given a small population of *A. tridentata* (6x) receiving intense pollen rain of race Occidentalis (4x), much of the reproductive capacity of the hexaploids would be taken up with production of sterile pentaploid hybrids, so that they would seldom reproduce. The pentaploids would produce occasional 2x and 3x euploid gametes, and so, under the pollen rain from tetraploids, their relatively rare offspring would be mostly tetraploid and pentaploid (2x + 2x = 4x; 3x + 2x = 5x). After the original hexaploid plants had reached the end of their lifespans, only pentaploid and tetraploid plants would remain. The newly formed tetraploid offspring should reproduce more abundantly, in comparison with the meager reproductive ability of the mostly sterile pentaploids. When the pentaploids in turn had dwindled and died out, the population would then consist entirely of introgressants at the tetraploid level. These would continue to receive genetic influence from the Occidentalis pollen rain as long as the population of Occidentalis continued to exist nearby, which continues to be the case at most of the Bonnevillensis sites. Another much simpler alternative for the origin of Bonnevillensis could have been by hybridization of Occidentalis with the less common tetraploid race of *A. tridentata*.

Race Canescens (4x)

Taxonomic names: *Calligonum canescens* Pursh, Flora Americae Septentrionalis 370. 1814. *Atriplex canescens* (Pursh) Nutt., Genera of North American Plants 1:197. 1818.

Type collection: South Dakota: Lyman County, Big Bend of the Missouri, *Lewis on Sept. 21, 1804* (holotype PH).

Low shrubs or suffrutescent, spreading through root sprouting, sometimes to 20 x 20 m. Single-sex clones visible where plants are sufficiently far apart, otherwise sexes intermingling. Leaves somewhat longer and narrower than those of race Aptera, with which there may be some intergradation, 6-methoxy flavonols present.

Found on badlands and shale, mostly along the Missouri River. Both race Aptera and race Canescens occur as localized, widely separated populations, and may have gained their present distributions at a time of greater aridity, when competition from grasses was less.

Race Cunescens (4x)

Taxonomic names: none.

Low shrubs, about 1–2 dm in height, resembling Occidentalis, but with fruits having reduced or missing wings fairly common, 6-methoxy flavonols present.

Found in Carbon and Emery Counties, Utah. Cunescens may have arisen as a segregant from the hybridization Occidentalis x *Atriplex cuneata,* the latter a common species in the Colorado Plateau, and hence the name "Cunescens."

Race Mexicana (4x)

Taxonomic names: none.

Bush size and leaf form are variable between populations, although generally resembling race Occidentalis, 6-methoxy flavonols absent.

The presence of Mexicana has been documented by flavonoid and chromosome number samples, from Entronque San Roberto in southern Nuevo Leon, to at least as far as the city of San Luis Potosi, but its distribution needs further study. There appears to be wide morphological variation between presently known locations, suggesting that it contains more than one phylogentic unit. Shorter forms may have given rise to the hexaploid race Prostrata of southern Nuevo Leon. Unlike the more northerly tetraploid Occidentalis, it exhibits a 6-methoxy flavonol negative flavonoid pattern, like the Sonoran and Chihuahuan Desert higher polyploids (table 1). It would, therefore, be a likely candidate as their ancestor at the tetraploid level. Probably, tetraploids of this flavonoid type were once somewhat more widespread, but have been overwhelmed genetically by introgression from Occidentalis.

Race Navajoensis (4x)

Taxonomic names: *Atriplex navajoensis* C. A. Hanson, Studies in Systematic Botany 1: 3. 1962. *Atriplex garrettii* var. *navajoensis* (C. A. Hanson) Welsh & Crompton, Great Basin Naturalist 55: 326. 1995.

Type: Arizona: Coconino County, east side of Navajo Bridge (abundant), *C. A. Hanson 388* (holotype BRY, isotypes K, GH, POM, UC, US).

Low shrub to 0.5 m in height, usually 1–2 dm in height exclusive of the inflorescence. Leaves to about 1 cm wide, obovate to obcuneate, 6-methoxy flavonols variably present.

Found on the Vermillion cliffs of Coconino County, Arizona, for a few miles in each direction from Lee's Ferry. As suggested by the describer, this entity appears to have had the hybrid origin Occidentalis x Garrettii. As would be expected, there is a strong resemblance between Garrettii and Navajoensis, and there is variation in the direction of Garretti in Navajoensis populations near the Colorado River at Lee's Ferry (Stutz and Sanderson, unpublished data on file at Brigham Young University). Hybridization with Occidentalis continues at the present time at Lee's Ferry.

Race Occidentalis (4x)

Taxonomic names: *Pterochiton occidentale* Torr. & Frem., Rep. exped. Rocky Mts. 318. 1845. *Atriplex canescens* var. *occidentalis* (Torr. & Frem.) Welsh & Stutz, Great Basin Naturalist 44: 188. 1984.

Type: Utah: "probably from the borders of the Great Salt Lake," *Fremont in 1843* (holotype NY).

Woody shrub 0.75–1.5 (2) m in height, leaves linear oblanceolate or linear ovate, the smaller often folded, apices acute or obtuse. Distinctive winter foliage of small, reflexed-appressed leaves occurring in many populations. Fruiting beak small or absent, fruiting wings entire or somewhat dentate, usually variable within a population, fruit usually 0.7–1.0 cm wide, 6-methoxy flavonols present.

This race is vigorous and widespread, occurring in the Western United States and Northern Mexico. It tolerates a variety of substrates, although sometimes demonstrating a preference for sand. It has been reported that spreading by root sprouts occurs in occasional plants in some New Mexican populations (Barrow 1997). Occidentalis plants are erect, woody shrubs, in contrast to those of race Canescens on the Missouri River. Plants of most populations of Occidentalis resprout from the roots when cut off or burned, but have not been otherwise observed to reproduce by rootsprouting.

Race Diegensis (6x)

Taxonomic name: none.

Moderate to large shrubs, leafy. Foliage color greenish, usually rather dark, pubescence relatively thin, 6-methoxy flavonol positive.

All our chromosome counts for the Pacific Coast from Los Angeles to the border between Baja California Norte and Baja California Sur have been hexaploid, and flavonoid samples have shown the plants to be 6-methoxy flavonol positive. Flavonoid pattern and morphological similarity would suggest a relationship of hexaploid Diegensis with the widespread tetraploid race Occidentalis, or perhaps with Angustifolia-4x or Vallis 6x. More study is needed regarding distribution and characteristics of this race.

Race Nana (6x)

Taxonomic names: none.

Low shrubs, most often 2 dm tall or less, although sometimes taller, depending on genotype and moisture availability. Fruits small, 5–7 mm wide including wings, highly variable within and between plants. Fruiting wings laciniate and often irregular with some of the wings incomplete or with wing fragments growing in the areas between the normal four wings, or wings in some individuals reduced to small ridges on the fruit, or else absent, 6-methoxy flavonols are produced in a minority of plants.

Nana occurs in southern Eureka and northern Nye Counties in Little Smokey Valley and in the Black Rock volcanic area. Its enormous variability and its intermediacy between *Atriplex canescens* and the suffrutescent species indicate it is of hybrid origin. In comparing Nana to the two *A canescens* races present in the area that might have participated in its origin, failure to detect 6-methoxy flavonols in most plants suggests Race Nevadensis (6x) as the fourwing saltbush parent rather than Occidentalis (4x). The suffrutescent parent of Nana might have been *Atriplex falcata* (2x, 4x) or *A. tridentata* (4x, 6x). Wingless fruit variants mostly have fruiting bracts that are toothed or have “shoulders,” ordinarily indicative of *A. tridentata* influence. However, there is a widespread entity of apparent falcata-tridentata parentage in eastern Nevada (*A. anomala*, 6x) that may be a more likely suffrutescent ancestor.

As noted in the key there is a population of plants similar to some variants of Nana in Buena Vista Valley below Unionville, Pershing County, that may be derived from the hybridization Nevadensis x *A. tridentata.* DNA analysis would be desirable to definitively determine origins of the various hybrid taxa, including Bonnevillensis (4x), Nana (6x), and *A. nuttallii* according to Stutz (6x).

The latter is not treated here because its fruits have only irregular wing segments and tubercles, not four definite wings. Flavonoids (consistently 6-methy flavonol positive) would favor Occidentalis rather than Nevadensis as the fourwing saltbush ancestor of *A. nuttallii*, while instances of sympatry and intergradation by *Atriplex tridentata* would suggest that species as another major contributor.

Race Nevadensis (6x)

Taxonomic name: none.

Shrub slightly smaller than Occidentalis, usually 3–6 dm in height, fruiting wings usually more deeply toothed than those of Occidentalis, primary (not clustered) leaves of the male inflorescence usually 5–7 mm wide or more, in contrast to those of Occidentalis in Nevada, which are more often less than 5 mm in width, 6-methoxy flavonol negative.

Found in the borders of the Mojave Desert in western and central Nevada. Occidentalis is found both to the north and to the south of the zone occupied by Nevadensis. The flavonoid constitution of race Nevadensis suggests derivation from the tetraploid race Mexicana, currently limited to central Mexico, rather than from Occidentalis, the widespread tetraploid of northern Mexico and the Western United States.

Race Occidentalis-6x (6x)

Taxonomic name: none.

Similar to Occidentalis (4x), but leaves wider.

Several isolated hexaploid populations are known from southern Arizona and other areas. Since populations of tetraploid Occidentalis frequently contain a few hexaploid individuals, the formation of hexaploid populations from these should take place readily. The relatively southern distribution of hexaploid populations suggests they may be inherently less cold tolerant than tetraploids. More study is needed to compare Occidentalis-6x, Diegensis, and Vallis, which in view of their 6-methoxy flavonol-positive flavonoid patterns, are all related to Occidentalis (4x).

Race Prostrata (6x)

Taxonomic names: none.

Low plants hedged by heavy grazing, most only 1–2 cm in height, but doubtlessly capable of growing somewhat taller under more favorable circumstances, 6-methoxy flavonol negative.

Found in the valley of Entronque San Roberto and La Paz, about 50 miles southbound from Saltillo on Mexico Federal Highway 57. Prostrata usually grows with grasses, also very close cropped. A similar to much taller tetraploid found in the same valley and in other areas to the south is designated “Mexicana.”

Race Rachelensis-6x (6x)

Taxonomic names: none.

Shrub, commonly 0.5 m in height or less. Primary inflorescence leaves do not seem to be retained into summer and autumn as in Nevadensis, larger foliage leaves wider than those of Occidentalis. Winter leaves also seem to be slightly wider than those of Nevadensis when they are viewed side by side, 6-methoxy flavonol positive.

Found on lower slopes in Sand Springs Valley, Lincoln County, Nevada, where the town of Rachel is located (upper slopes sometimes have Occidentalis). A possible origin for this entity might be Rachelensis (8x) x Occidentalis (4x + 2x = 6x). Rachelensis-6x closely resembles the octoploid except that it is less gray-canescent. It grows a little above the octoploid in the valley and is more abundant.

Race Tooelensis (6x)

Taxonomic names: none.

Shrubs to 0.5 m in height, leaves averaging wider than those of tetraploid Occidentalis, 6-methoxy flavonol positive.

Found on both sides of Utah Highway 112 in a restricted area between the towns of Tooele and Grantsville, Utah, it is threatened by agriculture and urbanization. This is an area of silt dunes that were active in producing dust storms during the 1930s due to drought and overgrazing. The area was rehabilitated by the CCC and planted with seeds of *Atriplex canescens,* said to have come from a warehouse in Colorado. It is possible that the seeds may have been mostly those of race Vallis (6x). Tooelensis differs from Vallis in flowering until late in the summer, and probably in its climatic tolerances. It is observed to hybridize with *Atriplex tridentata* (6x), which may, therefore, have contributed genetically to its origin. A somewhat different possibility is that Tooelensis was formed more anciently by hybridization of Occidentalis and *A tridentata*. Presence of spontaneous hexaploid individuals within Occidentalis could have allowed introgression of fourwing saltbush traits into an *A. tridentata* population, which in an unusually favorable situation (namely, a very small population of *A. tridentata* surrounded by abundant Occidentalis) could have driven introgression far in the direction of fourwing saltbush. The formation of mostly sterile pentaploid hybrids (2x + 3x = 5x), from which occasional euploid derivatives at the hexaploid or tetraploid levels might be expected (Stutz and others 1979), could have also contributed. Because the area of occurrence was observed to be devoid of vegetation in the 1930s, origin from race Vallis seems more likely.

Race Vallis (6x)

Taxonomic names: none.

Shrubs, usually shorter than those of race Occidentalis, often less than 0.5 m in height, flowering later than other races in the same area, forming large stands. Leaves averaging wider than those of Occidentalis (4x), foliage appearing slightly darker gray, 6-methoxy flavonol positive.

Found in bottomlands along the Rio Puerco, the Rio Grande as far south as west Texas, and at the south of White Sands and Alamogordo. There are also populations appearing to be Vallis between Las Cruces, New Mexico, and southeastern Arizona, but their chromosome number in most cases has not been determined.

Vallis can easily be distinguished from other fourwing saltbushes in central and southern New Mexico because of its distinctively later flowering time (June rather than May). Flavonoid composition would suggest a derivation from Occidentalis.

Race Cuyamaensis (8x)

Taxonomic names: none.

Shrubs 1–2 m in height, leaves averaging larger than those of Occidentalis, fruiting wings with large toothlike lobes, 6-methoxy flavonol negative.

Found in lowlands near the river in Cuyama Valley, Kern County, California. Occidentalis (4x) is also locally present but seems to prefer slopes. Flavonoids suggest that Cuyamaensis is not affiliated with Occidentalis, but with Mexicana (4x), Nevadensis (6x), and the Mexican higher polyploids.

Race Obtusifolia (8x)

Taxonomic names: *Atriplex canescens* var. *obtusifolia* Sanderson & Stutz, **var. nov.**

Type: Mexico: Coahuila, 5 miles south of Cuatro Cienegas. 28 May 1980, *Stutz 8573* (holotype BRY).

Atriplex prosopidium Johnston affinis sed statura minori, foliis flavo-viride-pallidis non caeruleo-viridi-pallidis.

Shrubs 1–5 dm in height, leaves yellowish-green pallid rather than bluish-green pallid as in Prosopidium, widely oblanceolate to oblong, apically rounded to retuse, fruiting wings crenate to irregularly lobed, sometimes with partial wings, or with wing fragments appearing between normal wing positions, 6-methoxy flavonol positive.

Obtusifolia resembles race Prosopidium (*Atriplex prosopidium*) to a considerable degree in leaf shape, but differs from it in having a shorter stature, a greener, not bluish foliage color, and in producing 6-methoxy flavonols. Prosopidium from its type locality is 10x, but Prosopidium plants from the valley of Monclova are 8x, like Obtusifolia. The sometimes irregular fruits suggest hybridization, perhaps with the suffrutescent species *A. obovata* (6x, 6-methoxy flavonol negative), but since A. obovata is 6-methoxy flavonol negative, 6-methoxy flavonoid production by Obtusifolia would not be expected if those were the only parents. Obtusifolia is found in bottomlands in the valley of Cuatro Cienegas, Coahuila, where it forms a major element of the vegetation.

Race Prosopidium-8x (8x)

Taxonomic names: see Prosopidium (10x).

Shrubs 5–12 dm in height, leaves small, relatively short and broad, the larger usually 15–20 mm in length, apices obtuse to retuse, foliage bluish-pallid, 6-methoxy flavonol negative.

Found in the valley of Monclova. According to the descriptor, it is found mostly north of the city, growing in gypsiferous soils with *Prosopis glandulosa*. The occurrence of Prosopidium-8x may have been reduced by urbanization and agriculture.

A small and isolated 8x population was observed on the west side of the valley that appeared intermediate with Occidentalis. A cross between Occidentalis and 8x

Prosopidium might initially produce a hexaploid that, by way of an unreduced gamete, could backcross to Occidentalis to produce occasional progeny at the octoploid level, probably along with a lot of mostly sterile odd-ploids. The origin of 8x Prosopidium might have been by the hybrid combination Mexicana x *Atriplex obovata*, the latter a 6-methoxy flavonol negative suffrutescent species.

Race Rachelensis (8x)

Taxonomic names: none.

Shrubs 0.2–1 m in height, foliage heavily gray-furfuraceous, 6-methoxy flavonols present.

Found near the playa (dry lake bottom) in Sand Springs Valley near Rachel. A very similar hexaploid is also present at slightly greater elevations around the valley that is not as gray. Both 6x and 8x Rachelensis have 6-methoxy flavonols, suggesting the parentage of race Occidentalis. A possible scenario is that the octoploid originated through hybridization between Nevadensis (6x) and Occidentalis (4x), both found nearby, with an unreduced gamete from Nevadensis (6x + 2x = 8x). Rachelensis-6x in turn might have been generated from hybrids between Rachelensis (8x) and Occidentalis (4x), by the combination of normal gametes from each (4x + 2x = 6x).

Race Prosopidium (10x)

Taxonomic names: *Atriplex canescens* var. *prosopidium* (Johnston) Sanderson & Stutz **comb. nov.** *Atriplex prosopidium* Johnston, Journal of the Arnold Arboretum 24: 227. 1943.

Type: Mexico, Coahuila: south of El Oso, rounded bush 2–3 ft tall, *Johnston 8877* (holotype GH).

Shrubs 0.5–1.2 m in height, leaves oblanceolate to widely oblanceolate or oblong-ovate, fruiting wings prominently paucidentate.

Found in the southern part of the Valle las Calaveras, which begins about 17 km North of the town of Cuatro Cienegas, and also near the town of Sacramento, between Cuatro Cienegas and Monclova. More study is desirable to look for possible differences in morphology between 8x and 10x Prosopidium. Both were examined by the descriptor (Johnston 1943). A possible origin for 10x Prosopidium could have been the combination of a reduced with an unreduced gamete within 8x Prosopidium to produce a 12-ploid, followed by backcross to the 8x (4x + 8x = 12x; 6x + 4x = 10x). Any further crossing would expectedly lead to sterile products, but if isolated, 10x plants could cross among themselves.

Race Laciniata (12x)

Taxonomic names: *Atriplex canescens* var. *laciniata* Parish, Flora of California 1: 442. 1914.

Type: California, Riverside County: Caleb (a town at the southern end of the Salton Sea), *Parish 8256* (holotype CAS, isotype GH, photograph POM).

Large shrubs, 1–2 m in height, leaves usually up to 25 (30) mm in length, the apex commonly rounded. Fruits, including wings up to 1.5 (2) cm wide, usually pedicellate, the wings fimbriately or laciniately cleft or lobed, lobe tips often appearing slightly swollen, fruiting beak with "shoulders" to 3-toothed, relatively inconspicuous, 6-methoxy flavonols absent.

Found in California in the Sonoran and the western Mojave Deserts and in northeastern Baja California Norte, often on sand. Macilenta (12x) is similar, but with smaller fruits. The dissected fruiting wings of Laciniata are suggestive of an origin by hybridization. The most apparent candidate would be *Atriplex polycarpa* (4x, 8x), except that it has the wrong flavonoid composition (6-methoxy flavonol positive). Some other species might be possible but most of them are diploid. The flavonoids of Laciniata (6-methoxy flavonol negative) would suggest race Cuyamaensis (8x), Nevadensis (6x), or Mexicana (4x) as the fourwing saltbush parent, rather than Occidentalis.

Race Macilenta (12x)

Taxonomic names: *Atriplex canescens* var. *macilenta* Jepson, Flora of California 1: 442. 1914.

Type: California, Imperial County: Bluffs of the Alamo, Calexico, *Parish 8258* (lectotype GH).

Medium shrubs, usually 0.5–1 m in height, leaves usually up to 25 mm in length, the apex commonly rounded. Fruits small, often like a laciniata fruit in miniature, width including wings about 5–7 mm, fruiting bracts fimbriately to laciniately lobed, fruiting beak with "shoulders" to 3-toothed, inconspicuous in comparison to the projections of the wings, 6-methoxy flavonols absent.

Found in the Sonoran Desert of California. Fruit and shrub size vary from one place to another and intergrade with Laciniata. Small fruit size and variability are suggestive of hybridization, but leaf shape does not suggest a parent with leaves greatly different than those of Laciniata. Two acceptable candidates might therefore be *Atriplex polycarpa* (4x, 8x), which has *A. canescens*-like leaves in wetter seasons, and race Linearis (2x). *Atriplex polycarpa* 8x might have formed a 12-ploid via an unreduced gamete, and the 12-ploid might then have hybridized readily with Laciniata. In the case of Linearis, a mostly sterile 13-ploid could be produced by union of an unreduced Laciniata gamete plus a normal linearis gamete (12x + x = 13x), and euploid gametes (6x) should then occasionally be produced by segregation. Neither origin seems clearly satisfactory. On the one hand, 6-methoxy flavonols are present in *Atriplex polycarpa,* but not in Macilenta (nor Laciniata). On the other, a very slight genetic contribution from Linearis would hardly seem enough to change the fruit characteristics to the extent seen in Macilenta, unless there was a gene of strong effect involved or the introgression was long recurrent. If Linearis was indeed involved, however, it might explain the sometimes confusing similarity between Linearis and Macilenta.

Race Laciniata-14x (14x)

Taxonomic names: see Laciniata (12x).

Large shrubs, fruits fimbriate to laciniate or coarsely dentate, 6-methoxy flavonols absent.

Known from a few miles east of the Colorado River mouth in westernmost Sonora to the resort town of Golfo de Santa Clara, and perhaps further eastward. Because we did not travel extensively in the Gran Desierto, distributions of Laciniata-14x and Grandidentatum are incompletely known.

Race Grandidentatum (20x)

Taxonomic names: *Atriplex canescens* var. *grandidentatum* Sanderson & Stutz, American Journal of Botany 81: 1045-1053. 1994.

Type: Mexico, Sonora: 25 km east of Puerto Peñasco, *Sanderson 93047* (holotype BRY, isotype MEXU).

Large shrubs, larger leaves usually 15–60 mm in length, slightly to moderately blue-green pallid, 5–10 mm in width, apically obtuse to acute or occasionally emarginated, fruits about 1–2 cm in width, including wings, large-toothed or laciniate, 6-methoxy flavonols mainly absent.

Found along the upper Sonoran coast in the Desierto de Altar and at least the western side of the Gran Desierto, mostly on sand.

As noted in a previous publication (Sanderson and Stutz 1994), Grandidentatum has been observed to hybridize with *Atriplex polycarpa* 8x. This may be the reason for small amounts of 6-methoxy flavonols that can be occasionally detected in Grandidentatum samples.

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Preliminary Key to Fourwing Saltbush Races

1. Plants suffrutescent, stems dieing at the end of the season. Leaves linear to oblong or lanceolate, oblanceolate, the larger often with several teeth along the margin and the margins wavy. El Bolson de Mapimi (Mapimi Basin), Coahuila, Mexico . . . . **Race Stewartii** (2x, 6-methoxy flavonol negative)
1. Plants usually shrubby. Leaf margin teeth very rare, or if more common, leaves roundish and often 1 cm or more wide
  2. Leaves less than 5 times as long as broad, the larger usually 1 cm wide or more. Plants a bright yellowish green during much of the year but green or gray-green during growth, less than 0.5 m in height, growing within a few miles of the Colorado River in Utah or Arizona
    3. Leaves ovate or obovate, mostly less than 3 times as long as broad. Found in drainages above Glenn Canyon Dam in Utah and Arizona . . . . **Race Garrettii** (2x, 6-methoxy flavonol negative)
    3. Leaves obovate to obcuneate, 2 to 4 times as long as broad and about 1 cm wide. Vermillion Cliffs near Lee's Ferry, Arizona . . . . **Race Navajoensis** (4x, 6-methoxy flavonol negative or positive)
  2. Leaves narrower or smaller, plants usually larger. *Atriplex canescens* in the narrower sense, keyed by geographic area, as follows:

Plants of the Pacific Northwest (4x only) . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of the western Great Plains (4x only)

1. Aboveground stems short lived, plants usually 0.5 m or less in height. Strongly rootsprouting, individual clones often covering many square meters. Found in South Dakota, especially along the Missouri River, on badland soils . . . . **Race Canescens** (4x, 6-methoxy flavonol positive)
1. Aboveground stems woody, persistent, most plants not spreading clonally
  2. Fruit wings small, usually lobed, laciniate or irregular. Fruits including wings, 5–7 (10) mm wide or less. Low plants with wide leaves. Alberta, Saskatchewan, Montana, North and South Dakota, Wyoming . . . . .Race Aptera** (4x, 6-methoxy flavonol positive)
  2. Fruit wings normal in form and size, the margins entire to toothed. Fruits including wings about 7–10 mm wide. Mostly Nebraska southward . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of Nevada or northern Arizona (2x, 4x, 6x, 8x)

1. Plants of Sand Springs Valley (near the town of Rachel), Lincoln County, Nevada
  2. Larger leaves in the fall usually 5 mm or less in width. Plants of higher elevations around the valley edges, especially along the highway approaching Rachael from the east . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)
  2. Larger leaves in the fall usually more than 5 mm in width. Lower elevations
    3. Gray-canescent plants of low elevations known from the area between the highway and the dry lake bed (playya) . . . . **Race Rachelensis** (8x, 6-methoxy flavonol positive)
    3. Plants of similar appearance but not as gray, growing above the previous on lower valley slopes. Large populations in some areas, especially north of the playa . . . . **Race Rachelensis 6x** (6x, 6-methoxy flavonol positive)
1. Plants of other areas
  4. Length-width ratio of larger leaves about 10:1 or greater during most of the year
    5. Plants growing at elevations of 1,500 m (5,000 ft) or greater in Lake Valley at Pioche, Lincoln County, also known from the vicinity of Tuba City, Arizona . . . . **Race Piochensis** (2x, 6-methoxy flavonol negative)
    5. Plants at lower elevations or other locations. Known from Valley of Fire and Overton, Nevada, and scattered plants in northern Arizona and northwestern New Mexico, intergrading with Occidentalis . . . . **Angustifolia 4x** (4x, 6-methoxy flavonol positive)
  4. Length-width ratio of larger leaves usually below 10:1
    6. Fruiting wings small, fruits to about 5 (7) mm in width including wings, deeply lobed, often irregular in size and sometimes in position. Fruits strongly variable within and between plants, usually including some plants of a population with a few wingless fruits. Found in southern Eureka, and northern Nye Counties. Plants growing in the bottom of northern Buena Vista Valley, below Unionville, Pershing County, may have larger fruits but could perhaps also be classified here. (Not included in the key, because it cannot be said to have four wings, but only wing fragments, is the putative hybrid derivative *Atriplex nuttallii,* in the sense of Stutz (Stutz and Sanderson 1998), of the Humboldt River valley and other locations in the Battle Mountain area) . . . . **Race Nana** (6x, mostly 6-methoxy flavonol negative, with occasional plants positive)
    6. Fruiting wings normal in size, sometimes strongly dentate but extending the length of the fruit and growing in only the four ordinary positions, fruits usually 7–10 mm in width
      7. Larger leaves of the male inflorescence, when under 25 mm in length, 7 mm or more in width in the majority of plants of a population. Anthers mostly 0.75 to 1.00 mm in length. Borders of the Mojave Desert in western and central Nevada . . . . **Race Nevadensis** (6x, 6-methoxy flavonol negative)
      7. Larger leaves of the male inflorescence usually less than 7 mm in width. Anthers usually 0.50 mm in length or less. More generally distributed than Nevadensis (above), both to the north and south . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of Utah or western Colorado (2x, 4x, 6x)

1. Length-width ratio of larger summer leaves 10:1 or greater. Plants of the Little Sahara Dunes, Juab County, Utah . . . . **Race Gigantea** (2x, 6-methoxy flavonol negative)

Length-width ratio of larger summer leaves less than 10:1

- 3. Fruiting wings small and irregular or occasionally absent, fruits, including wings usually 5 (7) mm or less in width. Known from Juab and Millard Counties of western Utah . . . . **Race Bonnevillensis** (4x, 6-methoxy flavonol positive)
- 3. Fruiting wings sometimes small or more often normal in size, usually entire to moderately toothed. Fruits, including wings usually 7–10 mm wide
  - 4. Plants of Tooele County, Utah, between the towns of Tooele and Grantsville on the north and south sides of Utah Highway 112, about 2 miles east of Grantsville. Grayish, shorter plants with wider leaves, flowering until late summer (plants closer to Grantsville are race Occidentalis) . . **Race Tooelensis** (6x, 6-methoxy flavonol positive)
  - 4. Plants widespread or of other areas
    - 5. Plants mostly about 2 dm in height or less, of Carbon or Emery County, Utah . . . . **Race Cunescens** (4x, 6-methoxy flavonol positive)
    - 5. Plants averaging well over 2 dm in height. Widespread . . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of New Mexico, or San Luis Valley, southern Colorado (2x, 4x, 6x)

1. Plants of San Luis Valley, Colorado, or Taos County, New Mexico
   - 2. Plants generally over 0.5 m in height . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)
   - 2. Plants mostly about 0.5 m or less in height
     - 3. Width of largest summer leaves 2–3 mm during seasons of drought, foliage usually yellowish. Occurring west of the Rio Grande in Taos County, New Mexico, and south of Antonito in Conejos County, Colorado . . . . **Race Brevis** (2x, 6-methoxy flavonol negative)
     - 3. Width of larger leaves usually about 5 mm or greater except in winter, foliage more greenish. More widespread than the previous . . . . **Occidentalis x Brevis introgressants** (4x, 6-methxy flavonol positive)
1. Plants not of San Luis Valley or Taos County, New Mexico
   - 4. Length-width ratio of larger leaves about 10 or greater
     - 5. Larger leaves at some seasons only 2–3 mm in width in most populations, foliage with a pronounced yellowish color in dry hot seasons. Typically growing on sand dunes or mesquite hummocks, usually on uplands above tetraploids and hexaploids; however, mixed 2x-4x populations are rather common in the Rio Grande Valley . . . . **Race Angustifolia** (2x, 6-methoxy flavonol negative)
     - 5. Larger leaves usually wider than 2–3 mm at all seasons, foliage color not as yellow. Leaf length-width ratio not much exceeding 10:1, usually less at some seasons. Occurring on a variety of substrates . . . . **Race Angustifolia-4x** (4x, 6-methoxy flavonol positive)
   - 4. Leaf length width ratio less than 10, larger leaves wider than 2–3 mm during all seasons. Foliage more consistently grayish during all seasons
     - 6. Plants with new flowers appearing only in June, if not of northern New Mexico. Low bottomland plants of a slightly darkish foliage color . . . . **Race Vallis** (6x, 6-methoxy flavonol positive)
     - 6. Plants with new flowers appearing in May, except at higher elevations in the north. Larger plants, often occurring on slopes, with a somewhat more yellowish dry-season foliage color than the previous . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of California, southern Arizona, Baja California, or Sonora (2x, 4x, 6x, 8x, 12x, 14x, 20x)

1. Length-width ratio of larger leaves about 10:1 or greater
   - 2. Fruits with small or irregular wings, width, including wings usually 5 (10) mm or less. Bottomland plants, the foliage usually with a slight bluish cast. Fruits usually not pedicellate, but prominently beaked . . . . **Race Linearis** (2x, 6-methoxy flavonol negative)
   - 2. Fruit with well developed wings, width including wings usually 7–10 mm or more. Plants usually of well-drained sites, fruits pedicellate, fruiting beaks usually obscure or absent
     - 3. Plants of Imperial Valley, California, and the western Sonoran and Mojave Deserts . . . . **Race Angustifolia-4x** (4x, 6-methoxy flavonol positive)
     - 3. Plants of the Arizona portion of the Sonoran Desert, especially south of Tucson . . . . **Race Angustifolia** (2x, 6-methoxy flavonol negative)
1. Length-width ratio of larger leaves mostly less than 10:1
   - 4. Fruit wings usually entire to moderately toothed
     - 5. Plants of the Pacific Coast of Baja California Norte and California, below Los Angeles . . . . **Race Diegensis** (6x, 6-methoxy flavonol positive)
     - 5. Plants of other areas
       - 6. Leaves narrower at a given season. Plants widespread . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)
       - 6. Leaves wider by comparison. Isolated populations . . . . . . **Race Occidentalis-6x** (6x, 6-methoxy flavonol positive)
   - 4. Fruiting wings of all or most plants having large teeth, or prominently lobed or incised

6. Plants of Cuyama valley, California, mostly in bottomlands. Fruiting wings with large irregular teeth. (Occidentalis present in the general locality also, on slopes) . . . . **Race Cuyamaensis** (8x, 6-methoxy flavonol negative)
6. Plants of the southern Mojave or Sonoran Deserts
   7. Southern California and Baja California Norte
      8. Plants usually 1 m in height or more, fruiting bracts normal to large in size, fruits about 7–15 (20) mm in width including wings . . . . **Race Laciniata** (12x, 6-methoxy flavonol negative)
      8. Plants usually less than 1 m in height, fruiting bracts small, fruit usually 5–7 (10) mm or less in width, including wings
         9. Plants normally 0.5 m in height or less, fruits mostly sessile, foliage with a bluish cast in the field (a few populations with wider leaves will key out here) . . . . **Race Linearis** (2x, 6-methoxy flavonol negative)
         9. Plants mostly greater than 0.5 m in height, fruits mostly pedicellate, foliage often pale, but greenish. Apparently intergrading with Laciniata . . . . **Race Macilenta** (12x, 6-methoxy flavonol negative)
   7. Coastal northern Sonora
      10. West of Gran Desierto . . . . **Race Laciniata 14x** (14x, 6-methoxy flavonol negative)
      10. Gran Desierto(?) and Desierto de Altar . . . . **Race Grandidentatum** (20x, 6-methoxy flavonol negative)

Plants of the Chihuahuan Desert of Mexico (2x, 4x, 6x, 8x, 10x)

1. Length-width ratio of larger leaves 10:1 or more, larger leaves during dry seasons usually 2–3 mm in width or less, dry season foliage color markedly yellowish. . . . . **Race Angustifolia** (2x, 6-methoxy flavonol negative)
1. Length-width ratio of larger leaves usually less than 10:1, larger leaves, even during drier seasons, usually over 2–3 mm in width. Foliage color not as strongly yellowish
   2. Foliage bluish-green pallid, leaf apices usually rounded, leaves short and fairly wide
      3. Plants of Coahuila
         4. Plants of Valle Las Calaveras, between the towns of Ocampo and Cuatro Cienegas, or at Sacramento, Coahuila. Pure large stands (where not extirpated by agriculture) or growing with Race Occidentalis . . . . **Race Prosopidium** (10x, 6-methoxy flavonol negative)
         4. Plants of the valley of Monclova, Coahuila . . . . **Race Prosopidium-8x** (8x, 6-methoxy flavonol negative)
      3. Plants of Chihuahua . . . . Prosopidium? (6x, 6-methoxy flavonol status unknown)
   2. Foliage grayish-green or yellowish-green pallid, leaf apices rounded or not
      5. Plants of the valley of Cuatro Cienegas, Coahuila. Leaf apices rounded, leaves relatively short and wide, plants usually below 0.5 m in height, forming large uniform stands. Differing from races of Prosopidium by shorter stature and non-bluish foliage color . . . . **Race Obtusifolia** (8x, 6-methoxy flavonol positive)
      5. Plants widespread or of other localities, leaves not particularly short and wide
         6. Plants of southern Nuevo Leon or San Luis Potosi
            7. Plants 2 or 3 dm in height or less, most often only a few cm, growing in the valley bottom from Ent. San Roberto for about 20 km northward . . . . **Race Prostrata** (6x, 6-methoxy flavonol negative)
            7. Plants of various populations ranging in stature from very low like Prostrata to much taller, growing from La Paz southward to about 20 km north of Ent. San Roberto, and from San Roberto to at least as far as the city of San Luis Potosi. . . . . **Race Mexicana** (4x, 6-methoxy flavonol negative)
         6. Plants more northern . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)