

LEAF ANATOMY AND SUBGENERIC AFFILIATIONS OF C₃ AND C₄ SPECIES OF *SUAEDA* (CHENOPODIACEAE) IN NORTH AMERICA¹

DEBORAH D. FISHER,² H. JOCHEN SCHENK,³ JENNIFER A. THORSCH, AND
WAYNE R. FERREN, JR.

Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106-9610

The halophytic genus *Suaeda* (Chenopodiaceae) includes species with the C₃ and C₄ photosynthetic pathways. North American species of this genus were investigated to determine whether C₃ and C₄ leaf anatomy are consistent within the two sections of *Suaeda*, *Chenopodina* and *Limbogermen*, present on this continent. All species from section *Chenopodina* were found to possess C₃ anatomy, whereas all species from section *Limbogermen* were found to be C₄ species. Characteristics of leaf anatomy and chloroplast ultrastructure are similar to those reported from C₃ and C₄ species, respectively, from the Eastern Hemisphere. All species from section *Limbogermen* have the *suaedoid* type of leaf anatomy, characterized by differentiation of the mesophyll into palisade parenchyma and a chlorenchymatous sheath surrounding central water-storage tissue, as well as leaf carbon isotope ratios ($\delta^{13}\text{C}$) of above -20 . All species from section *Chenopodina* have *austrobassoid* leaf anatomy without a chlorenchymatous sheath and $\delta^{13}\text{C}$ values of below -20 . According to our literature review, the photosynthetic pathway has now been reported for about half (44) of the *Suaeda* species worldwide. The C₃ and C₄ photosynthetic syndromes are with few exceptions distributed along sectional or subsectional lines. These findings throw new light on the infrageneric taxonomy of this genus.

Key words: C₃/C₄ photosynthesis; Chenopodiaceae, *Chenopodina*; infrageneric taxonomy; leaf anatomy; *Limbogermen*; *Suaeda*.

Four large genera in the Chenopodiaceae, *Atriplex*, *Kochia*, *Bassia*, and *Suaeda*, include both C₃ and C₄ species (Welkie and Caldwell, 1970; Carolin, Jacobs, and Wesk, 1975; Osmond, Björkman, and Anderson, 1980; Shomer-Ilan, Nissenbaum, and Waisel, 1981). The C₄ photosynthetic syndrome consists of anatomical, physiological, and biochemical components, all of which must be present to facilitate proper functioning of the CO₂-concentrating mechanism that C₄ plants possess in addition to the Calvin-Benson (C₃) pathway of carbon fixation (Björkman, 1973; Percy and Ehleringer, 1984; Ehleringer and Monson, 1993). Presence or absence of the C₄ syndrome has been recognized as an important taxonomic character in plant families and genera that include both C₃ and C₄ species, for example in the Poaceae (Brown and Smith, 1972; Ehleringer and Monson, 1993), especially in the genus *Panicum* (Poaceae) (Zuloaga, Dubcovsky, and Morrone, 1993). In the Chenopodiaceae, the C₄ syndrome as an infrageneric character has only been

studied extensively in the genus *Atriplex* (Osmond, Björkman, and Anderson, 1980). Although the taxonomic importance of leaf anatomy in *Suaeda* had been recognized almost a century ago (Solms-Laubach, 1901), this is the first study of the distribution of the C₃ and C₄ syndromes in different sections of the genus *Suaeda*.

The Chenopodiaceae have evolved a number of very different C₄ leaf anatomies, ranging from typical bundle sheath arrangements in the genus *Atriplex* (Downton, Bisalputra, and Tregunna, 1969; Osmond, Troughton, and Goodchild, 1969; Napp-Zinn, 1984/1988) to cylindrical chlorenchyma-sheaths surrounding internal water-storage tissue in the leaf-succulent genera *Salsola* and *Suaeda* (Metzler, 1924; Evenari, 1938; Olesen, 1974; Carolin, Jacobs, and Wesk, 1975; Napp-Zinn, 1984/1988). These different anatomies correspond with different biochemical pathways (Glagoleva et al., 1990; P'yankov, 1991; Gamaley et al., 1992; P'yankov et al., 1992a).

The genus *Suaeda* consists mostly of halophytic leaf-succulents that grow in saline and alkaline wetlands and deserts worldwide, but primarily outside the tropics. A number of species have been found to be valuable feed for livestock in arid areas (Iljin, 1936a), while others have been utilized to desalinate irrigated farmlands (e.g., Zhao, 1991). The genus is known to be taxonomically very difficult (Standley, 1917; Hopkins and Blackwell, 1977; Boulos, 1991). According to our review of the literature, it is currently thought to include ~90 species worldwide, but almost twice as many names have been published. The difficulty lies in the fact that the genus includes wide-ranging polymorphic species, such as the coastal salt marsh plant *Suaeda maritima*, which has a worldwide extratropical distribution, as well as a number of narrowly distributed endemic taxa. This means that the taxonomy

¹ Manuscript received 7 October 1996; revision accepted 29 January 1997.

² Current address: Department of Biology, The Pennsylvania State University, 208 Mueller Lab, University Park, PA 16802.

³ Author for correspondence.

The authors thank George W. Welkie for giving access to his personal notes, the herbarium curators at Utah State University and Harvard University for loan of specimens, Katherine Esau for translations from the Russian, Luis Rodriguez for translations from the Spanish, Hadas Parag for help with illustrations, Lucy St. Omer for assistance in early project development, and Bruce Mahall for his support of the final stages of this project. Special thanks go to Chuck Kennicut and James Brooks of the Geochemical and Environmental Research Group at Texas A&M University for the carbon isotope analyses. Financial support for this work was provided by the Museum of Systematics and Ecology at the University of California Santa Barbara and partially by the Andrew W. Mellon Foundation.

of *Suaeda* should be considered within a continental or even global context.

The overall goal of this project was to clarify the systematics of the genus *Suaeda* and its sections in North America. More specifically, species of *Suaeda* were investigated to determine whether characteristics of C_3 or C_4 leaf anatomy are consistent within each of the two sections of the genus present on this continent, *Chenopodina* Moquin-Tandon and *Limbogermen* Iljin. Additionally, a review of the literature on the distribution of C_4 vs. C_3 leaf anatomy in the sections of *Suaeda* worldwide was conducted.

The specialized leaf anatomy found in all known C_4 species of *Suaeda* is very distinctive. It had been described in a number of anatomical publications long before the discovery of the C_4 pathway of photosynthesis (Solms-Laubach, 1901; Paulsen, 1912; Evenari, 1938; Shields, 1951; Pyykkö, 1966). Like those of numerous other C_4 species, this leaf anatomy deviates from the typical bundle-sheath (Kranz-type) anatomy (Brown, 1975; Carolin, Jacobs, and Wesk, 1975; Napp-Zinn, 1984/1988). Two distinct cell layers of chlorenchyma are located between the epidermis and a central water-storage tissue. In contrast, C_3 species of *Suaeda* do not show a differentiation of the chlorenchyma into distinct layers (Shomer-Ilan, Beer, and Waisel, 1975; Shomer-Ilan, Neumann-Ganmore, and Waisel, 1979; Glagoleva et al., 1990). Biochemical and physiological studies of *Suaeda* species have revealed both C_3 and C_4 pathways of carbon fixation, and C_4 photosynthesis has been found exclusively in species exhibiting the specialized C_4 anatomy (Shomer-Ilan, Beer, and Waisel, 1975; Shomer-Ilan, Neumann-Ganmore, and Waisel, 1979; Bil' et al., 1981; Frey and Kürschner, 1983; Venkatesalu and Chellappan, 1988; Glagoleva et al., 1990; P'yankov et al., 1992a; P'yankov, 1993; Kolchevskii, Kocharyan, and Koroleva, 1995). All C_4 species of *Suaeda* examined utilize the NAD-ME biochemical type of C_4 photosynthesis and predominantly use aspartate as the first stable product of carbon fixation (Shomer-Ilan, Neumann-Ganmore, and Waisel, 1979; Bil' et al., 1981; Glagoleva et al., 1990, 1992; P'yankov et al., 1992a; P'yankov, 1993).

Studies of the anatomy, morphology, and ecology of *Suaeda* species often have been hampered by incorrect identification of species or by the confusing taxonomy that has led to a proliferation of synonyms. For example, the North American species *Suaeda moquinii* (Torrey) Greene is known by 19 other names. Likewise, herbarium specimens labeled *Suaeda californica* S. Watson may be any one of three different species from two different sections of the genus: *S. californica*, *S. taxifolia* Standley, or *S. esteroa* Ferren & Whitmore. This situation has resulted in contradictory observations about the anatomy, morphology, and biochemistry of the same species of *Suaeda*, contributing further to the confusion (Welkie and Caldwell, 1970; Winter, 1981).

Various genera, subgenera, and sections have been proposed in the past for the taxa that comprise the genus *Suaeda* (Moquin-Tandon, 1840, 1849; Grenier and Godron, 1856; Volkens, 1894; Ulbrich, 1934), including most recently the system by Iljin (1936a, b), who described seven sections, based largely on gynoecium and seed morphology. Two additional sections have been proposed

by Townsend (1980) and Tsvelev (1993), who revised Iljin's system based on an examination of eastern European species. Tsvelev also renamed two of Iljin's sections, using names that he assumed to have priority over the names chosen by Iljin, including the name *Schoberia* (C. A. Meyer) Volkens for Iljin's section *Heterosperma*, based on the genus *Schoberia* C. A. Meyer now submersed into *Suaeda*. However, a recent review of the nomenclatural history of *Suaeda* by H. J. Schenk and W. R. Ferren (unpublished data) revealed that the section name *Chenopodina* Moquin-Tandon has priority over both *Heterosperma* and *Schoberia*. *Chenopodina* is treated here as a synonym for *Heterosperma* Iljin, excluding section *Conosperma* Iljin, which Tsvelev (1993) proposed to merge in section *Schoberia* nom. illeg..

Of the species examined in this study, *Suaeda calceoliformis* (syn. *S. depressa* name misapplied) and *S. linearis* have been assigned to section *Chenopodina* (syn. *Heterosperma*) by Iljin (1936b). (For authorities for species names see Tables 1 and 6.) This section includes predominantly annuals with axillary clusters of flowers, horizontal, often dimorphic seeds, and slender, very short and smooth to slightly papillous stigmas, which are inserted on the constricted tip of the ovary. *Suaeda esteroa* and *S. puertopenascoa* also show these characteristics (Ferren and Whitmore, 1983; Watson and Ferren, 1991; Ferren, 1993). *Suaeda taxifolia*, *S. moquinii* (syn. *S. ramosissima*), *S. tampicensis*, and *S. palmeri* were assigned to section *Limbogermen* by Iljin (1936b). This section includes shrubs and subshrubs with axillary flower clusters, horizontal and/or vertical, monomorphic seeds, and filiform, pilose-papillate stigmas, which are subsessile or on a short style that arises from a pit in the top of the ovary. These characteristics are also found in *Suaeda conferta* and *Suaeda californica*, the latter of which was assigned to section *Chenopodina* (syn. *Heterosperma*) by Iljin (1936b), presumably because of a misidentification.

MATERIALS AND METHODS

Suaeda californica, *S. taxifolia*, *S. moquinii*, *S. calceoliformis*, and *S. esteroa*, were collected in their native habitats in California. Localities and voucher numbers are listed in Table 1. Entire shoots were fixed in the field on ice in 6% glutaraldehyde buffered with 0.05 mol/L sodium cacodylate (pH 6.8) for 6 h. Leaves were excised from the stems, cut into 1.0-mm pieces, and fixed under vacuum for an additional 2 h. Samples were postfixed in 2% osmium tetroxide in sodium cacodylate buffer overnight at 4°C. The tissue was dehydrated through a graded acetone series and embedded in Spurr's epoxy resin (Spurr, 1969). Sections were cut on a Porter-Blum MT2B ultramicrotome. Thick sections were stained with 1% toluidine blue in water and photographed on a Zeiss Ultraphot. Thin sections were stained with uranyl acetate and lead citrate and photographed on a Siemens Elmiskop 101 transmission electron microscope (TEM).

Leaves from these five species were also used for $\delta^{13}\text{C}$ carbon isotope ratio determinations. Dried leaves were prepared in a Craig-type combustion system with CO_2 determination on a Finnigan MAT 251 isotope ratio mass spectrometer. Values are reported as $\delta^{13}\text{C}$ (‰) relative to the PeeDee belemnite (PDB) standard.

Suaeda tampicensis, *S. linearis*, *Suaeda conferta*, and *Suaeda puertopenascoa* were collected in their native habitats (see Table 1 for localities). Entire shoots were fixed in the field in 95% ethanol on ice, and subsequently stored in a freezer. Leaves were hand-sectioned for

TABLE 1. Sources and voucher numbers of specimens used in this study. Preserved specimens collected by the authors are kept at the UCSB herbarium of the Museum of Systematics and Ecology at the University of California Santa Barbara.

<i>Suaeda calceoliformis</i> (Hooker) Moquin-Tandon. Carpinteria, Santa Barbara County, California. Ferren, Fisher & Thorsch, 1989, No. 3212.
<i>Suaeda californica</i> S. Watson. Morro Bay, San Luis Obispo County, California. Ferren, Fisher & Thorsch, 1989, No. 3213.
<i>Suaeda conferta</i> (Small) I. M. Johnston. Along the Arroyo Salado, Zapata County, Texas. Schenk, 1994, No. 94 S8.
<i>Suaeda esteroa</i> Ferren & Whitmore. Mugu Lagoon, Ventura County, California. Ferren, Fisher & Thorsch, 1989, No. 3210.
<i>Suaeda linearis</i> (Elliott) Moquin-Tandon. NE of Brownsville, Cameron County, Texas. Schenk, 1994, No. 94 S4B.
<i>Suaeda mexicana</i> (Standley) Standley. Hacienda de Angostura, San Luis Potosi, Mexico. Pringle, 1891, No. 3788. (Isotype (H).)
<i>Suaeda moquinii</i> (Torrey) Greene. Soda Lake, San Luis Obispo County, California. Ferren, Fisher & Thorsch, 1989, No. 3230.
<i>Suaeda palmeri</i> (Standley) Standley. North of Rancho Estacas, Nuevo Leon, Mexico. M. C. Johnston, T. L. Wendt & F. Chiang, 1973, No. 10219 (UCSB).
<i>Suaeda puertopenascoa</i> C. Watson & Ferren. Northwest of Puerto Peñasco, Sonora, Mexico. Ferren & Watson, 1985, No. 2807. (Holotype).
<i>Suaeda tampicensis</i> (Standley) Standley. Cameron County, Texas, northeast of Brownsville. Schenk, 1994, No. 94 S4A.
<i>Suaeda taxifolia</i> (Standley) Standley. Goleta, Santa Barbara County, California. Ferren, Fisher & Thorsch, 1989, No. 3211.

light microscopy to determine the general organization of their leaf tissues.

Leaves from *S. palmeri* and *S. mexicana* were detached from herbarium specimens. They were placed in distilled water until they sank and hand sectioned within a few hours for light microscopy to determine presence or absence of specialized C₄ leaf anatomy.

RESULTS

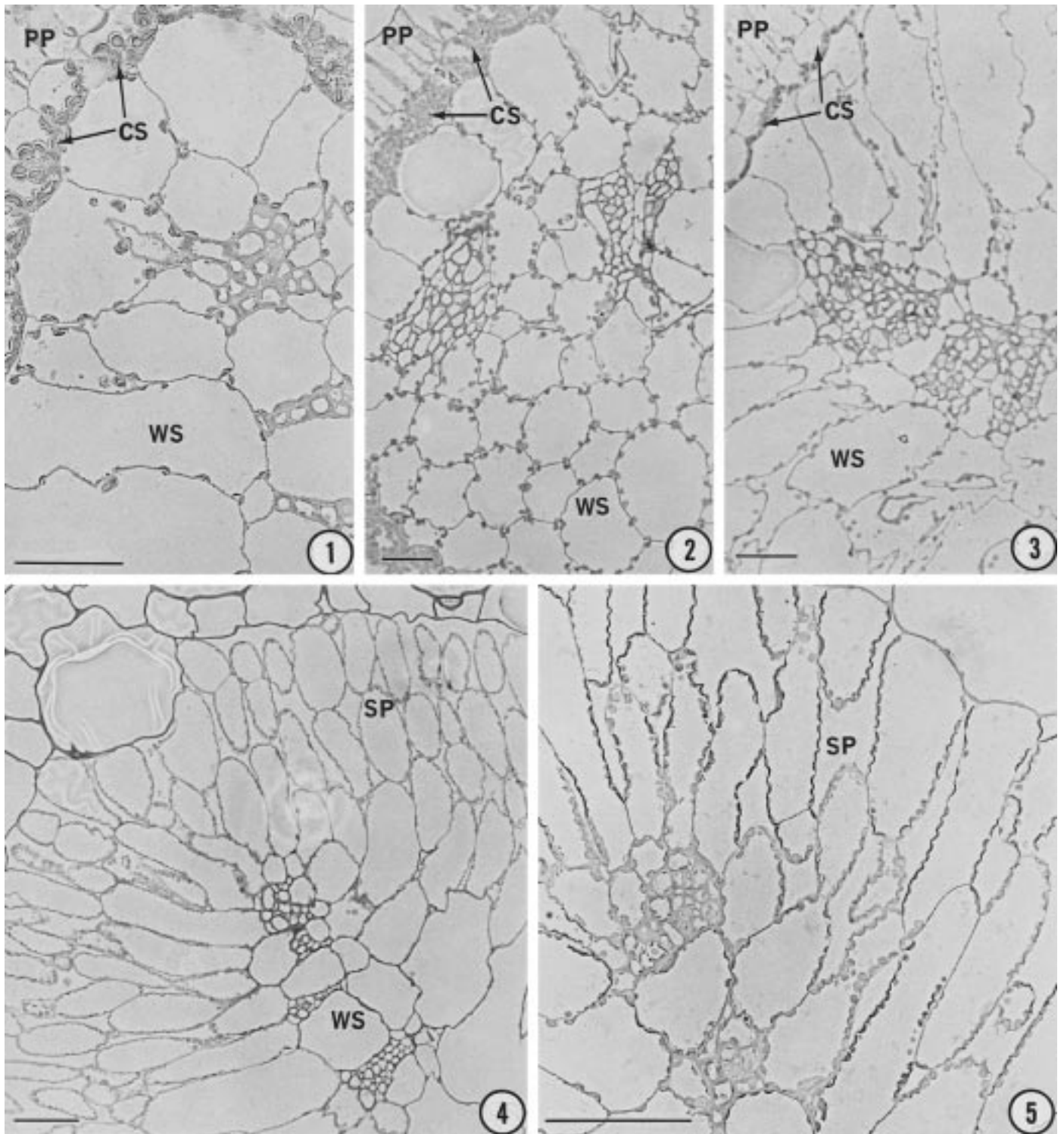
Arrangement of leaf tissues—All species examined have relatively centric leaves. The epidermal cells contain few chloroplasts and have relatively thin cuticles. Stomata are located on both sides of the leaves and are aligned with the other epidermal cells. Results are summarized in Table 2.

Suaeda californica, *S. taxifolia*, *S. moquinii*, *S. tampicensis*, and *S. conferta* have isolateral leaf arrangements (Figs. 1–3). The mesophyll is differentiated into three distinct layers: a layer of palisade parenchyma below the epidermis, an inner chlorenchymatous sheath, and central water-storage tissue, containing vascular bundles. This specialized anatomy, termed the *suaedoid* (Carolin, Jacobs, and Wesk, 1975), is typical for C₄ species of *Suaeda*. The chlorenchymatous sheath, restricted to the leaf blade, does not extend into the petiole or stem.

Leaves from *Suaeda calceoliformis*, *S. esteroa*, and *S. linearis* have varying degrees of bifaciality (Figs. 4–5, Table 2), but in some cases, palisade parenchyma surrounds the central water-storage tissue on all sides, creating an almost isolateral arrangement. In most leaves, the palisade parenchyma layer is most pronounced on the abaxial side. Leaves from these three species also contain small amounts of spongy parenchyma, which primarily consists of elongate cells that resemble palisade cells. Spongy parenchyma is not present in leaves from *S. puer-*

TABLE 2. Organization of tissue in leaves from North American species of *Suaeda*, determined by light microscopy. The following abbreviations are used: A = annual herb; P = perennial herb; S = perennial shrub; Chl. sheath = chlorenchymatous sheath; WST (%) = water-storage tissue (in % of cross-sectional area); ab = austrobassoid leaf anatomy; sd = suaedoid leaf anatomy.

Characteristic	Section <i>Chenopodina</i>					Section <i>Limbogermen</i>				
	<i>S. calceoliformis</i>	<i>S. esteroa</i>	<i>S. linearis</i>	<i>S. puertopenascoa</i>	<i>S. californica</i>	<i>S. taxifolia</i>	<i>S. moquinii</i>	<i>S. conferta</i>	<i>S. tampicensis</i>	
Life form	A	P	A, P	P	S	S	S	S	S	
Habitat	saline and alkaline wetlands	intertidal marshes and estuaries	intertidal marshes, estuaries, beaches	intertidal marshes, estuaries	intertidal marshes, shorelines	coastal bluffs, estuary marshes	alkaline wetlands	alkaline wetlands	alkaline wetlands; coastal marshes	
Chl. sheath	none	none	none	none	present	present	present	present	present	
C ₄ /C ₃ anatomy	C ₃ ; ab	C ₃ ; ab	C ₃ ; ab	C ₃ ; ab	C ₄ ; sd	C ₄ ; sd	C ₄ ; sd	C ₄ ; sd	C ₄ ; sd	
WST (%)	<33%	≈20%	≈25%	≈25%	≈60%	≈60%	≈75%	≈50%	≈50%	
Leaf symmetry	bifacial	± bifacial	± bifacial	± isolateral	isolateral	isolateral	isolateral	isolateral	isolateral	
Bundle arrangement	large main and minors	large main and minors	large main and minors	large main and minors	main and small minors	main and large minors	main and large minors	main and large minors	main and large minors	



Figs. 1–5. Transverse sections of leaves of *Suaeda* species, with the abaxial side of the leaf on top. The approximate location of these figures on the cross-sectional leaf area is indicated in Fig. 12. Scale bars = 50 μ m. 1. *S. californica*. 2. *S. taxifolia*. 3. *S. moquini*. 4. *S. calceoliformis*. 5. *S. esteroa*.

Figure Abbreviations: C, crystalloid; CS, chlorenchymatous sheath; G, grana; M, mitochondrion; P, plastoglobules; PP, palisade parenchyma; S, starch; SP, spongy parenchyma; WS, water-storage tissue.

topenascoa. In these four species, internal water-storage tissue surrounds the vascular bundles, and a distinct chlorenchymatous sheath is not observed. This anatomy, termed *austrobassioid* (Carolin, Jacobs, and Wesk, 1975), is typical for most C_3 plants of the genus.

Water-storage tissue is more abundant in the *suaedoid* species, where it fills at least 50% of the volume of the leaf, and it comprises < 30% of the leaf volume in the *austrobassioid* species (Table 2).

Anatomical features of leaf tissues—Sections of leaves from *Suaeda californica*, *S. taxifolia*, *S. moquinii*, *S. tampicensis*, and *S. conferta* (all section *Limbogermen*) reveal a distinct inner chlorenchymatous sheath located between the palisade parenchyma and the water storage tissue (see Figs. 1–3 for examples). This sheath is generally one cell layer thick, and consists of small cubical cells that are densely packed with chloroplasts, located centripetally along the cell wall (Fig. 7). This chlorenchymatous sheath can be seen with a hand lens at 10 \times magnification in unstained, free-hand, leaf cross sections as a dark green ring of cells.

Species assigned to the section *Limbogermen* have vascular bundles embedded in the central water-storage tissue, which in *S. taxifolia*, *S. moquinii*, *S. tampicensis*, and *S. conferta* also contains numerous chloroplasts. Intervascular distances are minimal between the small bundles (Figs. 1–3), and the bundles are not in direct contact with the chlorenchymatous sheath. Compact bundle sheath cell arrangements surrounding these veins are not observed, but in *S. taxifolia*, the water-storage tissue cells surrounding the bundles vaguely resemble typical bundle sheath cells (Figs. 2, 7).

In leaves from *Suaeda calceoliformis*, *S. esteroa*, *S. linearis*, and *S. puertopenascoa* (section *Chenopodina*), large vascular bundles are surrounded by water-storage tissue containing few chloroplasts. An exception is the water-storage tissue of *S. puertopenascoa*, which contains almost as many chloroplasts as that of the C_4 species from section *Limbogermen*. Species from section *Chenopodina* have small vascular bundles, mostly not in contact with intercellular spaces, and enclosed by nonuniform parenchyma. Distinctions among adjacent palisade, spongy, and possible bundle sheath cells are not obvious and in many cases palisade and spongy parenchyma appear to be in direct contact with the small bundles (Figs. 4–6). Small intervascular distances are observed, with mostly only one parenchyma cell separating the lateral bundles.

Chloroplast characteristics—Quantitative and structural correlations between chloroplasts from the various mesophyll cell types of five species were observed at both the light and TEM level. Results are summarized in Table 3. Some epidermal chloroplasts of *S. taxifolia* and *S. californica* contain crystalloids (Fig. 8). The chloroplasts in the water-storage tissue of *S. calceoliformis* and *S. esteroa* (*Chenopodina*) generally contain limited amounts of well-defined grana. The thylakoids of *S. calceoliformis* chloroplasts are more loosely aligned; those of *S. esteroa* more tightly stacked. The numerous chloroplasts in the palisade and spongy parenchyma of both species contain starch and plastoglobules, lack crystalloids, and have slightly more pronounced stacking of thy-

lakoids (Fig. 11). Chloroplasts of *S. calceoliformis* often appear more rounded than the typical disc shape and contain greater quantities of plastoglobules.

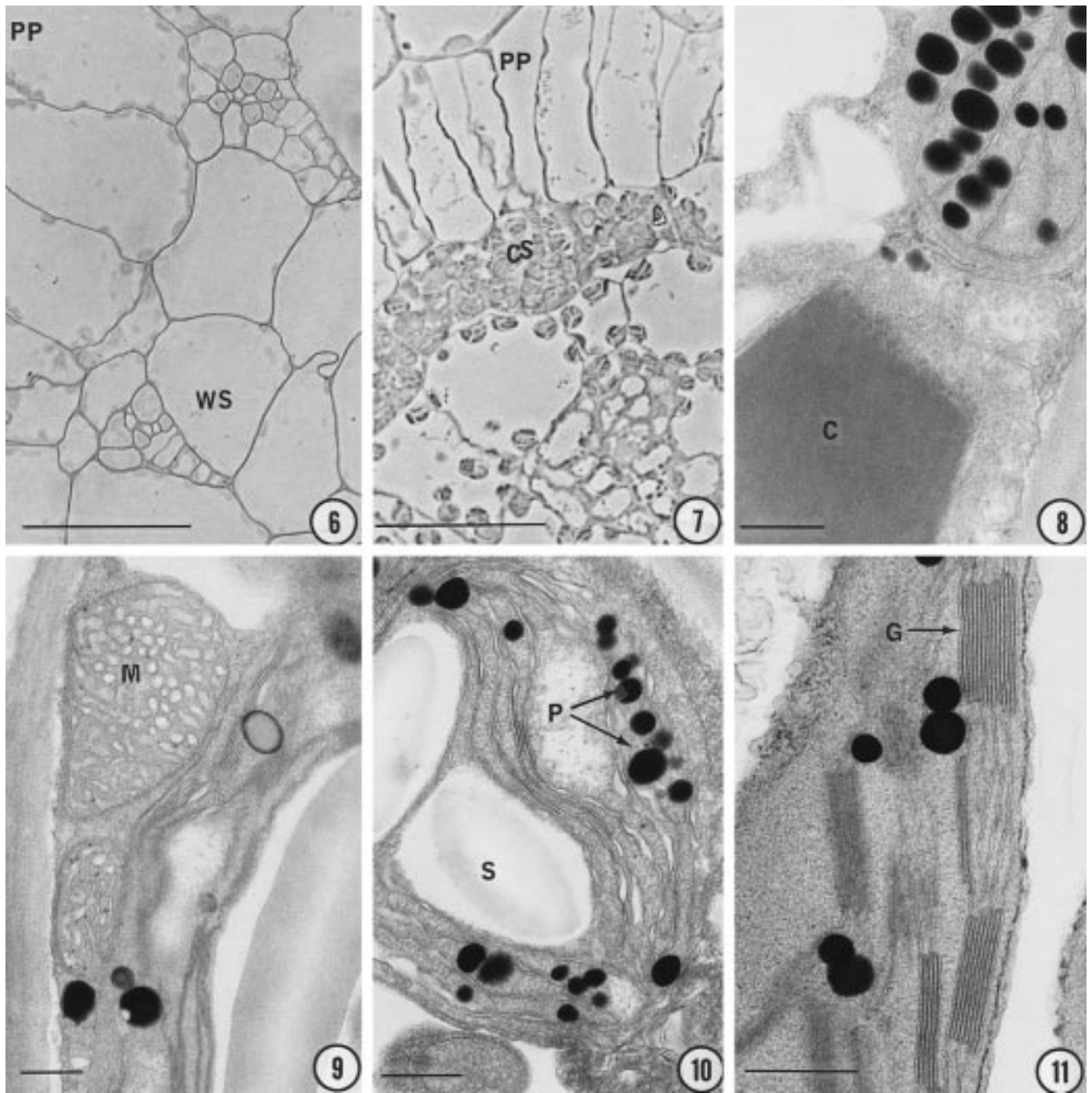
In species from section *Limbogermen*, chloroplasts are more abundant in the water-storage tissue than in any of the C_3 species, especially in *S. taxifolia* (Figs. 2, 7) and *S. moquinii* (Fig. 3). The cells surrounding the smaller bundles of *S. taxifolia* have the largest number of chloroplasts (Fig. 7). Well-defined grana, starch, and plastoglobules, but not crystalloids, are found in chloroplasts from water-storage cells of *S. taxifolia* and *S. californica*. These features are more difficult to discern in *S. moquinii* chloroplasts, due to numerous, large lipid-like deposits located within the stroma, but grana are observed and stromal thylakoids are minimal. The palisade cells of these three species contain similar numbers of chloroplasts in their palisade cells. Starch, plastoglobules, and crystalloids are present, but unlike in the C_3 species, stacked grana are minimal to absent (Fig. 10).

The inner chlorenchymatous sheath is the distinguishing feature of the *suaedoid* C_4 anatomy. The chloroplasts of the sheath cells of *S. californica*, *S. taxifolia*, and *S. moquinii* are predominantly centripetally aligned and contain large quantities of starch and plastoglobules (Figs. 1–3, 7, 9). Granular and crystalloid inclusions are abundant in the chloroplasts of *S. taxifolia*. Grana are observed in all three species (Fig. 9), but thylakoids are more loosely organized in *S. taxifolia* and *S. moquinii*, and in the latter species, stacking is generally minimal. Particularly conspicuous are the numerous, large mitochondria, usually positioned between the chloroplasts and the plasmalemma (Fig. 9). The cristae of these mitochondria are highly developed and phytoferritins are abundant (Fig. 9).

$\delta^{13}C$ values—Results from the measurements of $\delta^{13}C$ in five species of *Suaeda* are summarized in Table 4. *S. calceoliformis* and *S. esteroa* have values below -20% , indicating a high degree of ^{13}C discrimination typical for C_3 species, while *S. californica*, *S. moquinii*, and *S. taxifolia* have values above -20% , which is typical of C_4 species.

DISCUSSION

C_4 anatomy and physiology—Our findings show that North American species of *Suaeda* from the section *Limbogermen* are consistently C_4 species, whereas species examined from section *Chenopodina* are C_3 species. Species from section *Limbogermen* are characterized by the typical *suaedoid* leaf anatomy described from other C_4 species of *Suaeda*, as well as carbon isotope discrimination ratios typical of C_4 species (Winter and Troughton, 1978; Osmond, Björkman, and Anderson, 1980; Winter, 1981). Ultrastructural features of the chloroplasts and mitochondria of species from *Limbogermen* are similar to those reported from other C_4 species of *Suaeda* in the sections *Lachnostigma*, *Schanginia*, and *Conosperma*. Features found in our studies, such as reduced thylakoid stacking in chloroplasts from palisade parenchyma cells, large, centripetally arranged chloroplasts with abundant starch and large stacks of grana, and many, large mitochondria with well-developed cristae in the sheath cells,



Figs. 6–11. Transverse sections of leaves of *Suaeda* species. **6.** Vascular bundles in water-storage tissue of *S. estroea*. Bar = 50 μm . **7.** Chlorenchymatous sheath of *S. taxifolia*. Bar = 50 μm . **8.** Epidermal crystalloid in *S. californica*. Bar = 0.5 μm . **9.** Mitochondria associated with a chloroplast in a chlorenchymatous sheath cell of *S. californica*. Bar = 0.5 μm . **10.** Stroma thylakoids in a chloroplast from the palisade parenchyma of *S. taxifolia*. Notice absence of grana. Bar = 0.5 μm . **11.** Stroma thylakoids and grana in a chloroplast from the palisade parenchyma of *S. estroea*. Bar = 0.5 μm .

also have been reported from *S. monoica* (Shomer-Ilan, Beer, and Waisel, 1975; Shomer-Ilan, Neumann-Ganmore, and Waisel, 1979), *S. altissima*, and *S. confusa* (Glagoleva et al., 1990). These characteristics are typical for C₄ plants of the NAD-ME biochemical type (Hatch, Kagawa, and Craig, 1975; Ku and Edwards, 1975; Gla-

goleva et al., 1990, 1992; P'yankov, 1991, 1993; P'yankov et al., 1992a).

Biochemical studies in the C₄ species *Suaeda monoica* have shown that fixation of atmospheric CO₂ by the C₄ cycle takes place in the primary carbon assimilation (PCA) cells of the palisade parenchyma, which exhibit

TABLE 3. Chloroplast characteristics of five North American species of *Suaeda*, determined by TEM microscopy. Because all chloroplasts have stroma thylakoids, only presence or abundance of grana is listed. Abbreviations used in this table: cp = centripetally aligned; pp = peripherally aligned; CR = crystals present; GR = grana present; PG = plastoglobules present; ST = starch present; NA = not applicable.

Characteristic	Section <i>Chenopodina</i>		Section <i>Limbogermen</i>		
	<i>S. calceoliformis</i>	<i>S. esteroa</i>	<i>S. californica</i>	<i>S. taxifolia</i>	<i>S. moquinii</i>
Chloroplasts in palisade parenchyma	Many, mostly cp; GR; ST; PG; no CR	Many, pp; GR; ST; PG; CR	Many; few GR; ST; PG; CR	Many; no GR; ST; PG; CR	Many; no GR; ST; PG; CR
Chloroplasts in spongy parenchyma	Many; GR; ST; PG	Many, pp; GR; ST; PG	NA	NA	NA
Chloroplasts in chlorenchymatous sheath (Kranz cells)	NA	NA	Many, cp; GR; many ST; PG	Many, packed or cp; loosely stacked GR; ST; PG; CR	Many, cp; few GR; ST; PG
Chloroplasts in water-storage cells	Few; GR; few ST; CR; PG	Few; GR; few ST; CR; PG	Few; GR; ST; PG	Many; GR; ST; PG, no CR	Many; no GR; ST

high activities of PEP carboxylase (Shomer-Ilan, Neumann-Ganmore, and Waisel, 1979). The C_4 acids, formed in the PCA cells, are transported to the photosynthetic carbon reduction (PCR) cells of the chlorenchymatous sheath, which contain all the components of the Calvin-Benson (C_3) cycle (Shomer-Ilan, Neumann-Ganmore, and Waisel, 1979).

The abundant chloroplasts in the water-storage tissue reported herein for *S. taxifolia*, *S. moquinii*, *S. tampicensis*, and *S. conferta* have also been reported for the central Asian species *S. arcuata* and *S. crassifolia* (Bil' et al., 1981). These cells apparently contribute substantially to carbon fixation. Enzymes for both the C_3 and C_4 pathway of photosynthesis have been found in water-storage cells of *Suaeda monoica* (Shomer-Ilan, Neumann-Ganmore, and Waisel, 1979) and *S. arcuata* (P'yankov et al., 1992b). Bil' et al. (1981; Bil' and Fomina, 1992) observed diurnal fluctuations of acidity in the cell sap of leaves, as well as small rates of CO_2 fixation at night and postulated that the cells of the water-storage tissue fix carbon at night by the CAM pathway of photosynthesis. P'yankov et al. (1992b), however, found very low rates

of dark fixation in the C_4 species *S. arcuata* and *S. microphylla*, and reported similar daily oscillations of acidity in these C_4 species and in the C_3 species *S. paradoxa*. They concluded that there was no evidence for CAM photosynthesis in *Suaeda*, and postulated that the observed acidity fluctuations reflected synthesis of osmotic agents and protective substances during the day.

C_3 anatomy and physiology—The anatomical features reported here from section *Chenopodina* are also consistent with those reported from other C_3 species of *Suaeda* (Carolin, Jacobs, and Wesk, 1975; Mateu Andrés, 1989; P'yankov et al., 1992a). Our findings concerning chloroplast ultrastructure in this section are similar to those for other C_3 species in the Chenopodiaceae (Downton, Bisalputra, and Tregunna, 1969; Osmond, Björkman, and Anderson, 1980). Carbon isotope discrimination values found for *S. esteroa* and *S. calceoliformis* are typical for C_3 plants (Winter and Troughton, 1978; Osmond, Björkman, and Anderson, 1980; Winter, 1981). Martin, Lubbers, and Teeri (1982) reported a similar $\delta^{13}C$ value of -25‰ for *S. linearis* from North Carolina, and Guy, Reid, and Krouse (1986) reported a value of -25.6‰ for a species from Alberta, Canada, identified as *S. maritima*, but very likely *S. calceoliformis* (Bassett and Crompton, 1978).

Organization of leaf tissues—All species from section *Limbogermen* have an isolateral leaf anatomy, whereas the species from section *Chenopodina* show varying degrees of bifaciality, due to the differentiation of the leaf mesophyll into densely packed palisade parenchyma and more loosely packed tissue, somewhat resembling spongy parenchyma. The thickness of the palisade parenchyma

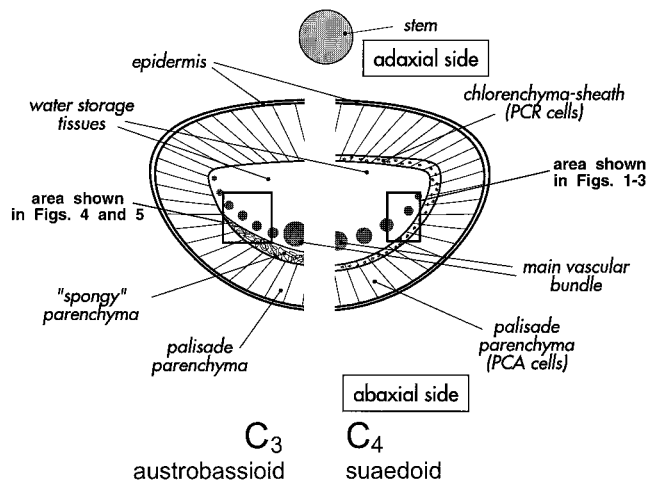


Fig. 12. General organization of leaf tissues in species of *Suaeda* with austrobassioid (C_3) and suaedoid (C_4) types of leaf anatomy (modified after Carolin, Jacobs, and Wesk, 1975). The rectangles show the approximate locations of Figs. 1-5 in the cross-sectional area of the leaves.

TABLE 4. Carbon isotope ratio in leaves from species of *Suaeda* collected in California. The data are expressed in the δ notation, where the data are reported against the PDB standard and $\delta^{13}C = [(^{13}C/^{12}C_{\text{sample}})/(^{13}C/^{12}C_{\text{standard}}) - 1] \times 1000$.

Species	$\delta^{13}C$ value (‰)
<i>Suaeda calceoliformis</i>	-25.7
<i>Suaeda esteroa</i>	-24.4
<i>Suaeda californica</i>	-12.7
<i>Suaeda moquinii</i>	-13.0
<i>Suaeda taxifolia</i>	-18.5

on the adaxial or abaxial side of the leaves may be related to leaf angle, but our observations on leaf position in species of section *Chenopodina* only partially agree with this notion. Leaves of *S. calceoliformis* are often in a tightly ascending arrangement, which may explain the adaxial position of spongy parenchyma, but this is also true for *S. linearis* and *S. esteroa*, which have small amounts of spongy parenchyma on the abaxial side. A survey of plants from different locations indicated that the amount and location of spongy parenchyma appear to vary substantially among individuals and populations of species from section *Chenopodina* (H. J. Schenk, unpublished data).

Isolateral (unifacial) leaf anatomy is common in plants that grow under high light conditions and in leaves that are held in a more or less vertical (orthotropic) position (Heinricher, 1884; Napp-Zinn, 1984/1988). This feature is a common characteristic found in plants from hot and arid environments because it tends to minimize heating of the leaves and thus reduces transpirational demands (Ehleringer and Forseth, 1980). However, vertical leaf position combined with isolateral leaf anatomy should be advantageous in all high-light environments, regardless of aridity, as long as there is enough scattered radiation to reach all sides of the leaf (Heinricher, 1884; Nobel, 1991). This is true in desert environments and on shorelines, the habitat for many species of *Suaeda*.

In addition to the two kinds of leaf anatomy found in this study (Fig. 12), Paulsen (1912) described and illustrated a third kind of leaf anatomy for the central Asian species *S. microsperma*. In this type, water-storage tissue is situated below the epidermis, forming a hypodermis that surrounds what appears to be internal palisade parenchyma and/or a chlorenchymatous bundle sheath. Pyykkö (1966) described a similar anatomy for herbarium specimens from Patagonia identified as *S. fruticosa*, which are very likely *S. argentinensis* (Soriano, 1942, 1945). Such peripheral water-storage tissues are known in the Chenopodiaceae from the genus *Atriplex* (Volkens, 1887; Jürgens, 1985; Weiglin and Winter, 1991). Yet another anatomical type may be the C₃ anatomy in *S. vera*, which appears to be of a different kind from the one observed in section *Chenopodina*. According to Solms-Laubach (1901), water-storage tissue and chlorenchyma in this species are not differentiated into separate layers. These earlier reports are currently under investigation to determine whether they in fact represent distinct anatomical types and to evaluate the taxonomic importance of any differences observed.

Functional anatomy and ecology—The C₄ species of section *Limbogermen* are largely restricted to the south and the semiarid west of the North American continent, from Mexico north to 50° N latitude, west of 95° longitude, but largely excluding the Pacific coast north of central California, whereas C₃ species are widely distributed on the continent. This agrees with the notion that C₄ plants are most abundant in hot, dry, high-light environments (Björkman, 1973; Percy and Ehleringer, 1984; Ehleringer and Monson, 1993).

Species from section *Limbogermen* have the superior water-use efficiency of the C₄ syndrome, as well as a higher degrees of leaf succulence, compared to the C₃

species from section *Chenopodina*. This fits in well with observations regarding habitat range of the species studied. North American species of section *Chenopodina* are largely restricted to more or less saline wetlands, while species from section *Limbogermen* extend from wetlands to upland areas. In wetlands, C₃ and C₄ species of *Suaeda* commonly grow side by side, for example *S. moquinii* and *S. calceoliformis* in alkaline habitats of the Great Basin, or *S. tampicensis* and *S. linearis* along the coast of southern Texas. Studies of such sympatric populations along gradients of salinity and aridity would be informative. Other studies of such gradients have often found C₄ species to be more abundant in drier and more saline sites (Syvertsen et al., 1976; Eickmeier, 1978; Shomer-Ilan, Nissenbaum, and Waisel, 1981). However, a number of small-scale distributional studies have found no correlation between the abundance of C₄ species and environmental factors (Percy and Ehleringer, 1984; Barbour et al., 1987; Weiglin and Winter, 1991). This is not very surprising as the photosynthetic pathway is only one factor of many influencing the ecological behavior of plants.

Phenology and life histories—The phenology of North American C₃ and C₄ species of *Suaeda* is largely similar. All are active throughout the summer, which may include prolonged periods of drought in the southwestern part of the continent. Thus, they do not show the difference in phenology observed in many other C₃ and C₄ taxa. In the semideserts of North America, C₃ species are mostly active from fall to spring, whereas C₄ species tend to be active in summer, especially under conditions of summer precipitation (Syvertsen et al., 1976; Ehleringer and Monson, 1993; Ehleringer, 1994). It seems likely that all *Suaeda* species are enabled by their succulence to persist throughout the dry season.

Any ecological differences among species from the sections *Limbogermen* and *Chenopodina* may result from their different life histories. The fact that C₃ species of *Suaeda* in North America are herbaceous annuals and perennials, whereas the C₄ species are semishrubs and shrubs appears to be a phylogenetic and biogeographical coincidence. In central Asia, C₄ species of *Suaeda* are mostly annuals (Glagoleva et al., 1990; P'yankov et al., 1992a).

Taxonomy and phylogeny—Our results on the distribution of C₃ and C₄ photosynthesis in North American species of *Suaeda* mostly agree with those of Welkie and Caldwell (1970). A taxonomic re-examination of the specimens used by these authors enabled us to clarify the differences found. Of nine specimens labeled as *S. californica*, we re-identified seven as *S. taxifolia*, one as *S. californica*, and one as *S. esteroa*. The photosynthetic syndrome of the only specimen of *S. californica* could not be determined (G. W. Welkie, personal communication). Five specimens originally identified as *S. depressa* var. *depressa* and reported by Welkie and Caldwell to be a C₄ species turned out to be *S. moquinii*. The corrections proposed here to the reports regarding specialized leaf anatomy in *Suaeda* in Welkie and Caldwell (1970) are summarized in Table 6.

Four other North American species belonging to section *Chenopodina* have not been included in the present

TABLE 5. C₃ and C₄ anatomy and physiology in *Suaeda*. The determinations are partly based on anatomical descriptions and drawings made before the discovery of the C₄ syndrome (Solms-Laubach, 1901; Monteil, 1906; Paulsen, 1912; Evenari, 1938; Shields, 1951; Pyykkö, 1966). More recent determinations were based on leaf anatomy, biochemistry, and δ¹³C values (see the references listed for further details). Sectional affiliations determined by Iljin (1936a, b), with the following exceptions: *S. aegyptiaca* (Townsend, 1980), *S. esteroa*, *S. californica* (Ferren, 1993), *S. puertopenascoa* (Watson and Ferren, 1991), *S. conferta* and *S. mexicana* (W. R. Ferren and H. J. Schenk, unpublished data), *S. patagonica* (determined from herbarium specimens and original description), *S. australis*, *S. carnosissima*, and *S. asphaltica* (tentatively determined from original descriptions). For a discussion of the sectional affiliations of *S. fruticosa*, *S. vera*, and *S. heterophylla* see the text and footnotes below.

Section	C ₃	C ₄
<i>Suaeda</i> * (syn. sect. <i>Platystigma</i> Iljin) (shrubs)	<i>S. vera</i> ^{b,f,h,i,j,x,y*}	
<i>Chenopodina</i> Moquin-Tandon (syn. <i>Heterosperma</i> Iljin nom. illeg.; <i>Schoberia</i> † (annuals and perennials))	<i>S. australis</i> ^b <i>S. calceoliformis</i> ^{a,g} <i>S. corniculata</i> ^v <i>S. esteroa</i> ^a <i>S. linearis</i> ^{g,p} <i>S. maritima</i> ^{b,g,h,j,k,l,y} <i>S. mexicana</i> ^a <i>S. occidentalis</i> ^g <i>S. olufsenii</i> ^{m,t} <i>S. patagonica</i> ^c <i>S. puertopenascoa</i> ^a	<i>S. crassifolia</i> ⁿ
<i>Schanginia</i> (C. A. Meyer) Volkens subsect. <i>Schanginia</i> (Syn. <i>Spermococca</i> Iljin) (annuals)	<i>S. glauca</i> ^b <i>S. linifolia</i> ^t <i>S. paradoxa</i> ^d	
<i>Schanginia</i> (C. A. Meyer) Volkens subsect. <i>Leiosperma</i> Iljin (annuals to shrubs)		<i>S. altissima</i> ^{b,c,h,i,y***} <i>S. microphylla</i> ^{b,g,††}
<i>Lachnostigma</i> Iljin (mostly shrubs)	<i>S. vermiculata</i> ^{b,‡}	<i>S. arucata</i> ^{d,t} <i>S. asphaltica</i> ^{h,s} <i>S. dendroides</i> ^{b,t} <i>S. fruticosa</i> ^{f,o,q,x*} <i>S. monoica</i> ^{b,f,l,x} <i>S. pruinosa</i> ^{w,x} <i>S. vermiculata</i> ^{f,h,x}
<i>Conosperma</i> † Iljin (annuals)		<i>S. acuminata</i> ^h <i>S. carnosissima</i> ^h <i>S. confusa</i> ^c <i>S. splendens</i> ^{b,f,h,y***}
<i>Limbogermen</i> Iljin (perennials, shrubs)		<i>S. californica</i> ^a <i>S. conferta</i> ^a <i>S. moquini</i> ^{a,g} <i>S. palmeri</i> ^a <i>S. suffrutescens</i> ^t <i>S. tampicensis</i> ^a <i>S. taxifolia</i> ^{a,g}
<i>Brezia</i> (Moquin-Tandon) Volkens (annuals)		<i>S. heterophylla</i> ^{d**,†††}
<i>Immersa</i> Townsend (annuals to perennials)		<i>S. aegyptiaca</i> ^{b,f,h,i,o}
<i>Physophora</i> Iljin (shrubs)	<i>S. physophora</i> ^s	
Sectional affiliation unknown:	<i>S. ifniensis</i> ^u <i>S. palaestina</i> ^{h,i}	<i>S. arguinensis</i> ^u <i>S. divaricata</i> ^e

† Tsvelev (1993) proposed to submerge sections *Heterosperma* and *Conosperma* into section *Schoberia* (C. A. Meyer) Volkens nom. illeg.

†† Tsvelev (1993) suggested *S. microphylla* to be more closely related to *S. dendroides* than to *S. altissima*.

‡ According to Winter (1981) this report of C₃ photosynthesis in *S. vermiculata* was probably due to incorrect taxonomy.

* See the discussion section regarding sectional affiliations of *S. vera*, *S. fruticosa*, and other species of section *Lachnostigma*.

** Iljin (1936a, b) assigned *S. heterophylla* to section *Heterosperma*. This assignment to section *Brezia* follows Volkens (1894) and Tsvelev (1993). Moquin-Tandon (1849) and Ulbrich (1934) recognized *Brezia* Moq. as a separate genus.

*** Freitag (1989) reports *S. splendens* and *S. altissima* to be C₃ species, apparently based on a casual report in Solms-Laubach (1901). Tsvelev (1993) assigned *S. altissima* to a new monotypic section called *Macrosuaeda*.

References: a = Present study; b = Carolin, Jacobs, and Wesk, 1975; c = Glagoleva et al., 1990; d = P'yankov et al., 1992a; e = Pyykkö, 1966; f = Shomer-Ilan, Nissenbaum, and Waisel, 1981; g = Welkie and Caldwell, 1970; h = Winter, 1981; i = Freitag, 1989; j = Mateu Andrés, 1989; k = Venkatesalu and Chellappan, 1988; l = Winter and Troughton, 1978; m = P'yankov, 1993; n = Bil' and Fomina, 1992; o = Frey and Kürschner, 1983; p = Martin, Lubbers, and Teeri, 1982; q = Weiglin and Winter, 1991; r = Shields, 1951; s = Evenari, 1938; t = Paulsen, 1912; u = Maire, 1962; v = Gamaley, 1984; w = Mommaerts-Billiet, 1971; x = Solms-Laubach, 1901; y = Monteil, 1906.

TABLE 6. Corrections to the determinations of specialized leaf anatomy in the genus *Suaeda* (Chenopodiaceae) in Welkie and Caldwell (1970, page 2138), based on a re-examination of the herbarium specimens used in that study. (+) species that exhibit the specialized (C₄) leaf anatomy; (–) species that do not exhibit the specialized leaf anatomy (C₃).

<i>Suaeda</i>	
(+)	<i>S. californica</i> S. Watson
	<i>S. moquinii</i> (Torrey) Greene
	name used in Welkie and Caldwell (1970):
	<i>S. fruticosa</i> (Linnaeus) Forsskal auct. mult., name misapplied
	synonyms:
	<i>S. intermedia</i> (S. Watson) Heller
	<i>S. nigra</i> (Rafinesque) Macbride
	<i>S. moquini</i> (Greene) Nelson
	<i>S. torreyana</i> S. Watson var. <i>torreyana</i>
	<i>S. torreyana</i> S. Watson var. <i>ramosissima</i> (Standley) Munz
	<i>S. suffrutescens</i> S. Watson
	<i>S. taxifolia</i> Standley
(–)	<i>S. calceoliformis</i> (Hooker) Moquin-Tandon
	name used in Welkie and Caldwell (1970):
	<i>S. depressa</i> (Pursh) S. Watson var. <i>depressa</i> auct. mult. name misapplied
	synonyms:
	<i>S. depressa</i> (Pursh) S. Watson var. <i>erecta</i> S. Watson
	<i>S. minutiflora</i> S. Watson
	<i>S. esteroa</i> Ferren & Whitmore
	<i>S. linearis</i> (Elliott) Moquin-Tandon
	<i>S. maritima</i> (Linnaeus) Dumortier
	<i>S. occidentalis</i> S. Watson

study. One of these is *S. maritima*, a polymorphic taxon with a worldwide distribution in coastal marshes. This is a C₃ species with austrobassoid leaf anatomy (Welkie and Caldwell, 1970; Carolin, Jacobs, and Wesk, 1975; Venkatesalu and Chellappan, 1988; Mateu Andrés, 1989). *Suaeda rolandii*, a rare species of coastal marshes of northeastern North America from New Jersey to Nova Scotia, is thought to be allotetraploid in origin, derived from the closely related *S. calceoliformis* and *S. maritima* (Bassett and Crompton, 1978; Clemants, 1992). Therefore, it is likely a C₃ species, as also suggested by its distribution. *Suaeda occidentalis*, a taxon that is closely related to *S. calceoliformis* (Watson, 1874), possesses C₃ anatomy (Welkie and Caldwell, 1970). We also attempted to determine the presence of C₄ anatomy in herbarium specimens of *S. jacoensis*, but found that leaves from these specimens did not rehydrate adequately to make a determination possible.

In the section *Limbogermen*, other shrubby desert species than the ones included in this study have been reported from North America, including *S. nigrescens*, and *S. suffrutescens*, which two of the authors of this study consider to be synonymous with *Suaeda moquinii* (W. R. Ferren and H. J. Schenk, unpublished data). The leaf anatomy of *Suaeda suffrutescens* has been described in detail by Shields and colleagues (1951; Shields, Mangum, and Ludi, 1958). It is identical to the C₄ anatomy described here for *S. moquinii*.

In our study, presence of the C₄ syndrome was restricted to species from section *Limbogermen*. Other studies of genera containing both C₃ and C₄ species have shown that these two photosynthetic syndromes can be found in taxa that are closely enough related to allow them to hy-

bridize (Osmond, Björkman, and Anderson, 1980). Intermediate C₃-C₄ species also exist, including species of Chenopodiaceae (Osmond, Björkman, and Anderson, 1980; P'yankov, Voznesenskaya, and Kondrachuk, 1993). However, research in two large genera that include both C₃ and C₄ species, *Atriplex* and *Panicum*, has shown that these two syndromes apparently do not occur within the same species complex, or even in the same section of the genus (Osmond, Björkman, and Anderson, 1980; Zuloaga, Dubcovsky, and Morrone, 1993). An earlier review by Carolin, Jacobs, and Wesk (1975) found three sections of the genus *Atriplex* to include both C₃ and C₄ species, while 15 sections were exclusively C₃ or C₄. According to Zuloaga, Dubcovsky, and Morrone (1993), presence or absence of the Kranz syndrome is one of two characters that contribute foremost to the delimitation of major groups in the genus *Panicum*.

A literature review of sectional affiliations of C₃ and C₄ species of *Suaeda* gave the results summarized in Table 5. Two sections appear to include both C₃ and C₄ species. In section *Schanginia*, C₃ and C₄ species are divided along subsectional lines. Tsvelev (1993) recently proposed to dissolve subsection *Leiosperma*, suggesting to place *S. microphylla* in the affinity of *S. dendroides* and *S. altissima* in the monotypic section *Macrosuaeda*. Section *Schanginia* is certainly in need of study; it is the only one of Iljin's (1936b) sections defined by inflorescence type rather than stigma morphology, and the data on photosynthetic types suggest artificiality of this section. Only one C₄ species, *S. crassifolia*, is reported from section *Chenopodina*, which is otherwise C₃. There are a number of potential explanations for this. *Suaeda crassifolia* may belong in a different section or may have been incorrectly identified in the study by Bil' and Fomina (1992). Alternatively, the origin of C₄ photosynthesis in *Suaeda* may be polyphyletic as postulated for the genus *Atriplex* (Osmond, Björkman, and Anderson, 1980), or reversals from C₄ to C₃ may have occurred. However, it is likely that the C₄ syndrome in *Suaeda* has evolved only once in the genus from a C₃ ancestor common to all C₄ species of *Suaeda*. This is suggested by the unique suaedoid leaf anatomy common to all C₄ species of *Suaeda* examined so far. The global distribution of C₄ species in *Suaeda* suggests that C₄ photosynthesis may have originated very early in the evolution of the genus, in the upper Cretaceous or early Tertiary, possibly in seasonally arid areas of the continental interior of Gondwana land before its final breakup into the continents Africa, Australia, and America (P'yankov, 1991; P'yankov et al., 1992a). A reversion of C₄ to C₃ photosynthesis could also explain the presence of C₃ species in a section containing C₄ species, but there is currently no evidence for this. No data are available to clarify the potential evolutionary pathways from C₃ to C₄ forms or vice versa, as C₃-C₄ intermediates are not known from *Suaeda*. The genus is obviously in need of a phylogenetic analysis, including species from all sections and both photosynthetic syndromes.

The proposal by Tsvelev (1993) to combine section *Conosperma* with *Chenopodina* (syn. *Heterosperma*) would merge a group of C₄ annuals with a group of almost exclusively C₃ annuals and perennials that also has a distinctly different stigma morphology (Iljin, 1936b). In

view of this, we propose to retain the sections *Chenopodina* (syn. *Heterosperma*) and *Conosperma* as delimited by Iljin (1936b).

Species from the sections *Lachnostigma* and *Suaeda* (syn. *Platystigma*) are often considered to be closely related (e.g., Tsvelev, 1993), although it was pointed out as early as 1901 that these species are easily separated by their different leaf anatomies (Solms-Laubach, 1901). The taxonomy and nomenclature of these groups have been complicated in the past by confusion of the two species *S. vera* Forssk. ex J. F. Gmelin and *S. fruticosa* Forssk. ex J. F. Gmelin (Schweinfurth, 1896; Soriano, 1942, 1945; Zohary, 1966; Pedrol and Castroviejo, 1988; Boulos, 1991), which apparently also affected Iljin's (1936b) sectional assignments of these species. This issue is discussed in a separate paper (H. J. Schenk and W. R. Ferren, unpublished data). For the purpose of the topic under discussion here it suffices to say that the gynoecium morphology of *S. vera* clearly shows that it belongs in Iljin's *Platystigma* (a synonym for section *Suaeda*) (see the illustrations in Iljin [1936b] for gynoecium morphology in *Platystigma* and Pedrol and Castroviejo [1988] and Freitag [1989] for *S. vera*), whereas *S. fruticosa* belongs in section *Lachnostigma*. The proposal by Tsvelev (1993) to include both of these taxa in section *Suaeda* would again combine species with different photosynthetic pathways and different gynoecium morphologies in one section. In light of this, we retain section *Lachnostigma* (Table 5). Further studies are necessary to clarify the relationships among the C₃ species *S. vera* and the C₄ species *S. fruticosa*, *S. vermiculata*, *S. monoica*, *S. dendroides*, and *S. microphylla*, as well as the relationship between these taxa and the North American taxa from section *Limbogermen*.

The sectional affiliations of four species listed in Table 5 could not be determined. In the case of two of these species, *S. palaestina* and *S. ifniensis*, the photosynthetic pathway and a number of other characteristics suggest affiliation with *Suaeda vera* (Maire, 1962; Freitag, 1989).

Hopefully, a phylogenetic analysis and an in-depth look at the characters delimiting sections in *Suaeda* will clarify some of the problems described above. For the sections *Chenopodina* and *Limbogermen* in North America, the consistent differences in leaf anatomy correlate with a number of other characters separating these sections (W. R. Ferren and H. J. Schenk, unpublished data).

Section *Chenopodina* in North America includes glabrous annuals and herbaceous or rarely suffrutescent perennials with sessile leaves that lack specialized C₄ anatomy. Bractlets in the inflorescence are always without marginal trichomes. The flowers are bisexual and more or less bilateral; the calyx is hooded and keeled, horned, and/or horizontally or vertically wing-margined; there are two to four slender, short, and smooth to papillose stigmas, inserted on the constricted tip of the ovary. Seeds are positioned horizontally and are dimorphic in some species and individuals.

Section *Limbogermen* includes shrubs and subshrubs (often flowering in the first year) that are glabrous or pubescent. Leaves are sessile or constricted at the base and short petiolate; they have specialized C₄ anatomy. Bractlets in the inflorescence often have several marginal scattered hairs. The flowers are bisexual or unisexual and

radial; the calyx lobes are rounded, hooded, or keeled, but not horned or wing-margined, and there are two to mostly three filiform, pilose-papillate stigmas, which are subsessile or on a short style, from a pit in top of ovary, often on a neck-like extension. The seeds are always monomorphic, in a horizontal or vertical position.

These consistent differences could justify a treatment of these groups as different genera, or at least subgenera. However, such a split would have to be made on the basis of a global taxonomic treatment of the genus. Hopefully, such a treatment will be possible in the near future to clarify the difficult taxonomy of *Suaeda*. Knowledge of the global distribution of C₃ and C₄ species of *Suaeda* could also explain much about the ecology of these photosynthetic syndromes and the evolution of C₄ photosynthesis in the Chenopodiaceae.

LITERATURE CITED

- BARBOUR, M. G., M. REJMÁNEK, A. F. JOHNSON, AND B. M. PAVLIK. 1987. Beach vegetation and plant distribution patterns along the northern Gulf of Mexico. *Phytocoenologia* 15: 201–233.
- BASSETT, I. J., AND C. W. CROMPTON. 1978. The genus *Suaeda* (Chenopodiaceae) in Canada. *Canadian Journal of Botany* 56: 581–591.
- BIL', K. Y., AND I. R. FOMINA. 1992. Possibility of cooperative interaction of phototrophic and heterotrophic tissues during carbon dioxide photoassimilation. *Photosynthetica* 26: 609–616.
- , V. Y. LYUBIMOV, R. N. DEMIDOVA, AND T. GEDEMOV. 1981. Assimilation of CO₂ by plants of the family Chenopodiaceae with three types of autotrophic tissues in the leaves. *Soviet Plant Physiology* 28: 808–815.
- BJÖRKMANN, O. 1973. Comparative studies on photosynthesis in higher plants. *Photophysiology* 8: 1–63.
- BOULOS, L. 1991. Notes on *Suaeda* Forssk. ex Scop.. Studies in the Chenopodiaceae of Arabia: 2. *Kew Bulletin* 46: 291–296.
- BROWN, W. V. 1975. Variations in anatomy, associations, and origins of Kranz tissue. *American Journal of Botany* 62: 395–402.
- , AND B. N. SMITH. 1972. Grass evolution, the Kranz syndrome, ¹³C/¹²C ratios, and continental drift. *Nature* 239: 345–346.
- CAROLIN, R. C., S. W. L. JACOBS, AND M. WESK. 1975. Leaf structure in Chenopodiaceae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 95: 226–255.
- CLEMANTS, S. E. 1992. Chenopodiaceae and Amaranthaceae of New York State. *New York State Museum Bulletin* 485: 1–26.
- DOWNTON, W. J. S., T. BISALPUTRA, AND E. B. TREGUNNA. 1969. The distribution and ultrastructure of chloroplasts in leaves differing in photosynthetic carbon metabolism. II. *Atriplex rosea* and *Atriplex hastata* (Chenopodiaceae). *Canadian Journal of Botany* 47: 915–919.
- EHLERINGER, J. R. 1994. Variation in gas exchange characteristics among desert plants. In E.-D. Schulze and M. M. Caldwell [eds.], *Ecophysiology of photosynthesis*. *Ecological Studies* 100: 361–392.
- , AND I. FORSETH. 1980. Solar tracking by plants. *Science* 210: 1094–1098.
- , AND R. K. MONSON. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* 24: 411–439.
- EICKMEIER, W. G. 1978. Photosynthetic pathway distributions along an aridity gradient in Big Bend National Park, and implications for enhanced resource partitioning. *Photosynthetica* 12: 290–297.
- EVENARI, M. 1938. The physiological anatomy of the transpiratory organs and the conducting systems of certain plants typical of the Wilderness of Judaea. *Journal of the Linnean Society of London, Botany* 51: 389–407.
- FERREN, W. R., JR. 1993. *Suaeda*. In J. C. Hickman [ed.], *The Jepson manual: higher plants of California*, 514–515. University of California Press, Berkeley, CA.
- , AND S. A. WHITMORE. 1983. *Suaeda esteroa* (Chenopodiaceae),

- a new species from estuaries of southern California and Baja California. *Madroño* 30: 181–190.
- FREITAG, H. 1989. Contributions to the Chenopod flora of Egypt. *Flora (Jena)* 183: 149–173.
- FREY, W., AND H. KÜRSCHNER. 1983. Photosyntheseweg und Zonierung von Halophyten an Salzseen in der Türkei, in Jordanien und im Iran. (Photosynthetic pathways and ecological distribution of halophytes from some inland salines of Turkey, Jordan, and Iran. In German, with English summary). *Flora (Jena)* 173: 293–310.
- GAMALEY, Y. V. 1984. Anatomija lista u rasteniy pustyni Gobi. (The leaf anatomy of Gobi plants. In Russian with English summary). *Botanicheskii Zhurnal* 69: 569–584.
- , T. A. GLAGOLEVA, K. G. KOL'CHEVSKII, AND M. V. CHULANOVSKAYA. 1992. Ekologiya i evolyutsiya tipov C₄-sindroma v svyazi s filogeniej semejstv *Chenopodiaceae* i *Poaceae*. (The C₄-syndrome types: ecology and evolution in connection with phylogeny of *Chenopodiaceae* and *Poaceae*. In Russian with English summary). *Botanicheskii Zhurnal* 77: 1–12.
- GLAGOLEVA, T. A., M. V. CHULANOVSKAYA, M. V. PAKHOMOVA, E. V. VOZNESENSKAYA, AND Y. V. GAMALEY. 1992. Effects of salinity on the structure of assimilating organs and ¹⁴C labelling patterns in C₃ and C₄ plants of Ararat plain. *Photosynthetica* 26: 363–369.
- , E. V. VOZNESENSKAYA, K. G. KOL'CHEVSKII, N. I. KOCHARYAN, M. V. PAKHOMOVA, M. V. CHULANOVSKAYA, AND Y. V. GAMALEY. 1990. Structural-functional characteristics of halophytes of the Ararat Valley. *Soviet Plant Physiology* 37: 822–829.
- GRENIER, M., AND M. GODRON. 1856. Flore de France, vol. 3. F. Savy, Paris.
- GUY, R. D., D. M. REID, AND H. R. KROUSE. 1986. Factors affecting ¹³C/¹²C ratios of inland halophytes. II. Ecophysiological interpretations of patterns in the field. *Canadian Journal of Botany* 64: 2700–2707.
- HATCH, M. D., T. KAGAWA, AND S. CRAIG. 1975. Subdivision of C₄-pathway species based on differing C₄ acid decarboxylating systems and ultrastructural features. *Australian Journal of Plant Physiology* 2: 111–128.
- HEINRICHER, E. 1884. Ueber isolateralen Blattbau mit besonderer Berücksichtigung der europäischen, speciell der deutschen Flora. *Jahrbücher für wissenschaftliche Botanik* 15: 502–567.
- HOPKINS, C. O., AND W. H. BLACKWELL. 1977. Synopsis of *Suaeda* (Chenopodiaceae) in North America. *Sida* 7: 147–173.
- ILJIN, M. M. 1936a. Chenopodiaceae Less. In V. L. Komarov and B. K. Shishkin [eds.], *Flora of the U.S.S.R.*, vol. VI, Centrospermae (English translation, 1970, by N. Landau), 4–272. Israel Program for Scientific Translation, Jerusalem.
- . 1936b. K sistematike roda *Suaeda* Forssk. i tri'by *Suaedeae* Rchnb. (On the systematics of the genus *Suaeda* Forssk. and the tribe *Suaedeae* Rchnb. In Russian.) *Sovietskaja Botanik* 1936(5): 39–49.
- JÜRGENS, N. 1985. Konvergente Evolution von Blatt- und Epidermismerkmalen bei blattsukkulenten Familien. (Convergent evolution of leaf and epidermal characters in leaf succulent families. In German with English summary). *Berichte der Deutschen Botanischen Gesellschaft* 98: 425–446.
- KOLCHEVSKII, N. I. KOCHARYAN, AND O. Y. KOROLEVA. 1995. Effect of salinity on photosynthetic characteristics and ion accumulation in C₃ and C₄ plants of Ararat plain. *Photosynthetica* 31: 277–282.
- KU, S. B., AND G. E. EDWARDS. 1975. Photosynthesis in mesophyll protoplasts and bundle sheath cells of various types of C₄ plants. IV. Enzymes of respiratory metabolism and energy utilizing enzymes of photosynthetic pathways. *Zeitschrift für Pflanzenphysiologie* 77: 16–32.
- MAIRE, R. 1962. Flore de l'Afrique du Nord. Vol. VIII. Paul Lechevalier, Paris.
- MARTIN, C. E., A. E. LUBBERS, AND J. A. TEERI. 1982. Variability in Crassulacean acid metabolism: a survey of North Carolina succulent species. *Botanical Gazette* 143: 491–497.
- MATEU ANDRÉS, I. 1989. Anatomía foliar en plantas de saladares mediterráneos costeros. Dicotiledóneas. *Candollea* 44: 435–452.
- METZLER, W. 1924. Beiträge zur vergleichenden Anatomie blattsukkulenter Pflanzen. *Botanisches Archiv* 6: 50–83.
- MOMMAERTS-BILLIET, F. 1971. Note sur l'écomorphologie foliaire de quelques plantes gypsicoles d'Espagne. *Bulletin de la Société royale de Botanique de Belgique* 104: 21–27.
- MONTEIL, P. 1906. Anatomie comparée de la feuille des chénopodiacées. Lucien Declume, Lons-le-Saunier.
- MOQUIN-TANDON, C. H. B. A. 1840. *Chenopodearum monographica enumeratio*. P.-J. Loss, Paris.
- . 1849. Salsolaceae. In A. P. de Candolle [ed.] *Prodomus systematis universalis regni vegetabilis* 13.2, 41–219. Masson, Paris.
- NAPP-ZINN, K. 1984/1988. Anatomie des Blattes. II. Blattanatomie der Angiospermen. B. Experimentelle und ökologische Anatomie des Angiospermenblattes, 2 vols; Handbuch der Pflanzenanatomie, VIII. Gebrüder Bornträger, Berlin.
- NOBEL, P. S. 1991. *Physiochemical and environmental plant physiology*. Academic Press, San Diego, CA.
- OLESEN, P. 1974. Leaf anatomy and ultrastructure of chloroplasts in *Salsola kali* L. as related to the C₄-pathway of photosynthesis. *Botaniska Notiser* 127: 352–363.
- OSMOND, C. B., O. BJÖRCKMAN, AND D. J. ANDERSON. 1980. Physiological processes in plant ecology: toward a synthesis with *Atriplex*. *Ecological Studies* 36.
- , J. H. TROUGHTON, AND D. J. GOODCHILD. 1969. Physiological, biochemical and structural studies of photosynthesis and photorespiration in two species of *Atriplex*. *Zeitschrift für Pflanzenphysiologie* 61: 218–237.
- P'YANKOV, V. I. 1991. The origin and evolution of C₄ metabolism of the Chenopodiaceae as a result of global aridization of climate. In Y. P. Abrol, P. N. Watal, and A. Gnanam [eds.], *Impact of global climatic changes on photosynthesis and plant productivity*, 711–720. Oxford & IBH, New Delhi.
- . 1993. C-4-species of high-mountain deserts of eastern Pamir. *Russian Journal of Ecology* 24: 156–160.
- , A. N. KUZ'MIN, É. D. DEMIDOV, AND A. I. MASLOV. 1992a. Diversity of biochemical pathways of CO₂ fixation in plants of the families *Poaceae* and *Chenopodiaceae* from the arid zones of central Asia. *Soviet Plant Physiology* 39: 411–420.
- , A. A. VASIL'EV, A. N. KUZ'MIN, É. D. DEMIDOV, AND A. I. MASLOV. 1992b. Daily dynamics of physiological processes in succulent halophilic plants with the C₃ and C₄ types of photosynthesis from the arid zone of central Asia. *Soviet Plant Physiology* 39: 599–605.
- , E. V. VOZNESENSKAYA, AND A. V. KONDRACHUK. 1993. Mountain saltwort *Salsola oreophila* (Chenopodiaceae)—a possible stage between C₄ and C₃ species. (Translated from the Russian from Doklady Akademii Nauk 332(2):267–270). *Doklady Botanical Sciences* 332: 71–75.
- PAULSEN, O. 1912. Studies on the vegetation of the Transcaspian lowlands. Gyldendalske Boghandel—Nordisk Forlag, Copenhagen.
- PEARCY, R. W., AND J. EHLERINGER. 1984. Comparative ecophysiology of C₃ and C₄ plants. *Plant, Cell and Environment* 7: 1–13.
- PEDROL, J., AND S. CASTROVIEJO. 1988. A propósito del tratamiento taxonómico y nomenclatural del género *Suaeda* Forsskäl ex Scop. (*Chenopodiaceae*) en "Flora Iberica." *Anales Jardín Botánico de Madrid* 45: 93–102.
- PYYKKÖ, M. 1966. The leaf anatomy of East Patagonian xeromorphic plants. *Annales Botanici Fennici* 3: 453–622.
- SCHWEINFURTH, G. 1896. Sammlung arabisch-aethiopischer Pflanzen. *Bulletin de l'Herbier Boissier* 4, App. II: 9–266.
- SHIELDS, L. M. 1951. Leaf xeromorphy in dicotyledon species from a gypsum sand deposit. *American Journal of Botany* 38: 175–190.
- , W. K. MANGUM, AND M. LUDI. 1958. Leaf Kjeldahl nitrogen in relation to leaf structure for plant species growing in a semi-arid recent volcanic area. *Phytomorphology* 8: 265–277.
- SHOMER-ILAN, A., S. BEER, AND Y. WASEL. 1975. *Suaeda monoica*, a C₄ plant without typical bundle sheaths. *Plant Physiology* 56: 676–679.
- , R. NEUMANN-GANMORE, AND Y. WASEL. 1979. Biochemical specialization of photosynthetic cell layers and carbon flow paths in *Suaeda monoica*. *Plant Physiology* 64: 963–965.
- , A. NISSENBAUM, AND Y. WASEL. 1981. Photosynthetic pathways and the ecological distribution of the Chenopodiaceae in Israel. *Oecologia* 48: 244–248.
- SOLMS-LAUBACH, H., GRAF VON. 1901. Über die in der Oase Biskra und

- deren nächster Umgebung wachsenden spiroloben Chenopodeen. *Botanische Zeitung* 59: 159–186.
- SORIANO, A. 1942. Las especies del género *Suaeda* en la República Argentina. *Revista Argentina de Agronomía* 9: 343–353.
- . 1945. Notas sobre Quenopodiáceas Argentinas. *Revista Argentina de Agronomía* 12: 51–56.
- SPURR, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. *Journal of Ultrastructure Research* 26: 31–43.
- STANDLEY, P. C. 1917. The Chenopodiaceae of the North American flora. *Bulletin of the Torrey Botanical Club* 44: 411–429.
- SYVERTSEN, J. P., G. L. NICKELL, R. W. SPELLENBERG, AND G. L. CUNNINGHAM. 1976. Carbon reduction pathways and standing crop in three Chihuahuan Desert plant communities. *Southwestern Naturalist* 21: 311–320.
- TOWNSEND, C. C. 1980. Contributions to the flora of Iraq: XIII. Notes on some genera of *Chenopodiaceae*. *Kew Bulletin* 35: 291–296.
- TSVELEV, N. N. 1993. Zametki o marevykh (Chenopodiaceae) vostochnoy Evropy. (Notes on Chenopodiaceae of eastern Europe. In Russian with English summary). *Ukrains'kyi Botanichnyi Zhurnal* 50: 78–85.
- ULBRICH, E. 1934. Chenopodiaceae. In A. Engler and H. Harms [eds.], *Die natürlichen Pflanzenfamilien*, 16c, 379–584. Duncker & Humblot, Berlin.
- VENKATESALU, V., AND K. P. CHELLAPPAN. 1988. Photosynthetic studies in succulent halophytes. *Geobios* 15: 49–52.
- VOLKENS, G. 1887. Die Flora der ägyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen. Gebrüder Borntraeger, Berlin.
- . 1894. Chenopodiaceae. In A. Engler [ed.], *Die natürlichen Pflanzenfamilien*, III(1), 36–91. Wilhelm Engelmann, Leipzig.
- WATSON, M. C., AND W. R. FERREN, JR. 1991. A new species of *Suaeda* (Chenopodiaceae) from coastal Northwestern Sonora, Mexico. *Madroño* 38: 30–36.
- WATSON, S. 1874. *Suaeda*. *Proceedings of the American Academy* 9: 88–90.
- WEIGLIN, C., AND E. WINTER. 1991. Leaf structures of xerohalophytes from an East Jordanian salt pan. *Flora (Jena)* 185: 405–424.
- WELKIE, G. W., AND M. M. CALDWELL. 1970. Leaf anatomy of species in some dicotyledon families as related to C₃ and C₄ pathways of carbon fixation. *Canadian Journal of Botany* 48: 2135–2146.
- WINTER, K. 1981. C₄ plants of high biomass in arid regions of Asia—occurrence of C₄ photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR. *Oecologia* 48: 100–106.
- , AND J. H. TROUGHTON. 1978. Photosynthetic pathways in plants of coastal and inland habitats of Israel and Sinai. *Flora (Jena)* 167: 1–34.
- ZHAO, K. F. 1991. Desalinization of saline soils by *Suaeda salsa*. *Plant and Soil* 135: 303–305.
- ZOHARY, M. 1966. *Flora Palestina*. Part One. Text. Equisetaceae to Moringaceae. Israel Academy of Sciences and Humanities, Jerusalem.
- ZULOAGA, F., J. DUBCOVSKY, AND O. MORRONE. 1993. Infrageneric phenetic relations in new world *Panicum* (Poaceae: Panicoideae: Paniceae): a numerical analysis. *Canadian Journal of Botany* 71: 1312–1327.