

THE GENUS *KOCHIA* (CHENOPODIACEAE) IN NORTH AMERICA

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ABSTRACT

The genus *Kochia* and *Bassia* with which it has been combined, of Chenopodiaceae tribe Camphorosmeae, were at one time considered to include plants native to Eurasia, Australia, and North America, and included species of both C₃ and C₄ photosynthetic types. This aggregate has been reduced in size by removal of a large group of C₃ Australian genera and species. Because of their intercontinental disjunction, the presence of root sprouting, and the results of recent phylogenetic studies, it appears that the two North American species *Kochia americana* and *K. californica*, of C₃ photosynthetic type, should be removed as well, and we designate *Neokochia* as a new genus for them. In agreement with a study by other authors, comparison of pubescence characters and ploidy levels within *K. americana* did not give support recognition of the segregate *K. vestita*.

Key Words: Chenopodiaceae, *Kochia*, Kranz anatomy, *Neokochia*, polyploidy.

Kochia Roth and *Bassia* Allen are shrubs, subshrubs or herbs with indehiscent fruits, and with embryos that are horizontally oriented in the flower and ring-like rather than spiral. Tribe Camphorosmeae, to which these genera belong, has narrow, hairy leaves, and, similar to other Chenopodiaceae, has apetalous small flowers. A disseminule consists of a seed and its pericarp enclosed within a persistent perianth (Uhlbrich 1934). The name *Kochia* has usually been applied to taxa with horizontal wings growing from the perianth, whereas the name *Bassia* has been applied to taxa with spines. The form of these appendages is apparently related to method of dispersal, by wind or animals, a characteristic likely to experience strong and variable selection. As might not be entirely surprising, therefore, the distinction has been found untrustworthy, leading to a merger of these genera (Scott 1978). However, recent research indicates the need for a more extensive reorganization (Kadereit et al. 2005; Lee et al. 2005).

Kochia/Bassia was formerly a larger genus, but taxa native to Australia were portioned out as a number of separate genera, including *Maireana* Moquin and *Sclerolaena* R. Brown (Wilson 1975; Scott 1978). Recent studies have shown the Australian Camphorosmeae, which have C₃ photosynthesis, to be a distinct clade from the C₄ Eurasian group containing the majority of species of *Kochia*, *Bassia*, and related genera (Kadereit et al. 2003, 2005). In the same studies, North American *Kochia* came out either sister to the Australian Camphorosmeae or sister to a clade formed by the Australian Camphorosmeae plus the C₄ group. However, these relationships were

all rather weakly supported. Eurasia does contain a few members of the Camphorosmeae that are C₃ and are currently placed in *Kochia* and *Bassia*; these plants are related to the Australian C₃ taxa or to North American *Kochia* (Kadereit et al. 2003, 2005). The type species of both *Kochia* and *Bassia* are in the C₄ group. See Table 1 for a comparison of some of these taxa. Photosynthetic type has been identified as a character of considerable phylogenetic depth in Camphorosmeae, and in other parts of the Chenopodiaceae as well, but has been little utilized systematically (Pyankov et al. 2001; Kadereit et al. 2003, 2005). It appears that a large part of the present disorder in the tribe can be corrected by attention to photosynthetic type and its morphological correlate, the presence or absence of Kranz anatomy.

There are two species ascribed to *Kochia* that are native to North America, *K. americana* S. Watson, and *K. californica* S. Watson. Leaf morphology of these has been examined and found to be non-Kranz (Carolin et al. 1975). They are semi-shrubs growing in saline soils, the former widespread in saline deserts of the mountain west of North America, and the latter an uncommon plant of the Central Valley and the Mojave Desert in the state of California, and rarely of adjacent Nevada.

In this paper we examine the species of North American *Kochia* in order to confirm their photosynthetic type. We also reconsidered the separation of *K. vestita* A. Nelson from *K. americana*. *Kochia vestita* was segregated on the basis of indumentum, but examination of representative specimens by Blackwell et al. (1978) failed to reveal consistent differences. However, as

TABLE 1. COMPARISON OF CHARACTERISTICS OF *NEOKOCHIA* WITH OTHER GENERA.

	<i>Neokochia</i>	<i>Maireana</i>	<i>C₄ Kochia & Bassia</i>
Leaf anatomy	non-Kranz	non-Kranz	Kranz
Leaf type	Terete or half-terete	Complanate to terete	Complanate
Life form	Subshrubs	Mainly subshrubs, with some shrubs and perennial herbs	Annuals, or (one) subshrub
Perianth appendages	Winglike, developing from the base of the lobes of the perianth, thus the wings are free	Winglike, developing from the tubular part of the perianth, thus the wings are united into a single orbicular structure, or if free, at least the bases of the wings are united	Winglike, developing from the base of the lobes of the perianth, thus the wings are free
Sex	Bisexual or with some plants unisexual	Bisexual to dioecious	Bisexual
Root sprouting	Present	Absent	Absent
Perisperm	Absent	Present	Present

our preliminary observations showed both diploid and tetraploid populations existing within *K. americana*, it seemed desirable to examine correlation of the morphological characteristics with the ploidy level. We have to that end surveyed ploidy levels in *K. americana* and considered pubescence characters in relation to them.

METHODS

The C₃/C₄ status of *K. americana* and *K. californica* were determined by measurement of ¹³C/¹²C ratios, averaged for two determinations per species (Hatch et al. 2006), and presence or absence of Kranz anatomy was confirmed by examination of leaf cross sections of the species (Carolin et al. 1975).

Ploidy was determined by examination of meiosis in developing anthers and by flow cytometry of somatic leaf cells. Meiotic chromosome counts were made by acetocarmine squash methods (Sanderson and Stutz 1994). Flow cytometry was carried out using fresh leaves or winter buds, which were chopped finely with a razor blade in 0.3 ml of a DAPI (4' 6-diamidino-2-phenylindole) solution (CyStain UV Ploidy, Partec GmbH). An additional 1.7 ml of the solution was added, and the suspension was filtered and introduced into the flow cytometer. Ploidy values for peaks at different positions were determined by comparison with plants whose ploidies had been determined cytologically.

Pubescence in mid summer and fall was compared for diploid and tetraploid populations by sampling a branch from each of three plants per population for 23 populations. The plants were marked so that the same ones could be sampled at both times.

Response of leaf swelling and pubescence loss to substrate salinity was studied using plants of *K. americana*, which were brought to the greenhouse from several locations in the field and watered initially with tap water made 0 M, 0.1 M, 0.2 M, and 0.5 M in sodium chloride.

Voucher specimens were deposited at the Institute of Botany, Northwest Normal University, Lanzhou, China.

RESULTS

All six populations of *K. californica* that were examined for ploidy were diploid. Of 103 populations of *K. americana* examined, 63 were diploid and 40 were tetraploid (Fig. 1). The tetraploids were mainly found in western Utah in the basin of Pleistocene Lake Bonneville, including the area of the present Great Salt Lake and Bonneville Salt Flats, with a few additional tetraploid populations in eastern Nevada and at scattered locations in the Colorado Plateau. A triploid plant spreading by root sprouting was found growing within a diploid population at McElmo Creek, Montrose County, Colorado. Comparison of diploid DNA amounts of *K. americana* and *K. californica* by running samples of the species together in flow cytometry gave exactly overlapping peaks, and so their C-values (DNA contents of individual genomes) appear similar.

Examination of internal morphology of leaves of the American species *K. americana* and *K. californica* showed a radially organized palisade parenchyma and several vascular bundles without a bundle sheath or Kranz layer (Fig. 2), as was previously shown in diagrammatic form in Carolin et al. (1975). This may be contrasted with *K. prostrata* and *K. scoparia*, which had prominent bundle sheaths (Fig. 2). C¹²/C¹³ ratios were -23.89 for *K. americana* and -28.16 for *K. californica*, indicating a C₃ photosynthetic pathway for these species (Winter 1981).

Pubescence of *K. americana* consisted of elongate collapsed hairs attached to papillae on the leaf surface. Hairs of growing leaves were initially closely spaced but became more separated as the leaf expanded during growth. Early summer pubescence was often widely variable within populations and also varied between populations or regions. It was perhaps more

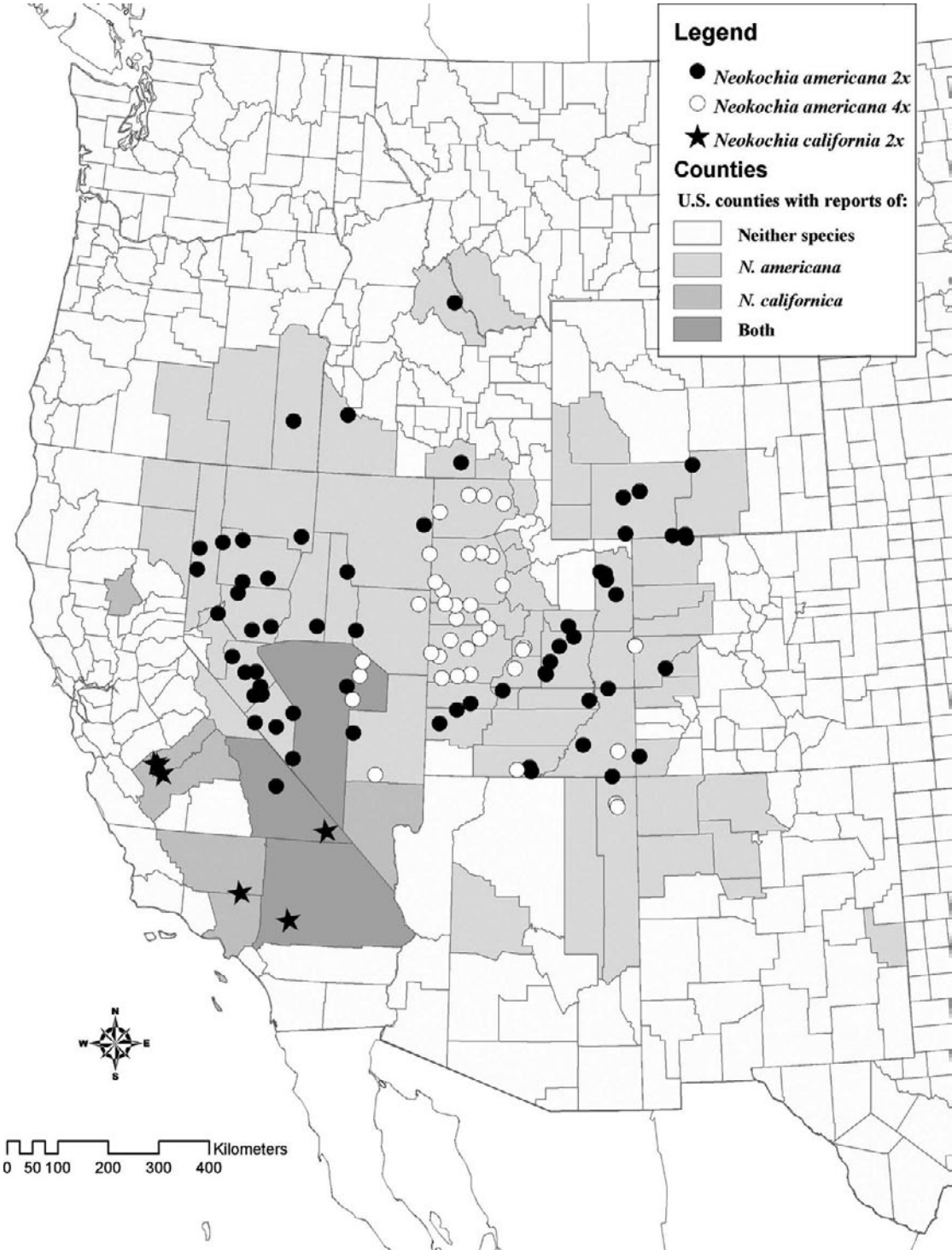


FIG. 1. Ploidy of sampled populations of *Neokochia americana* and *N. californica*. Shaded counties indicate reports of these species (USDA 2006).

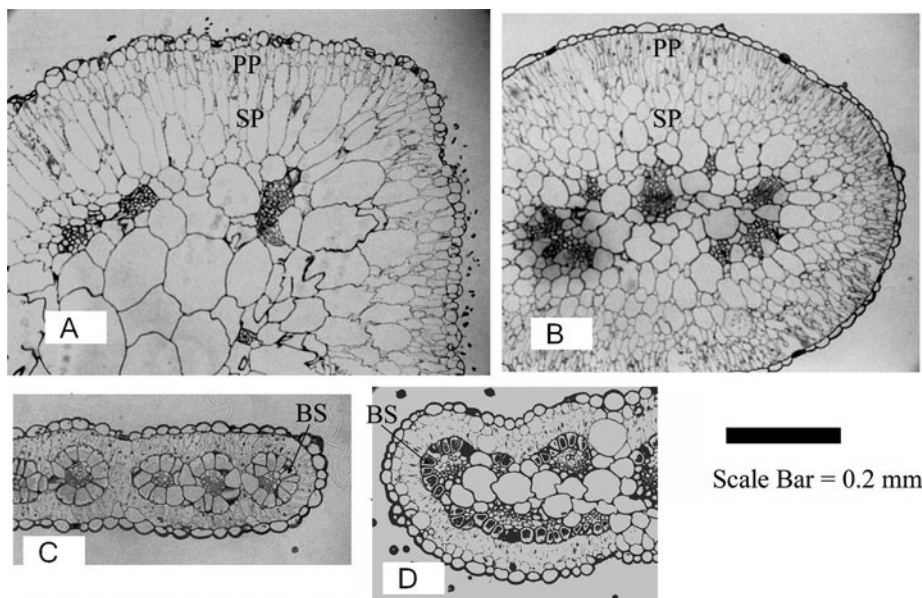


FIG. 2. Cross sectional views of leaves, showing presence or absence of bundle sheaths and Kranz anatomy; A) *Neokochia californica* S. Watson (non-Kranz). B) *N. americana* S. Watson (non-Kranz). C) *Kochia scoparia* (L.) Schrader (Kranz). D) *Kochia prostrata* (L.) Schrader (Kranz). PM = palisade mesophyll, SP = spongy parenchyma, BS = bundle sheath.

prominent in tetraploids, although we found some diploid populations with as much pubescence as the tetraploids.

Another factor affecting pubescence was apparently leaf swelling. Leaves may have swelled after maturity because of salt accumulation (Osmond et al. 1980), and patches of trichomes appeared to be then more easily lost by abrasion or other processes because swollen leaves in the field were mostly glabrous. All of the populations compared showed at least some loss of trichome patches by mid-autumn, but plants of eastern Utah and of the Escalante Desert in southwestern Utah started earlier and became more strongly glabrescent. The leaves of plants in the greenhouse that we watered with any of the salt solutions became grossly swollen and terete, whereas plants given water without the added salt remained slender and linear in shape. Leaves in the greenhouse experiments that had become swollen did not immediately lose their pubescence, however.

DISCUSSION

An alternative name for the native American taxa that we considered was "*Rhizomatosa*," from an herbarium annotation by Nuttall, referring to frequent vegetative reproduction by root sprouting. Unfortunately, Nuttall's name is not technically correct since sprouting in these species is from true roots, while rhizomes, horizontal stems with internodes and scalelike leaves, are absent. The presence of root sprouting in the North

American *Kochia* species, as well as their intercontinental separation from Asian taxa, justify their designation as a separate genus. In addition, absence of Kranz anatomy also clearly differentiates them from most of the old world taxa.

According to results of Kadereit et al. (2003), the origin of C_4 photosynthesis in the *Camphorosma* clade was Miocene, likely early Miocene. At the present there are multiple named genera within the C_3 and C_4 portions of Tribe Camphorosmeae, and the C_3 portion has radiated from the Eurasian continent into Australia and North America. The combination of photosynthetic pathway with Kranz morphology therefore represents a taxonomic character of higher-than-genus level within these taxa. American *Kochia* should clearly be separated from Asian C_4 *Kochia* and *Bassia*. It might be objected that if photosynthetic type is used as a genus level character, a split within the chenopod genus *Atriplex*, affecting many species, might also be required. While it does appear that changes in *Atriplex* are necessary, the time of origin for C_4 photosynthesis differs within the chenopod family (Kadereit et al. 2003), and the appropriate taxonomic level for the character might therefore best be evaluated on a case-by-case basis in conjunction with other evidence.

The *Kochia americana*–*K. vestita* Question

Serenio Watson (1874) described var. *vestita* of *K. americana* from what probably was tetraploid

material from the shores of the Great Salt Lake. Tetraploids appeared to have somewhat longer early season pubescence on average, although there was often high variation within populations, and some diploid populations were as pubescent as any of the tetraploids.

Later in the season, loss of pubescence becomes more visible than trichome length. Aven Nelson (Coulter and Nelson 1909) raised var. *vestita* to species level, apparently with pubescence loss in mind. Rydberg's Flora of the Rocky Mountains (1922) distinguishes the species *K. vestita* as plants that do not become glabrescent, as opposed to others that do regardless of pubescence that either may have had earlier in the season. Plants of western Utah, including both diploids and tetraploids, and of the Colorado Plateau, mostly diploid, show a greater degree of swelling and more shedding of patches of trichomes, and the shedding begins earlier in the summer than for plants of most other locations. However, we found that all 23 of the populations we examined in the autumn shed their pubescence to some degree. The greenhouse experiment showed that leaf swelling can be induced artificially in response to salinity. Therefore we concur with Blackwell et al. (1978) that var. *vestita* not be recognized.

TAXONOMY

Neokochia (Ulbrich) G. L. Chu et S. C. Sanderson, gen. et stat. nov.—Type: *Kochia americana* S. Wats.

Kochia Roth in Schrad. Journ. Bot. 1: 307. 1800 (1801) *pro parte*.

Sect. *Neokochia* Ulbrich in Engl. et Prantl, Nat. Pflanzenfam. 2 Aufl. 16c: 535. 1934. *p. p.*

Series *Neokochia* (Ulbrich) A.J. Scott, Feddes Rept. Spec. Nov. Regni Veg. 89: 108. 1978.

Subfrutices vel frutices, interdum ex radices horizontales pullulans. Caules numerosi, erecti, initio dense-tomentosi. Folia linearia ad anguste oblonga, sessilia, leviter succulenta, teretia ad semi-teretia, absque Kranz anatomiis. Flores 2–5 in glomerulos, axillares, sub floribus plerumque cum singulari foliacea (breviter) vel squamosa bractea, bisexuales vel unisexuales, necnon versu dioecii; perianthia fere globosa, 5-partita, 5-nervata, evoluta 5 alato-appendicibus ex basi segmentorum fructificationum, saepissime discreta; alae patulae horizontaliter, tenuibus venis; stamina 5, evidenter disco; stigmata 2, raro 3, stylo brevissimo. Utriculus ovatus, pericarpio leviter carnosus. Semen horizontale, testa membranaceo, embryo prope annulari, radícula laterali, cotyledone leviter ampliato et absque perispermate.

Subshrubs or shrubs, spreading by root sprouting. Stems numerous, erect, at first densely silky-tomentose. Leaves linear, sessile, slightly

succulent, terete to half-terete, anatomy non-Kranz. Flowers 2–5 in glomerules, axillary, each flower usually subtended by a foliaceous or scale-like bract, bisexual or unisexual and tending towards dioecy. Perianth nearly globular, 5-parted, 5-veined, developing 5 free wing-appendages from base of the segment at frutescence; the wings spreading, horizontal, with fine veins; stamens 5, filaments filiform, arising from a disc, anthers elliptic; stigmas 2, rarely 3, subulate or linear, style very short. Utricle depressed-ovate, pericarp slightly succulent. Seeds horizontal, testa pellucid-membranous, embryo near annular, radical lateral, cotyledons somewhat enlarged, without perisperm. $X = 9$.

Plants of *Neokochia* have a multi-veined perianth, with the wing-appendages developing from the lobes. The wings are therefore separate and orbiculate, but fall together with the fruit because of the united perianth. A genus of two species endemic to western North America.

Neokochia americana (S. Watson) G. L. Chu et S. C. Sanderson, comb. nov. *Kochia americana* S. Watson, Proc. Amer. Acad. 9: 93. 1874. *K. vestita* A. Nelson in J. M. Coulter & A. Nelson, New Man. Bot. Centr. Rocky Mt. 165. 1909.—Lectotype (Blackwell et al. 1978): “Western Nevada,” J. Torrey 465 (GH).

Distribution: USA: on saline soils, most abundant in Utah, Nevada, also present in parts of Arizona, California, Colorado, Idaho, Montana, Oregon, and Wyoming.

Neokochia californica (S. Watson) G. L. Chu et S. C. Sanderson, comb. nov. *Kochia californica* S. Watson, Proc. Amer. Acad. 9: 93. 1874. *Kochia americana* var. *californica* (S. Watson) M. E. Jones, Contr. West. Bot. 11: 19. 1903.—Lectotype (Blackwell et al. 1978): “Colton,” Parry 275 (GH).

Distribution: USA: Central Valley and Mojave Desert of California and southern Nevada.

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