THE GENETIC RELATIONSHIP BETWEEN *NAMA HISPIDUM* AND *NAMA STEVENSII*

By

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1976

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 1983

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AND *NAMA STEVENSII*

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ACKNOWLEDGMENTS

I would like to express my sincere and deep appreciation to my major adviser Dr. Ronald J. Tyrl, for his invaluable advice, guidance, and encouragement throughout the course of this study. I gratefully thank Dr. Paul E. Richardson and Dr. Glenn Todd for serving as members of my committee and for their many helpful suggestions.

Again I thank Dr. Paul E. Richardson and extend my thanks to Mr. Dave Ferris for their assistance in the use of the flourescent microscopy.

Special thanks for my wife, Ftayem, my son Aymen and daughter Huda for their patience and sacrifice provided throughout the stay in the United States far from our family and not being able to see them for three and a half years.

I wish also to thank Tina Ahern, Sandra Nobbe, and Donetta Bantle for the typing of this thesis.

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CHAPTER I

INTRODUCTION

The genus *Nama* in the Hydrophyllaceae is composed of 18 annual species with 16 varieties and 20 perennial species and six varieties. Thus the genus includes 60 variable taxa. More than one-half of the species are distributed in the drier habitats of the southwestern United States and northern Mexico. There are five species in South America, two in the Caribbean, and one in Hawaii. Many of the taxa are restricted to a particular soil type while others do not exhibit this restriction for soil type.

In southwestern Oklahoma and adjacent Texas, *Nama* is represented by only two species (Hitchcock, 1933b; Waterfall, 1969; Correll and Johnston, 1970). One is *Nama stevensii* collected by George W. Stevens in 1913 from near Alva in Woods County, Oklahoma, and described by C. L. Hitchcock when he monographed the genus in 1933. *Nama stevensii* is an obligate gypsophile found growing only on gypsum soils of western Oklahoma, Texas, and Mexico (Figure 1).

The second taxon is *N. hispidum* and was described by Asa Gray in 1861. It is an extremely variable and widespread taxon found on sandy, gravelly soils. Plants are not

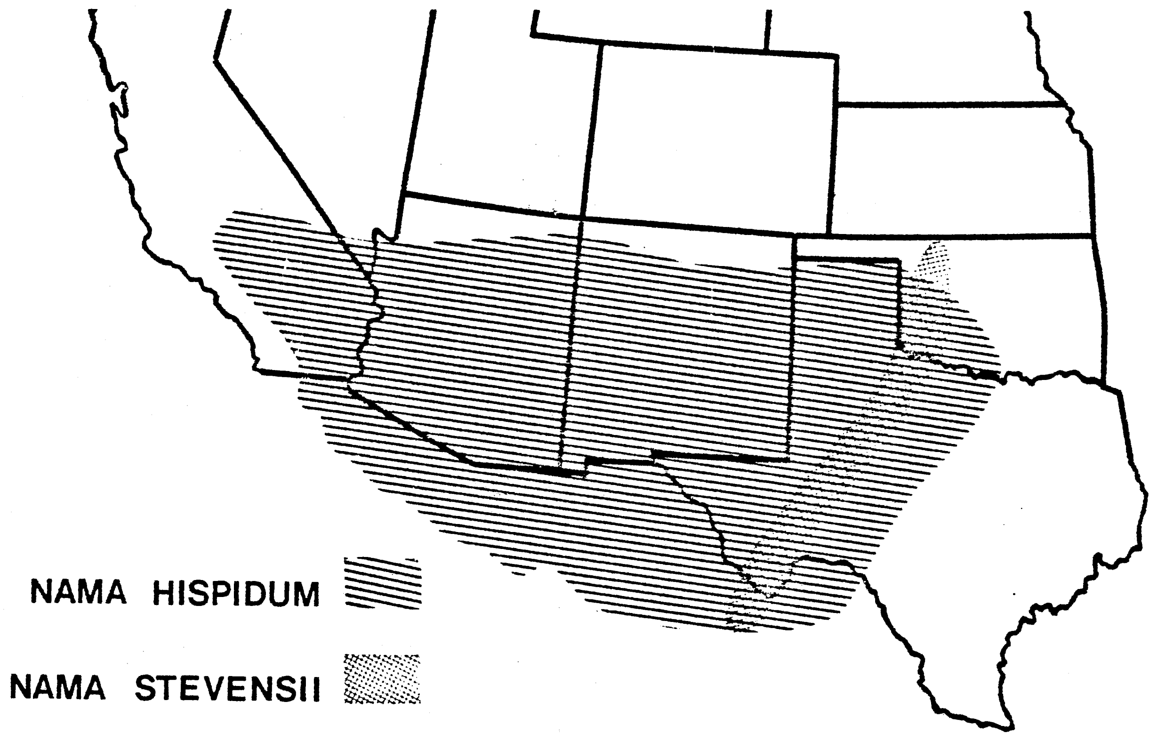

Figure 1. Distribution of Nama hispidum and Nama stevensii in the United States and Mexico.

found on gypsum soils. Populations of _N. hispidum_ occur from southwestern Oklahoma and Texas to southern California and northern Mexico (Figure 1).

Nama stevensii and _N. hispidum_ apparently are very closely related species. They differ, in addition to - soil type, in the nature of the pubescence, leaf shape and size, and the level of stamen filament insertion and the degree of filament fusion with the corolla. These characters are emphasized in the taxonomic keys used to differentiate the two taxa (Hitchcock, 1933b; Waterfall, 1969; Correll and Johnston, 1970). _Nama stevensii_ is characterized by appressed hairs, linear-lanceolate leaves, and the adnate portion of the filament is much wider or dilated at the base than the free portion. In contrast _N. hispidum_ has hispid hairs, linear-oblong to obovate leaves, and the adnate portion of the stamen filament is not much wider than the free portion. Further, _N. stevensii_ has a rounded appearance because it bears branches at the base with the upper branches and leaves crowded; whereas, _N. hispidum_ appears to be more erect due to the lack of branching at the base and less crowding of the upper branches and leaves.

Even though these two taxa have been accepted as two species (Hitchcock, 1933b; Waterfall, 1979; Correll and Johnston, 1970), there is still some questions as to whether the taxa are distinct. It was suggested by Correll and Johnston that _N. stevensii_ may be only a gypsophilous phase of *N. hispidum*. I. M. Johnston described a gypsophilic variety of *N. hispidum* from Nuevo Leon, Mexico in 1941 *N. hispidum* var. *gypsicola*. Bacon (1974), however, believed that the affinities of this variety lay closer to *N. stevensii* than to *N. hispidum*, except for its prostrate habit, its shorter less dense pubescence, and its smaller leaves and in 1982 renamed the taxon as *N. stevensii* var. *gypsicola*.

Preliminary studies of *N. stevensii* and *N. hispidum* by Tyrl (unpublished) revealed variability and overlap in the characters used to distinguish the two taxa. In addition, Benenati (1974) suggested that these two taxa exhibited phenotypic plasticity on the basis of her investigations of their ecology. Moreover, the presence of a population with plants identifiable as both *N. stevensii* and *N. hispidum* along the bluffs of the Red River in Harmon County, Oklahoma, suggests the taxa may not be distinct entities.

Nama, a most interesting genus, has received little detailed investigation since Hitchcock monographed the genus in 1933 and published additional work on Mexican species in 1939. During their investigations on the chromosome number of the Hydrophyllaceae, Constance and Cave (1947, 1950, 1959) and Constance (1963), reported chromosome numbers for about one-third of the species described by Hitchcock. Bacon (1974) reported chromosome numbers for about one-half of the species. Counts were also made by Tyrl *et al*. (1977).

The results of all three studies are smiliar. All plants exhibited a base chromosome number of seven with both *N. hispidum* and *N. stevensii* having 2*n*=14.

Biosystematic study of *N. stevensii* and *N. hispidum* was initiated by Tyrl in 1973. Grummer (1977) working with Tyrl studied the reproductive biology, analyzed the patterns of the morphological variation, characterized the flavonoid patterns by chromatography, and made intra- and interspecific crosses. However, the genetic information collected by Grummer was imcomplete and the genetic relationship of the two taxa was unresolved and needed to be clarified. Therefore, the objective of my study was to conduct an investigation of the genetic relationship of *N. stevensii* and *N. hispidum*. Work involved a determination of stigma receptivity, pollen fertility, selfcompatibility, and most importantly the genetic compatibility between the two taxa.

CHAPTER II

TAXONOMIC TREATMENT

In his 1933 monograph of the genus, Hitchcock described the taxonomic and nomenclatural history of *Nama*. Major points of his treatise are summarized below. In 1753, Linnaeus described the genus *Nama* and the species *N. zeylanicum*. He described a second species, *N. jamaicense* in 1759. In 1763, he transferred *N. zeylanicum* to the genus *Hydrolea* and published the binomial *H. zeylanica*. *Nama jamaicense* was left in *Nama*. In the 1800's, additional species were described by Choisy, Gray, Hemsley, and others. In 1871, Watson described the genus *Conanthus* into which Heller in 1898 subsequently transferred numerous western U.S. species of *Nama*.

Recognizing that the type species of *Nama*--*N. zeylanicum*--had been transferred to another genus-- *Hydrolea*--, Kuntze, in 1891 proposed that *Nama* be used only for *N. zeylanicum* and other species of *Hydrolea*, and that all other species of *Nama*, including *N. jamaicense*, be positioned in the new genus *Marilaunidium*.

Because of the problem created by Linnaeus when he transferred the type species of *Nama* to *Hydrolea* and the taxonomic and nomenclatural ambiguity surrounding *Nama*, the 1906 International Botanical Congress conserved the generic name Nama to include N. jamaicense as the type. Conanthus and Marilaunidium thus became synonyms.

Nama was revised in the 1800's by Choisy and Gray. The latter published many revisions of various taxa. In 1861 he examined the species of Nama known to him and on the basis of leaf position on the stem, leaf morphology, pubescence, and inflorescence type recognied eight species. He continued his work and in 1862 described two new species of Nama. In 1870, Gray revised his previous work, added new information, and using mainly the same characters, recognized 15 species, four of which were new.

In his treatment of the Hydrophyllaceae, Brand in 1913 again revised the genus. There were 2 subgenera, 2 sections, 36 species, 4 subspecies, 15 varieties, 6 forms and 1 hybrid recognied in this revision. He reduced the genus Conanthus to a subgenus of Nama with seven species characterized by united styles. He also reduced Marilaunidium to a subgenus with two sections comprising the remainder of the species which are characterized by free styles. In distinguishing between the two sections, he used the level of stamen filament insertion from the corolla base. Species were differentiated from each other mainly by leaf length and serration, corolla length, stamen filament characters, and number of ovules.

Brand in his treatment of the Hydrophyllaceae segregated Andropus from Nama as a new genus. Unfortunately, as Hitchcock (1933a) points out Brand misinterpretated the stamen filament bases of Nama. Another new genus--Turricula--was proposed by Maedrib in 1917 to include N. parryi which he felt was markedly dissimilar to the other species of Nama.

Finally, Hitchcock in 1933, questioning the status of the segregate genera and the status of some of the species of Nama, published the most recent and thorough monograph of the genus. Hitchcock, using length of the calyx lobes, style connation, growth habit, leaf margin and capsule characters, divided the genus into 5 sections. Three of these sections had one species each and one section had two species, one with two varieties. He reduced the subgenus Conanthus of Brand to a section composed of two species each with one variety characterized by fusion of styles. The semi-inferior ovary of N. stenocarpum was used to position it in a separate section. Nama rothrockii was placed in a different section because of its capitate inflorescence and crenate-dentate margined leaves. The cartilagenous capsule with loculicidal and septicidal dehiscence of N. lobbii caused Hitchcock to classify it in a distinct section. The rest of the species are morphologically so homogeneous that he put them in a fifth section with 27 species and 18 varieties. The plants of this section (Eunama) are divided into perennials and annuals and then species of each group are distinguished on the basis of inflorescence type, leaf morphology, pubescence, habit, sepal characters, seed characters, and the length of the free portion of the filament in relation to the adnate portion (Table I).

The Eunama section includes N. stevensii and N. hispidum with its 4 varieties. Table II lists the annual plants of this section and the position of N. stevensii and N. hispidum.

Hitchcock's monograph of this most interesting genus encouraged many botanists to make an effort to collect plants. Numerous specimens were collected from Mexico and southern Texas. Hitchcock examined these species and published a second paper in 1939 describing three new species and one new variety.

TABLE I

SUMMARY OF HITCHCOCK'S TREATMENT OF NAMA

Section	Species	Section Distinguishing Characters
Zonolacus	N. stenocarpum	Partially inferior ovary; styles frequently 3, united 2/3 their length, readily separable, capsule 120-250 seeded; annual.
Conanthus	N. densum N. aretioides	Styles permanently connate at least 3/4 their length; filaments unappendaged or minutely appendaged; capsule 10-35 seeded; annuals.
Cinerascentia	N. rothrockii	Leaves crenate-dentate; inflorescence capitate; capsule 16-20 seeded; perennial.
Arachnoidea	N. lobbii	Capsule cartilagenous and dehiscing loculicidally and septicidally; capsule 8-14 seeded; perennial.
Eunama	17 annual species 10 perennial species	Capsule membranous and dehiscing loculicidally; capsule few -180 seeded; annuals and perennials.

TABLE II

SECTION EUNAMA ANNUAL SPECIES AND THE POSITION OF N. HISPIDUM AND N. STEVENSII

Species	Taxonomic and/or Ecological Notes
N. sandwicense	Endemic to Hawaii.
N. torynophyllum	Mexico; 50-90 seeds/ capsule.
N. pusillum	Leaves rhombic-ovate to obovate, 6-13 mm long; 20-40 seeds/ capsule.
N. depressum	Leaves linear spathulate to narrowly oblong-spathulate, 10-30 mm long; 16-30 seeds/ capsule.
N. schaffneri	Leaves oblong, oblong-lanceolate or spathulate, 2-6 cm long; filament scales widened and toothed above.
N. undulatum	Filament scales narrow, not toothed.
N. biflorum	Long-lived annual or biennial.
N. jamaicense	Leaves spathulate, 6-15 mm long.
N. stevensii	Obligate gypsophile; leaves linear-lanceolate, 5-8 mm long.
N. demissum	Leaves obovate to spathulate or linear-lanceolate, 5-8 mm long.
N. ehrenbergii	Leaves obovate, 15 mm long, styles connate to middle.
N. havardii	Long-lived annual or biennial; leaves oblong, elliptic to obovate, 2-4 cm long.

TABLE II (Continued)

Species	Taxonomic and/or Ecological Notes
N. dichotomum	Leaves linear elliptic, 5-30 mm long.
N. parvifolium	Leaves spathulate to obovate-oblong, 7-15 mm long; 60-80 seeds/ capsule.
N. prostratum	Leaves ovate rotund, 8-20 mm long and 6-12 mm wide.
N. coulteri	Leaves obovate or spathulate, 1-3 cm long.
N. hispidum	Leaves linear-oblong to obovate, 1-5 cm long.

CHAPTER III

STUDY SITES

Nama hispidum and *N. stevensii* were collected at twenty-two study sites in western and southwestern Oklahoma and Texas (Table III, Figure 2). The two taxa were growing together in only one population, located in Harmon County, Oklahoma. Selected plants were dug up, transplanted into pots, and subsequently transported to the University of Oklahoma Biological Station on Lake Texoma and/or to the Botany Department greenhouse at Oklahoma State University for further study and manipulation.

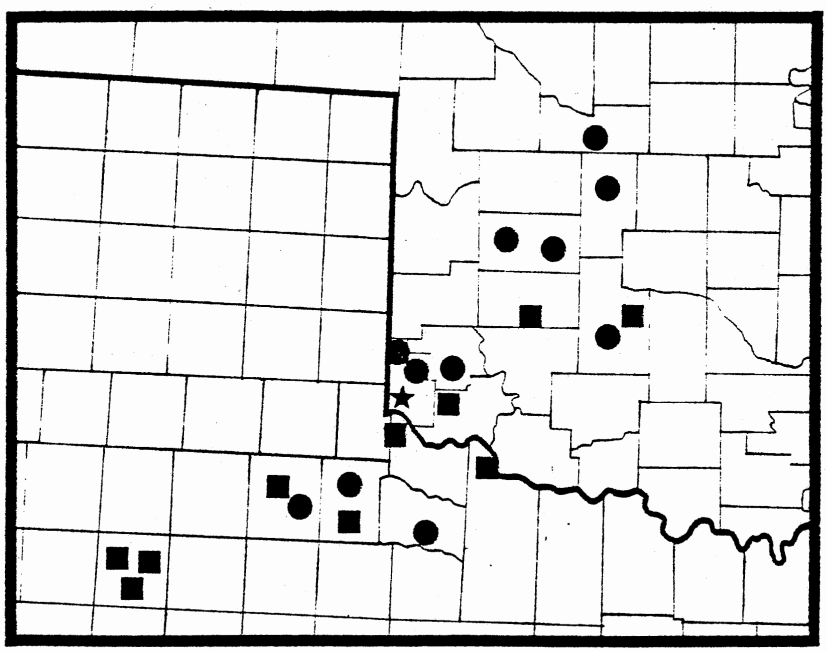

Figure 2. Collection Sites of <u>Nama hispidum</u> and <u>Nama stevensii</u> Used in Crossing Experiments. Squares, <u>N. hispidum</u>; Circles, <u>N. stevensii</u>; Star, Mixed Population.

TABLE III

NAMA HISPIDUM AND *N. STEVENSII* COLLECTION SITES

Population Number	County	Range	Township	Section	Notes
542 759	Blaine	R12W	T19N	27	*N. stevensii*. 8.3 miles W. of intersection of OK Hwy 58 with OK Hwy 51; 300 yds. N. of Hwy on section line road. Top of gyp ridge. Okeene, OK.
543 762	Custer	R15W	T13N	36	*N. stevensii*. Gyp outcrop S. side of paved section road. 1.3 mi. W. of OK Hwy 54 and 3 mi. N. of U.S. Hwy 66 junction, Weatherford, OK.

TABLE III (Continued)

Population Number	County	Range	Township	Section	Notes
544 761	Custer	R15W	T12N	11	N. stevensii. Gyp outcrop S. side of section road. 1.8 mi. W. of OK Hwy 54 and 1 mi. N. of U.S. Hwy 66 junction, due W. of Weatherford, cemetery, OK.
545	Washita	R14W	T11N	29	N. hispidum. Sandy waterway the base of sandstone butte W. of boat launch area. Crowder Lake ca. 5 mi. NE of Corn, OK.
546	Greer	R22W	T4N	5	N. stevensii. Gyp outcrop S. side of OK Hwy 34. Cut, about 2 mi. s. of Greer Co. Court House, Magnum, OK.

TABLE III (Continued)

Population Number	County	Range	Township	Section	Notes
547	Harmon	R24W	T5N	21	*N*. *stevensii*. Gyp outcrop S. side of OK Hwy 9. Ca. 0.8 mi. W. of Greer Co. line, OK.
548	Harmon	R26W	T1N	5	*N*. *hispidum* and *N*. stevensii.
549					Gyp bluffs abutting the Red River flood plain. 0.25 mi. NE of bridge over river on Hollis-Goodlet Road along ditch bank and fence row adjacent to field. OK.
550	Jackson	R26W	T15N	6	*N*. *hispidum*. 0.5 mi. N. of OK
773					Hwy 34-44 bridge across Red River. Stabilized sand dune E. side of Hwy next to abandoned RR building. OK.

TABLE III (Continued)

Population Number	County	Range	Township	Section	Notes
551 774	Wilbarger (Texas)	R20W	T2S	6	N. hispidum. 0.3 mi. S. of Red River bridge on U.S. Hwy 283. Stabilized sand dunes of river deep sand soil. Very common. Texas.
552 775	Caddo	R10W	T6N	35	N. stevensii. Western of Cement oil field adjacent to OK Hwy 8, Ca. 5.0 mi. W. of Cement OK Post Office. Exposed gyp ridge, scattered plants. OK.
553 776	Caddo	R10W	T9N	18	N. hispidum. 3.8 mi. W. of OK Hwy 152 and 8 junction. Open area SW facing slope at base of bluffs next to private driveway, Ca. 300

TABLE III (Continued)

Population Number	County	Range	Township	Section	Notes
					meters E. of Salary Lake. OK.
760	Major	R13W	T22N	6	<u>N</u>. <u>stevensii</u>. 5.2 mi. W. of Orienta. N. side of the OK Hwy 15. On top of a gyp butte. OK.
554 767	Motley (Texas)	--	--	--	<u>N</u>. <u>hispidum</u>. About 2.0 mi. N of Matador. W. side of Texas Hwy 70. Stabilized sand. Numerous small, weak plants due to the drought. Texas.
555 770	Lubbock (Texas)	--	--	--	<u>N</u>. <u>hispidum</u>. Lubbock. On N. side of the 4th St. W. of the Albertson food and drug store. Disturbed sand dune, area of the

TABLE III (Continued)

Population Number	County	Range	Township	Section	Notes
					city development. Huge prostrate plants. Few. Texas.
556 769	Lubbock (Texas)	--	--	--	<u>N</u>. <u>hispidum</u>. N of Lubbock city limits, S. of Regis St. Exit 847 W. of TX Hwy 27. Scattered plants. Texas
557 768	Lubbock (Texas)	--	--	--	<u>N</u>. <u>hispidum</u>. E. of Lubbock. 4th St. (=TX Hwy 82) and Quirt Ave. S. side of the 4th St. Sandy clayey soil. Common. Texas
558 765	Cottle (Texas)	--	--	--	<u>N</u>. <u>hispidum</u>. Ca. 0.2 mi. E. of Paducah city limits S. side of TX Hwy 70. Few plants. Endangered

TABLE III (Continued)

Population Number	County	Range	Township	Section	Notes
					plants. Texas.
763	Beckham	R25W	T8N	7	*N. stevensii*. 9.2 mi. S. of OK Hwy 30 from I-40. Roadside gyp outcrop.
764	Cottle (Texas)	--	--	--	*N. stevensii*. .47 mi. N. of river bridge, ca. 18.8 mi. N. of Paducah, Gyp bluffs W. side of TX Hwy 83-62. Plants are common.
766	Motley (Texas)	--	--	--	*N. stevensii*. Gyp S. side of TX Hwy 70-62 on ridges of waterway. Ca. 13.9 mi. E. of Matador, TX.
771	Foard (Texas)	--	--	--	*N. stevensii*. Gyp S. side of

TABLE III (Continued)

Population Number	County	Range	Township	Section	Notes
772	Hardman (Texas)	--	--	--	TX Hwy 70. 5.3 mi. W. of Crowell. Plenty of plants. Texas. <u>N</u>. <u>hispidum</u>. 5.1 mi. S. of bridge. Sandy S. side of Goodlet-Hollis Road. Scattered plants.

CHAPTER IV

MORPHOLOGY

The plants of Nama vary from herbaceous to suffrutescent, prostrate to erect, rarely glabrous to variously pubescent, and are 2 - 80 cm tall. The leaves are quite variable in shape and size. They range from linear to lanceolate, ovate, spathulate, obovate, oblanceolate,oblong, or a combination of each two of these shapes. They are 0.5 - 8 cm long and 0.1 - 3 cm wide, mostly alternate and entire. The flowers are born singly in the leaf axils or in reduced, lateral or terminal clusters of 2, 3, or 5. Pedicels are present or absent. The calyces are typically divided to the base with linear-lanceolate to spathulate lobes. The corolla is tubular to obconic-campanulate and glabrous. There are five stamens, typically unequal in length and subequal to unequally inserted. The filament bases are usually somewhat dilated and the adnate portion may or may not have free margins which are usually glabrous. The styles are typically two, usually free, but sometimes partially or almost completely united. The single ovary is one locular but seemingly two-chambered by the intrusions of the placenta. The ovary is typically pubescent. The fruit is ovoid to globose, many seeded capsule which is loculicidally, or rarely septicidally, dehiscent. It is membranous or cartilagenous. The seeds are yellow or brown, variously pitted, alveolate, reticulate, or smooth. They are sometimes minutely, transversely corrugated as well as pitted. The pollen grains are fairly uniform and differ primarily in the diameter of the lumina between the central zone of the mesocolpia and the area adjoining poles and colpia (Constance and Chung, 1982).

Taxonomic keys distinguishing N. stevensii and N. hispidum generally emphasize the leaf shape and pubescence and stamen features. For example, characters of N. stevensii are: leaves linear-lanceolate, calyx pubescence closely appressed and stamen filament bases dilated. In contrast, the characters of N. hispidum generally are: leaves linear-oblong to obovate, calyx pubescence somewhat spreading, and filament bases not dilated.

N. stevensii as observed by me and as described by Hitchcock (1933b) and Correll and Johnston (1970) is grayish strigose, erect or ascending, few branched, 4-8(25) cm tall. The plants branch at the stem base and form dense rounded clumps. The leaves are linear-lanceolate, acuminate, 1-3 cm long and 1.3 mm wide, strongly revolute, sessile and somewhat clasping. The flowers are borne in leafy terminal or axillary clusters of 2's or 3's. The leaves usually exceed the flowers which are lavender. The sepals are linear-lanceolate and 5-8 mm long. The corolla is tubular to funnelform and 8-10 mm long. The stamens are about half the corolla length. The stamen filaments are terete 1-2 mm long and the filament bases are dilated with narrow marginal wings. The base usually equals the free filament portion in length. The styles are two about 4 mm long. The capsules have 40-50 seeds which are yellow, 0.3 mm long and alveolate. N. hispidum is strigose-hirsute to hispid, erect or ascending and 8-35 (40) cm tall. The plants branch sparingly from the base or only above. The leaves are variable, linear to linear-oblong, spathulate to obovate, 1-3 (5) cm long and 1-7 mm broad; they are slightly to strongly revolute, mostly narrow toward the base. The flowers are solitary or borne in 2-3 flowered terminal cymes and are pink to bright purple. The sepals are linear lanceolate, 4.0-7.0 mm long. The corolla is tubular-campan- ulate, 8-15 mm long. The stamens do not exceed half the length of the corolla. The filaments are rather thick terete and very unequally inserted, 1-4 mm from the corolla base. The filament bases are scarcely dilated, i.e., the adnate portion is not much wider than the free filament. The margins are not winged. The two styles are 2-4 mm long. The capsules have 20-100 seeds. The seeds are 0.5 mm long, yellow and minutely alveolate-reticulate (Hitchcock, 1933b; Correll and Johnston, 1970).

CHAPTER V

GENETIC RELATIONSHIPS

With the exception of one mixed population in Harmon County, N. hispidum and N. stevensii grow in separate populations in Oklahoma and adjacent Texas. Morpholog, as noted above, is of limited value in determining relationships. The two taxa have the same chromosome number (2n=14). When taxa are allopatric, have intergrading morphology, and have the same chromosome number, as in Nama, a genetic approach to taxonomy involving artificial hybridization is needed (Thompson, 1960). The genetic approach measures the genetic relationship directly between taxa and the analysis of data from experimental hybridization gives a better understanding of this relationship. Elucidation of gene flow patterns within each taxon and between the two taxa were examined utilizing standard hybridization techniques (Radford et al., 1974). Crosses were performed on established potted plants at the University of Oklahoma Biological station and at the Botany Department greenhouse at Oklahoma State University in the summers of 1981 and 1982 respectively. The results of these hybridizations are summarized in Table IV and V.

The results of phenological studies made at the time

TABLE IV

SUMMARY OF FRUIT AND SEED SET IN HYBRIDIZATION EXPERIMENTS

Cross	Number of crosses	Number of fruits developed	% fruit set	Number of seeds/ovules	% seed set
Self Compatibility					
N. hispidum	33	0	0	0	0
N. stevensii	24	0	0	0	0
Intrapopulational					
N. hispidum x *N. hispidum*	13	13	100	495/597	83
N. stevensii x *N. stevensii*	1	1	100	53/53	100
Interpopulational					
N. hispidum x *N. hispidum*	57	28	49	582/946	63.3
N. stevensii x *N. stevensii*	61	39	64	1523/1686	90
Interspecific					
N. hispidum x *N. stevensii*	149	107	71.8	503/4284	11.7
N. stevensii x *N. hispidum*	164	109	66.5	66/2873	2.3

TABLE V

RESULTS OF EXPERIMENTAL HYBRIDIZATION

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
Interspecific			
550b X 543c	1	1	0/43
550b X 547d	1	0	0/0
550b X 552e	1	1	0/25
550c X 542e	1	1	0/46
550c X 544e	1	0	0/0
550c X 549a	1	1	0/57
550d X 546e	1	0	0/0
550d X 547b	1	0	0/0
551b X 544e	1	0	0/0
551b X 546a	1	0	0/0
551b X 546c	1	0	0/0
551c X 552a	1	1	0/25
551d X 547d	1	0	0/0
553b X 542c	1	1	0/45
553b X 544a	1	1	0/26
553b X 547b	1	1	5/34
553b X 552e	1	0	0/0
553c X 542a	1	1	12/18
553c X 549c	1	1	0/14
765d X 759c	3	0	0/0
765d X 766e	1	0	0/0
767e X 759a	1	1	0/57

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
767e X 762c	2	0	0/0
770d X 762c	1	1	0/0
772c X 761c	2	2	1/61
772c X 761e	1	1	0/10
773a X 759a	4	2	25/103
773a X 761b	2	1	2/40
773a X 761c	2	2	0/76
773a X 761d	2	2	2/64
773a X 761e	1	1	0/45
773a X 762a	2	2	9/114
773a X 762c	2	1	1/46
773a X 762b	1	0	0/0
773a X 762d	1	0	0/0
773a X 762e	1	1	*
773a X 763c	1	0	0/0
773a X 763e	1	0	0/0
773a X 766e	2	2	15/61
773b X 759a	2	0	0/0
773b X 760b	3	2	1/72
773b X 761c	1	1	0/30
773b X 762d	3	1	0/53
773b X 763d	1	1	0/15
773b X 759a	1	1	8/38
773c X 759b	2	2	0/90

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
773c X 759c	1	1	15/21
773c X 759e	2	2	23/67
773c X 760a	2	2	5/35
773c X 761c	1	1	0/21
773c X 761d	3	3	0/123
773c X 761e	2	2	0/88
773c X 762d	8	8	17/335
773c X 762e	1	1	0/20
773c X 763c	2	1	0/41
773c X 766c	1	1	1/36
773c X 775c	2	2	0/83
773c X 775e	3	3	2/121
773d X 763c	4	3	2/146
773e X 759a	1	1	0/52
773e X 759c	1	1	4/25
773e X 760b	3	3	0/136
773e X 762c	2	2	6/72
773e X 762d	3	3	7/147
773e X 775a	2	2	4/131
774b X 771b	1	0	0/0
774c X 760a	1	1	26/65
774c X 762d	7	7	64/416
774c X 763c	2	2	0/72
774d X 759a	1	0	0/0

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
774d X 760b	3	1	4/20
774d X 761d	1	1	8/46
774d X 762c	1	1	12/40
774d X 762d	5	4	47/147
774d X 763c	2	1	10/60
774d X 763d	4	4	67/202
774e X 760a	1	1	0/23
776a X 763c	1	0	0/0
776a X 766a	1	1	65/65
776b X 759a	4	0	0/0
776b X 760b	1	1	0/10
776b X 761d	2	1	3/60
776b X 762c	1	1	*
776b X 763a	1	0	0/0
776d X 762c	1	1	30/50
542a X 557a	1	0	0/0
542b X 553d	1	0	0/0
542c X 553b	1	0	0/0
542c X 557d	1	0	0/0
542d X 550d	1	0	0/0
542e X 550c	1	0	0/0
543b X 550d	1	1	0/45
543c X 557a	1	1	0/0
543c X 557d	1	1	0/55

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
543d X 550b	1	1	1/41
543d X 550d	1	0	0/0
543d X 553c	1	0	0/0
543d X 553d	1	1	0/55
543e X 557a	1	0	0/0
544a X 545b	1	0	0/0
544a X 553b	1	0	0/0
544b X 550d	1	1	0/13
544d X 557e	1	0	0/0
546a X 551b	1	0	0/0
546a X 558b	1	0	0/0
546b X 556e	1	0	0/0
546c X 556a	1	1	1/38
546c X 557a	1	1	0/39
546c X 558b	1	1	0/36
546d X 550c	1	0	0/0
546e X 550c	1	0	0/0
546e X 550d	1	1	0/33
547a X 558b	1	1	0/36
547b X 553b	1	0	0/0
547c X 558b	1	0	0/0
547d X 551d	1	0	0/0
547e X 556e	1	0	0/0
549a X 550c	1	0	0/0

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
549c X 553c	1	0	0/0
549c X 557a	1	0	0/0
552a X 551c	1	0	0/0
552a X 558b	1	0	0/0
552e X 550b	1	0	0/0
552e X 551c	1	0	0/0
759a X 773c	1	0	0/0
759c X 765d	2	2	3/28
759c X 773c	1	1	1/26
759d X 776e	1	0	0/0
759e X 769b	4	4	0/203
759e X 773a	1	1	0/20
759e X 773c	4	4	0/171
760a X 765b	2	0	0/0
760a X 776e	1	0	0/0
761b X 765d	1	0	0/0
761c X 765d	1	0	0/0
761c X 767f	1	1	0/20
761c X 773a	1	1	*
761c X 773c	1	1	0/49
761c X 774c	1	0	0/0
761d X 765d	1	0	0/0
761d X 773a	1	1	1/21
761d X 773c	6	5	1/169

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
761d X 773e	2	2	1/56
761d X 774d	3	3	3/90
761d X 776b	8	4	1/123
761e X 773e	1	1	0/43
762a X 773c	4	3	0/96
762b X 773a	5	5	13/151
762b X 773c	5	5	8/148
762b X 773e	1	0	0/0
762b X 774d	1	1	0/60
762c X 773a	1	1	2/22
762c X 773c	1	1	0/11
762d X 765a	1	0	0/0
762d X 767e	3	3	0/130
762d X 773b	3	1	0/18
762d X 773d	2	1	0/45
762dX 773e	2	1	0/25
762d X 774c	5	1	0/25
762d X 774e	2	1	0/20
762d X 776b	3	1	0/10
762d X 776d	1	1	10/60
762d X 776e	2	1	0/20
762e X 774c	4	4	0/155
763b X 776b	2	0	0/0
763c X 773c	2	2	2/89

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
763c X 774d	2	2	0/94
763c X 776b	3	3	1/125
763d X 773a	2	2	1/35
763e X 773c	3	1	0/14
766e X 765d	2	1	16/35
766e X 773a	2	1	0/13
766e X 773e	1	0	0/0
766e X 774c	2	0	0/0
775a X 768e	1	0	0/0
775a X 765d	1	1	0/32
775a X 773a	1	1	0/0
775a X 773c	1	0	0/0
775a X 773e	1	1	0/0
775e X 773c	2	1	0/30
775e X 773e	1	0	0/0
Interpopulational			
545b X 550b	1	0	0/0
550a X 558a	1	0	0/0
550b X 551c	1	1	12/63
550c X 556e	1	1	25/29
550d X 551c	1	0	0/0
551b X 558a	2	0	0/0
551b X 557a	1	0	0/0

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
551c X 550d	1	1	47/50
553c X 556a	1	0	0/0
553c X 557a	1	0	0/0
553c X 558a	1	0	0/0
553e X 550c	1	0	0/0
553e X 551c	1	0	0/0
557d X 556b	1	1	27/39
767f X 776c	1	1	29/31
770c X 773b	2	0	0/0
770d X 773d	1	1	0/25
772b X 768e	1	0	0/0
772c X 770c	2	1	22/23
772c X 774c	1	0	0/0
772c X 774e	1	0	0/0
772e X 770c	1	0	0/0
772e X 773c	1	1	*
772e X 776a	1	1	*
773a X 776a	1	1	44/47
773c X 765a	1	1	2/58
773c X 770a	2	2	26/99
773c X 770e	2	2	30/56
773c X 774c	4	4	170/170
773e X 770c	1	1	0/20
773e X 771d	1	1	79/79

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
773e X 775a	1	1	14/34
774b X 773e	1	1	20/27
774c X 770c	1	0	0/0
774c X 773c	1	0	0/0
774d X 768b	1	1	0/20
774d X 770b	1	1	35/35
774e X 767e	1	1	*
774e X 772c	1	0	0/0
776a X 768b	3	0	0/0
776a X 772e	2	1	0/14
776b X 773a	2	1	0/27
776b X 772e	3	0	0/0
542b X 543e	1	0	0/0
542b X 549c	1	0	0/0
543a X 546b	1	1	97/102
543a X 546e	1	0	0/0
543a X 547b	1	1	28/35
543c X 549c	1	1	89/89
543d X 542b	2	2	71/76
544b X 542c	1	1	8/15
544c X 543e	1	0	0/0
544c X 546c	1	1	31/34
544c X 546d	1	0	0/0

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
544d X 546a	1	0	0/0
544d X 546d	1	0	0/0
546a X 549a	1	1	14/17
546b X 543a	1	0	0/0
546b X 544d	1	0	0/0
546c X 543e	1	0	0/0
546e X 542b	1	1	14/17
546e X 544a	1	0	0/0
546e X 549a	1	0	0/0
547c X 546d	1	0	0/0
549a X 544d	1	0	0/0
549d X 542a	1	1	45/48
552a X 542a	1	1	27/29
552a X 549c	1	1	24/26
552d X 546b	1	0	0/0
759a X 763c	2	1	60/60
759a X 760e	1	1	33/33
760c X 763a	1	1	53/53
761b X 763e	1	0	0/0
761c X 760a	1	1	80/81
761c X 763c	1	1	41/44
761c X 763e	2	2	86/88
761c X 771d	4	4	262/269

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
761d X 763e	2	1	23/26
762a X 775c	1	1	15/15
762c X 761c	1	1	9/15
762d X 759a	3	3	150/173
762d X 775a	1	1	53/53
766e X 762d	9	5	140/153
775a X 762d	1	0	0/0
775c X 762d	3	3	70/94
Intrapopulational			
551c X 551b	1	1	21/26
767e X 767f	1	1	0/30
773a X 773b	1	1	53/56
773a X 773c	1	1	73/86
773b X 773a	2	2	45/56
773c X 773a	2	2	94/108
773c X 773b	1	1	34/34
773c X 773e	2	2	125/130
773e X 773c	1	1	50/58
776d X 776e	1	1	0/13
762d X 762f	1	1	53/53
Self Compatibility			
550b X 550b	1	0	0/0
550d X 550d	2	0	0/0

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
551a X 551a	1	0	0/0
551c X 551c	1	0	0/0
553c X 553c	1	0	0/0
767f X 767f	1	0	0/0
770d X 770d	2	0	0/0
770e X 770e	2	0	0/0
772c X 772c	4	0	0/0
772e X 772e	2	0	0/0
773a X 773a	5	0	0/0
773c X 773c	6	0	0/0
773d X 773d	2	0	0/0
774c X 774c	4	0	0/0
542d X 542d	1	0	0/0
543c X 543c	1	0	0/0
544c X 544c	1	0	0/0
544d X 544d	1	0	0/0
546a X 546a	1	0	0/0
546d X 546d	1	0	0/0
546e X 546e	1	0	0/0
549c X 549c	1	0	0/0
759e X 759e	1	0	0/0
761c X 761c	1	0	0/0
762d X 762d	7	0	0/0

TABLE V (Continued)

Cross	Number of Crosses	Number of Fruits Developed	Seed Set/ Ovules Produced
762e X 762e	2	0	0/0
763c X 763c	1	0	0/0
766e X 766e	1	0	0/0

* = Sample lost

that the crosses were performed, including flowering sequences and stigma receptivity, agree with those obtained by Grumer (1977). In these studies it was noted that the self-pollination does not occur naturally due to a slight spatial separation of the stigmas and anthers and the manner of anther dehiscence which is extrose. The presence of the insect pollinators Sphecodosoma and Nomadopsis is crucial in nature (Grummer, 1977).

Pollen fertility was determined by making slide counts of pollen grains stained with aniline blue-lactophenol. Fertility was 86 to 95%.

The results of the manual self-pollination of 57 flowers of both taxa revealed that both are genetically self-incompatible with no fruit development nor seed set. These results were supported by sequential sectioning of the style (technique of Ramming et al., 1973) which indicated a failure of continuing pollen tube growth. Even though there is germination of pollen grains on the stigmas and growth through the upper parts of the style, growth ceases before the ovules are reached. In contrast, the remnants of pollen tubes can be seen easily in the ovary and in the ovules of cross-pollinated flowers.

The crosses among the plants of an individual population were highly successful. Both fruit and seed set was high. The same was true for crosses among plants of different populations. Both taxa were similar.

Most important is the determinatin of gene flow between the two taxa. Two hundred-sixteen capsules developed in three hundred-fourteen reciprocal crosses. All capsules appeared normal in size; however, upon dissection, it was discovered that seed set was greatly reduced. Seeds ranged from very small, black, grayish-green and shriveled to full size and yellow. Seed development was determined to be 8.0%. This percent is much lower than that recorded by Grummer (1977) which was 26.73%. This reduction may be due to use of Texas populations of the variable *N. hispidum* rather than Oklahoma populations in the hybridizations. I was not able to germinate the seeds obtained from the crosses.

CHAPTER VI

CONCLUSIONS

Nama stevensii and *N. hispidum* are more similar to each other than to any other taxon in the genus. This similarity and the overlap in the characters usually used to distinguish the two taxa raised the question as whether they are distinct species or merely two genetic phases--ecotypes, varieties or subspecies of one species. The two taxa have similar phenological and genetic patterns. However, they differ consistently in only two distinguishable characters, namely the soil type on which they grow and the nature of their pubescence. They are highly restricted as to the soil type upon which they grew.

The data obtained in the experimental hybridizations give information about their genetic relationship. Gene flow between the two taxa is greatly reduced. Although capsules develop, seed set is highly reduced. It appears that there is an almost complete block to the exchange of genetic information between the two taxa. However, the development of the capsules and the formation of some seeds is significant, indicating there is a slight possibility of gene flow.

These genetic data when combined with those from morphology and phenology suggest that the taxonomic recognition of these two taxa as species best reflects their biological relationship. They are morphologically, ecologically, and genetically distinct.

On the basis of the information collected to date, one might hypothesize that the widely distributed and variable *Nama hispidum* has given rise to the gypsophilic *Nama stevensii*. This hypothesis is supported by the reclassification of *Nama hispidum* var. *gypsicola* (Johnston, 1941) to *Nama stevensii* var. *gypsicola* (Bacon, 1982). Examination and comparison of the plants of this variety convinced me to agree with Bacon that this taxon is *N. stevensii* rather than *N. hispidum*. The description of numerous gypsophiles in the genus *Nama* suggests that such an evolutionary phenomenon is possible. The marked similarities in morphology, insect visitors as described by Grummer (1977), flowering and the incomplete barrier to gene exchange are indicative of a relative recent origin.

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