Biology of Weeds in the *Solanum nigrum* Complex (*Solanum* Section *Solanum*) in North America

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Cover: *Solanum ptycanthum*, eastern black nightshade, drawn by Regina O. Hughes.

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ABSTRACT

Black nightshade and three related species of the *Solanum nigrum* complex have become economically important weeds in North America, particularly in the irrigated lands of the West. Numerous aspects of the biology of these species are poorly understood.

The importance of these species as competitive and poisonous weeds, disease vectors, and food sources is summarized. Taxonomic problems are fully reviewed and discussed. The breeding system and population genetics are described. Prominent and unique morphological features are described and illustrated. Aspects of plant-environment relationships and germination are reviewed. A method of field identification is presented. Implications for control research are discussed.

KEYWORDS: Black nightshade, hairy nightshade, taxonomy, morphology, economics, breeding, germination, *Solanum americanum*, *Solanum nodiflorum*, *Solanum ptycanthum*, *Solanum sarrachoides*.

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BIOLOGY OF WEEDS OF THE *SOLANUM NIGRUM* COMPLEX (*SOLANUM* SECTION *SOLANUM*) IN NORTH AMERICA

By Brant S. Rogers and Alex G. Ogg, Jr.[1]

INTRODUCTION

Nightshades are common agricultural weeds throughout the world. The most common of these are members of the *Solanum nigrum* complex, which constitute the species most closely related to black nightshade (*S. nigrum* L.). In North America, four species of the complex are the weeds most commonly referred to as black and hairy nightshade.

They have been considered minor weeds in most areas, but in recent years they have become known as serious pests in a variety of crops in many parts of the world. This has brought about an increase in control research, which has produced varying results. An incomplete understanding of the biology of these species is partially responsible for this variation.

As more effective control methods are sought, numerous aspects of the biological makeup of these weeds must be considered. The foundation of biological information in this context is a useable taxonomic system (*67*, *81*).[2] An understanding of such things as variability, genetic systems, ecology, and physiology necessarily follows (*58*). The following review summarizes the current state of knowledge of the biology of these species and will serve as a basis for further research.

ECONOMIC IMPORTANCE

Weeds

Members of the complex are known as weeds in at least 73 countries and are associated with 37 crops (*43*, *44*). They are found in temperate and tropical areas on every continent and grow especially well on fertile soils in moist

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[1]Botanist, Washington State University, and plant physiologist, Science and Education Administration-Agricultural Research (SEA-AR), U.S. Department of Agriculture, respectively, Irrigated Agriculture Research and Extension Center, Prosser, Wash. 99350.

[2]Italic numbers in parentheses refer to Literature Cited, p. 21.

areas and irrigated farmland. They are serious or principal weeds in a large variety of crops, including sugarbeets, corn, cotton, sugarcane, grapes, potatoes, tomatoes, peanuts, sweet potatoes, sunflowers, and many vegetables (*43*). In the United States, these nightshades have not generally been considered a major weed problem; however, in recent years they have been problems in many areas.

In Nebraska, black nightshade (UNK)[3] is a serious problem (*12*, *31*). When nightshade is harvested with field beans, juice from ruptured berries stains beans and causes soil particles to cling to beans, reducing quality. Burgert et al. (*12*) estimated a loss of $1.5 million a year in Nebraska due to nightshade damage to field bean quality. Losses due to competition there are appreciable also, but no estimate was made.

In California, nightshades are a major problem in tomatoes. They are also known as serious pests in potatoes, peppers, and melons and occur in cotton, onions, garlic, beets, safflower, grains, and grain sorghum (*49*, *50*).

Black nightshade (PT) is a severe problem in the north central Great Plains (*5*, *43*, *101*). It is a contaminant in canned peas and lima beans and may damage field beans, soybeans, and navy beans as mentioned above. Binning (*5*) noted that black nightshade did not compete well with other weeds in the area, but may be prevalent after other weeds have been controlled.

In the Pacific Northwest, nightshades have recently become a severe problem in beans (*63*).[4] They infest sugarbeets also (*20*). Data have shown that trifluralin[5] controls most annual grasses and certain broadleaf weeds, but not nightshade (*66*). It has been used extensively on beans in the area (*21*) and probably has increased the nightshade problem there.

In other countries, weeds of the complex are no less a problem. In eastern Canada, nightshade (UNK) is reported as a difficult to control weed (*13*). In New Zealand, they are some of the most important weeds. They may contaminate large seeded legume crops as mentioned above, compete strongly with certain crops, and stain wool of sheep that graze in infested areas (*37*, *57*). Recently, black nightshade (NI) has become abundant in England (*48*). In Israel, black night-

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[3] During the course of this review, numerous inconsistencies in the application of scientific and common names to these species were encountered. In order to further the accuracy of the literature cited herein, species designations follow all citations which are not known to be consistent with Ogg et al. (*67*) and Schilling (*81*) (AM = *S. americanum*, NI = *S. nigrum*, PT = *S. ptycanthum*, SA = *S. sarrachoides*, UNK = species identity unknown or unclear but definitely members of the *Solanum nigrum* complex).

[4] Don Hart, fieldman for Columbia Bean and Produce of Moses Lake, Wash., estimated that 44 percent of the 1975 dry bean crop in Washington State showed some degree of contamination by nightshade and that this contamination cost growers about $250,000 in lost revenue. Personal communication, 1976.

[5] α, α, α-trifluoro-2,6-dinitro-*N*,*N*-dipropyl-*p*-toluidine.

shade (UNK) is a serious weed in cotton and solanaceous vegetables.[6] Holm et al. (*43*, *44*) discussed the nightshade problem in other countries further.

Diseases

These nightshades are frequently associated with a broad spectrum of potentially destructive nematodes and phytopathic micro-organisms. Nightshades may be alternate hosts for these and therefore serve as potential disease vectors. There is also a potential for use of certain of these organisms as control agents. The following list provides a sampling of pathogens found in association with weeds of the *Solanum nigrum* complex. (Italic numbers in parentheses refer to the Literature Cited section, p. 21.):

Nematodes (*3*, *88*)

burrowing nematode (*Rotylenchus similis*, *Radopholus similis*)
foliar nematode (*Aphelenchoides ritzembozi*)
golden nematode of potato (*Heterodera marioni*, *Meloidogyne* spp.)
lesion nematode (*Pratylenchus neglectus*)
northern root-knot nematode (*Meloidogyne hapla*)
potato rot nematode (*Ditylenchus destructor*)
reniform nematode (*Rotylenchus reniformis*)
root-knot nematode (*Heterodera marioni*, *Meloidogyne* spp.)
silver-leaf nightshade nematode (*Ditylenchus phyllobis*, *Nothangirina phyllobia*)
southern root-knot nematode (*Meloidogyne incognito*)
stem nematode (*Ditylenchus destructor*)
stunt nematode (*Tylenchorhynchus claytoni*)
sugarbeet nematode (*Heterodera schachtii*)

Bacteria (*100*)

bacterial spot (*Xanthomonas vesicatoria*)
bacterial wilt (*Pseudomonas solanacearum*)
wildfire (*Pseudomonas tabaci*)

Fungi (*87*, *100*)

anthracnose (*Colletotrichum atramentarium*)
Cercospora nigrescens
Diporotheca rhizophila
early blight (*Alternaria solani*)
late blight (*Phytopthora infestans*)
leaf spot (*Cercospora atromarginalis*)
leaf spot (*Macrophoma subconica*)
powdery mildew (*Erysiphe cichoracearum*)

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[6] M. Horowitz, Agricultural Research Organization, Nve Yaar, Israel. Personal communication, 1979.

Fungi (*Continued*)

root rot (*Rhizoctonia solani*)
rust (*Puccinia subtriata*)
Septoria solanina
southern blight (*Sclerotium rolfsii*)
verticillium wilt (*Verticillium albo-atrum*)
violet root rot (*Rhizoctonia crocorum*)
white smit (*Entyloma australe*)

Viruses (*98*)

arabis mosaic
aster yellows
atropa belladona mosaic
chili pepper mosaic
cucumber green mottle mosaic
cucumber mosaic
curly top
leaf roll
lucerne mosaic
petunia mosaic
potato acuba mosaic
potato leaf roll
potato paracrinkle
potato stunt
potato virus A
potato virus M
potato virus X
potato virus Y
red current ring spot
tobacco etch
tobacco leaf curl
tobacco mosaic
tobacco necrosis
tobacco ring spot
tobacco ring spot No. 2
tobacco streak
tobacco yellow dwarf
tomato bunchy top
tomato spotted wilt
vaccinium false blossom
western aster yellows

Numerous destructive insects, such as the Colorado potato beetle (*7*), are frequently found in association with these species.

Poisonous Properties

Black nightshade (UNK) has a reputation for being poisonous to humans and livestock (*30*, *52*, *105*). Reputed toxicity is most frequently the result of steroidal alkaloid poisoning but may also be a result of high nitrate levels in the plant (*105*).

Most reports of poisoning and death to humans and livestock are secondhand information lacking detail (*34*, 74). Other reports of toxicity are more fully described but were recorded many years ago when the taxonomy of these species was highly confused (*79*).

Evidence that these species are not poisonous is more verifiable. Henderson (*42*) claimed personal experience in eating the raw fruit of *S. nigrum* and *S. nodiflorum* (AM) without ill effects. Similarly, Stebbins and Paddock (*95*) stated that the North American species are harmless. In New Zealand, Matthews (*57*) considered them harmless, and Healy (*37*) indicated that they are probably nonpoisonous. Henderson (*42*) reported that a heifer fed *S. nodiflorum* (AM) over a 4-day period suffered no ill effects. Bradley et al. (*6*) found that amounts of alkloids in members of the complex were small relative to other species of *Solanum*. The numerous instances of these species being used as food also indicates that they are probably harmless (*1*).

A probable explanation of the variability of reports of toxicity is that under certain conditions or in certain localities these species develop toxic levels of alkaloids (*59*, *78*). Weller and Phipps (*105*) further discussed toxicity in black nightshade (UNK).

Food

Historically, these nightshades have been a minor food source in many parts of the world. In China, it was a food plant, and the young shoots and berries were frequently eaten (*1*, *38*). Vegetative parts have been used in many places as a potherb (*38*, *42*).

Many examples of contemporary use can also be found. Luther Burbank introduced the sunberry or wonderberry (*S. retroflexum* Dun.), another member of the complex, into North America as a food plant (*39*). Fischer (*32*) described the methods of preparation and preservation of the garden huckleberry (*S. scabrum* Mill.), an allied species. Anthocyanins of this species are used as dyes in preserved fruits (*33*). Jams, preserves, and pies are made from the berries of other species (*12*, *24*, 42).

TAXONOMY

General Relationships

The Solanaceae is a large family of vascular plants composed of about 90 genera and over 2,000 species (*19*). It is primarily of Central and South America, but members are widespread and are commonly found on other continents.

The genus *Solanum* is the largest genus in the family and one of the largest genera in the plant kingdom. D'Arcy (*17*) noted that nearly 3,500 species have been referred to *Solanum*; however, a third to a half of these are probably not valid species because of nomenclatural duplication. D'Arcy (*17*) listed seven subgenera and 50 sections as belonging to *Solanum*.

Our concern in this paper is those members of *Solanum* that belong to the section *Solanum* (*Solanum nigrum* complex). Members are found on all continents in tropical and temperate environments from sea level to 3,000 m elevation. The greatest number of species are endemic to South America, where 18 species are currently recognized (*24*). In North America, 11 species are currently recognized by Schilling (*80*, *81*). The European species include 6 (*36*). Henderson (*42*) listed 11 species for Australia. It is unclear how many species are present in Africa, Asia, and the Pacific Islands. Edmonds (*27*) estimated that there are probably 30 species in the entire section *Solanum*.

Three species of the complex constitute a group of North American weed species which has most frequently been referred to as black nightshade in weed manuals and agricultural publications. These include American black nightshade (*S. americanum*), which is common in many southern and coastal areas; black nightshade (*S. nigrum*), locally common in the westernmost States; and eastern black nightshade (*S. ptycanthum*), the common black berried species east of the Rocky Mountains. The fourth North American weed of the complex is hairy nightshade (*S. sarrachoides*), which is found throughout most of North America. Four other species occur in certain areas, but they are geographically restricted, rather uncommon, and no evidence has been found that indicates that they occur as agricultural weeds in North America. They are *S. douglasii* Dun. of the Southwest, *S. psueudogracile* Heiser of the Southeast, *S. interius* Rydberg of the Midwest, and *S. villosum* Mill, which is uncommon in the United States (*80*, *81*). Other nightshades, such as cutleaf nightshade (*S. triflorum* Nutt.), a weed in the Pacific Northwest, are taxonomically distant from these species and much less common.

Taxonomic Problems

The section *Solanum* is generally considered extremely confusing taxonomically (*24*, *95*). Edmonds (*25*) and Heiser et al. (*41*) reviewed reasons for this difficulty in the complex. Concerning the four weed species of North America, there are four primary reasons for taxonomic confusion: gross similarity, phenotypic plasticity, genetic variability, and a confusing nomenclatural history (*67*).

Similarities

The most obvious reason for taxonomic difficulty is the general overall similarity between the species (fig. 1). All four species are herbaceous, usually annual broadleaf weeds of the same general size. Leaves, flowers, and fruits are frequently similar in obvious gross dimensions and color. To many, these species would most likely appear identical and are frequently considered so even by weed scientists (*62*).

Phenotypic Plasticity

Environmental factors play a large part in determining the expression of a number of morphological characteristics. Henderson (*42*) has observed that general form can be drastically altered by mowing, application of herbicides, grazing, and various insect infestations. Henderson (*42*) found that variation in flower color of *S. nodiflorum* (AM) is correlated with short days and cold temperatures. Similar variation has been found in *S. ptycanthum* (*80*). Edmonds (*25*) took seeds from a fully mature but small herbarium specimen (75 mm long) and from them, grew plants 50 cm tall. The specimen had been collected in a cattle pasture where it had been exposed to adverse conditions.

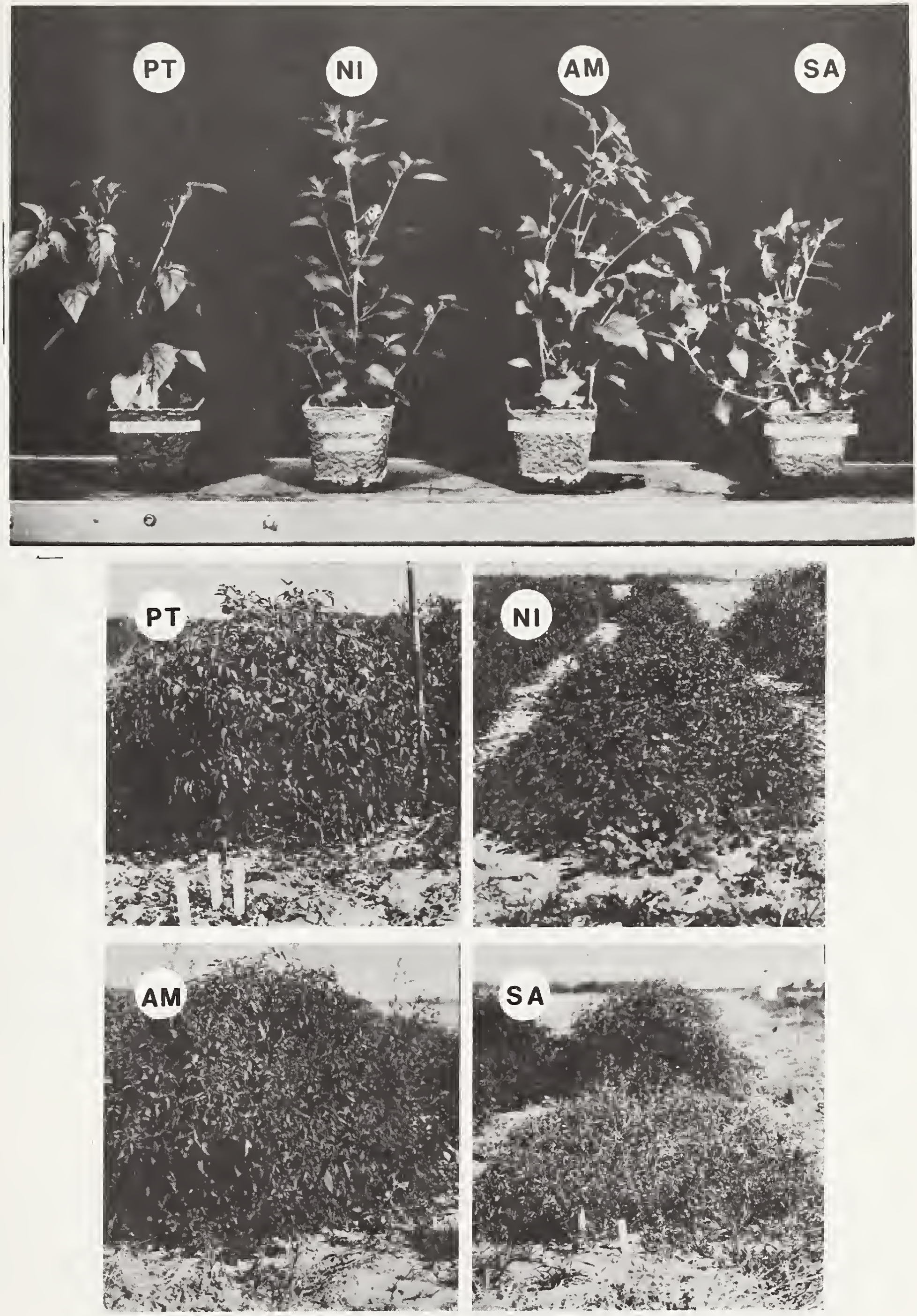

Figure 1.--The general appearance of all four North American species as 6-week-old plants grown in the growth chamber (above) and as mature plants in the field (PT = *S. ptycanthum*, NI = *S. nigrum*, AM = *S. americanum*, SA = *S. sarrachoides*).

According to Baylis (*2*), leaf size and form and stem winging are so variable that the exact limits within which they are fixed are difficult to define. Baylis (*2*), Edmonds (*27*), and Henderson (*42*) ascribed most of this variation to both environmental factors and plant age. Characteristics of the indumentum are also influenced by environmental factors and age (*42*).

Genetic Variability

Large variation in the genetic makeup of these species is a primary source of taxonomic confusion. Relationships between certain species are extremely close with poorly defined genetic barriers between them. Also, many species of the complex are allopolyploids derived from currently existing species. Such conditions make it difficult to define species relationships clearly on a genetic basis and might accurately describe certain taxa as "species in the making" (*95*).

Examples of genetic variability are numerous. *S. americanum* exhibits leaf margins ranging from entire to sinuate-dentate (*25*). Ogg et al. (*67*) illustrated the variability of leaf margins in all four North American weed species. Henderson (*42*) noted that presence or absence of purple striping on corollas of some species was unaffected by environmental influences. Schilling (*80*, *81*) has described distinct morphological types in *S. americanum* and significant genetic variation in populations of *S. ptycanthum* in terms of numerous morphological characters. Subspecies of both *S. americanum* and *S. nigrum* have been defined by numerous authors (*24*, *37*, *42*, *77*). Hairy nightshade has been considered by some to consist of two distinct species (*42*, *77*).

Hybridization may be a source of genetic variability in some cases. Schilling and Heiser (*83*) have described the lack of well-defined sterility barriers between certain species, and many investigators have found interspecific hybrids in nature (*2*, *18*, *42*, *55*, *80*, *95*).

Edmonds (*27*) has fully discussed polyploidy in the complex and pointed out that *S. nigrum*, a hexaploid, is an allopolyploid with definite genomes from *S. americanum* and probable genomes from *S. sarrachoides*. This may account for the similarity between the two diploid species and *S. nigrum*.

Nomenclature

The fourth reason for taxonomic confusion in this group is the large volume of literature produced by various botanists who studied the complex in the 19th and early 20th centuries. The high degree of variability and worldwide distribution of the species were probably confusing to early botanists who relied upon intuitive methods to help them define species.

In the 18th century, Linnaeus described six varieties of *S. nigrum*. Since then more than 300 varieties, subspecies, and species have been named. Many of these are synonyms and, as mentioned previously, only about 30 species are in the complex.

Georg Bitter, an early 20th century botanist, extensively changed the nightshade nomenclature of previous workers and named many new species based upon slight morphological variations. In the opinion of Edmonds (*25*), Bitter was responsible for much of the confusion in the group today. Since Bitter, numerous taxonomists have studied the group on a regional basis. In many cases, they recognized new taxa on the basis of an amount of variation, which in this group would be considered slight (*25*).

Among the four North American weed species, most nomenclatural problems have recently been clarified (*67*). The largest problem has been the persistent use of the name *S. nodiflorum* by most North American taxonomists for what we here call *S. americanum* (*41*, *80*, *95*). Nomenclature has recently been standardized to agree with the use of the name *S. americanum* for this species in North America (*67*, *81*). This is in agreement with the system of Edmonds (*24*, *25*, *27*) who plans to publish an article concerning nomenclatural problems in the section in the near future and a world monograph.[7]

The choice of an appropriate scientific name for *S. ptycanthum* also presents a problem. North America taxonomists until recently called this species *S. americanum*. The changes mentioned above now preclude the use of the name *S. americanum* for this species. Currently, the use of the name *S. ptycanthum* is accepted by North American workers (*67*, *81*). There is still some need to investigate the nomenclatural history of some species of the complex further, and minor changes may be necessary in the future. Of the four North American weed species, only the name *S. ptycanthum* is thought to be possibly tentative, pending further nomenclatural research.[7] It would be best to use the common names presented here in any literature citation.

A result of taxonomic confusion is the inconsistent usage of species names in weed floras, agricultural literature, and popularized plant books. In many weed manuals, *S. nigrum* is presented as the only major weed species of the section (*22*, *43*, *44*, *45*, *53*, *60*). Others present more thorough systems, which include other species (*74*). The Weed Science Society of America (*104*) provides the current standard for North American weed nomenclature. Their list includes only *S. nigrum* and *S. sarrachoides*.

Common names used for weeds of the section *Solanum* have proliferated to include no fewer than 16 within the group of four species as seen in the following list:

Scientific name	*Common name*
Solanum americanum (PT)	black nightshade (*80*) garden nightshade (*80*) nightshade (*80*) yerba mora negra (*15*)
S. nodiflorum (AM)	American black nightshade (*50*) black nightshade (*96*)

[7]Jennifer Edmonds, Cambridge University, Cambridge, England. Personal communication, 1979 and 1980.

S. nodiflorum (Continued).	common nightshade (*34*) chichiquelite (*80*) small flowered nightshade (*96*) yerba mora (*80*)
S. nigrum	black nightshade (*16*, *22*, *53*, *60*,-*80*, *96*, *104*). common nightshade (*27*, *53*) duscle (*22*). deadly nightshade (*16*, *22*, *60*,-*79*, *80*). European nightshade (*74*, *95*) garden nightshade (*22*, *27*, *60*,-*79*). houndsberry (*16*) nightshade (*22*) poisonberry (*16*, *22*, *60*) poison nightshade (*53*) stubbleberry (*16*, *22*)
S. sarrachoides	hairy nightshade (*34*, *50*, *74*, *104*)

Methods of Taxonomic Research

Crossability, numerical, and chemical studies have been useful in defining relationships within the complex in recent years. No method has been shown to be completely accurate alone, and therefore most recent students of the complex have employed all methods before making conclusions about taxonomic relationships.

Crossability Studies

Numerous investigators have studied crossing relationships among members of the complex (*2*, *25*, *29*, *40*, *42*, *51*, *68*, *70*, *71*, *72*, *73*, *80*, *81*, *82*, *95*, *97*). The assumption that crossing relationships reflect species relationships is founded upon the biological species concept (*56*), which has been frequently challenged (*83*).

The usefulness of crossing studies in helping to define taxonomic relationships within the complex varies. In general, genetic isolation reflects morphological variation (*25*); however, nearly all species successfully cross with at least one other species (*27*). Genetic isolation seems to be more complete between polyploids and diploids than between diploids. Among diploids, crosses between species are frequently successful; however, crosses between populations of the same species may be sterile. Schilling and Heiser (*83*) stated that crossing relationships between diploid species in North America are not useful in defining relationships.

Crossing relationships vary among the four North American weeds. *S. nigrum*, a hexaploid, is relatively well isolated and distinct although hybrids between this species and both *S. americanum* and *S. sarrachoides* are known (*25*, 55). *S. sarrachoides* is also relatively distinct and well isolated (*83*). *S. americanum* and *S. ptycanthum* are less isolated and frequently produce fertile interspecific crosses. Schilling (*80*) found that 2 percent of the progeny of plants of both species grown together in an experimental garden were hybrids.

The origin of polyploid species in the complex has been the subject of much study (*25*, *27*, *97*). Authors cite successful crosses between certain polyploids and plants of lower ploidy level as proof of contributions to the genomes of the polyploids. Edmonds (*27*) provided convincing evidence that *S. nigrum* is an allopolyploid with genomes contributed from *S. americanum*, a diploid, and *S. villosum*, a tetraploid.

Numerical Taxonomy

The use of quantitative techniques has helped define relationships within the complex (*26*, *40*, *46*, *80*, *82*, *91*). Three types of analysis have been used in these studies--cluster analysis, principal components analysis, and discriminant analysis.

In numerical studies, it is necessary to use those characteristics which are the least plastic and therefore least likely to vary from one individual to the next within a species. Generally, in species of the *S. nigrum* complex, vegetative characteristics, such as leaf size and shape and stem characteristics, are not useful for these analyses because of their variability. Floral and fruit characteristics have proven most valuable. Lists of those characters used in numerical studies are found in Edmonds (*24*, *25*), Heiser et al. (*40*), Jardine and Edmonds (*46*), and Schilling (*80*).

Numerical analysis of North American species has been reported by Schilling (*80*, *81*). He found that these species are generally well defined morphologically. He also found that *S. americanum* and *S. ptycanthum* are highly variable and probably consist of complexes of morphological types.

Numerical studies have provided evidence which helps define the ancestry of polyploids. Results strongly imply that *S. nigrum* is an allopolyploid product of *S. villosum* and *S. americanum*. Likewise, *S. sarrachoides* seems to be involved in the ancestry of the tetraploid *S. villosum* (*26*).

Chemotaxonomy

Chemotaxonomic techniques have been employed in two studies of the complex (*28*, *80*). The results of these studies are supportive of results of numerical and crossing studies.

Edmonds and Glidewell (*28*) studied band patterns of seed proteins produced by gel electrophoresis. The patterns generally reflected the morphological differences and genetical isolation of the species. Band patterns of hybrids matched well with those of parents.

Schilling (*80*) studied flavonoid chemistry of leaves and flowers of North American species. He found that most species have distinct flavonoid profiles and that polyploid species have a relatively simple flavonoid profile. He did not find evidence of polyploid ancestry relationships described by Edmonds (*25*, *26*).

BREEDING SYSTEM AND POPULATION GENETICS

Most members of the *Solanum nigrum* complex are primarily self-fertilizing (autogamous) species, although some cross-fertilizing (xenogamous) species occur and crossing of primarily selfing species has been documented. Fertilization in selfing species is from pollen of the same flower or, less frequently, of flowers on the same plant. The stigma and apical pores of the anthers are in close proximity in the selfing species, and flowers are usually inverted initially, promoting pollen deposition on the stigma of the same flower (*42*). Cross-fertilizing species of the complex have larger flowers with exerted stigmas in which anthers dehisce after the stigma is exerted past the anthers, increasing the possibility of pollination by wind or insects.

The four North American weed species are primarily selfing species. Schilling (*80*) found the pollen/ovule ratios and the amount of fruit set in the absence of pollinators indicated that the diploid species (AM, PT, SA) are definitely selfing species (facultatively autogamous). Observations of *S. nigrum* in the greenhouse by the authors indicate that this species is also primarily self-pollinated. Outcrossing is possible in these species, though, and many examples can be found in the literature (*42*, *80*). This is particularly true of *S. nodiflorum* (AM) (*2*).

The autogamous nature of the breeding system of these species gives rise to a high degree of homozygocity and concurrent genetic uniformity of plants within a population and from generation to generation. As a result, within each species a series of more or less uniform populations are highly homogeneous within but may be distinctively different from each other in many obvious morphological and ecological characters. Edmonds (*27*) described *S. americanum* as a highly variable "complex" of infraspecific units. Schilling (*80*) has found numerous morphological types within *S. ptycanthum* and *S. americanum* in North America. Stebbins (*94*) suggested that such plant groups as this might best be described as groups of "microspecies."

The autogamous breeding system in these species favors the rapid buildup of a population from a few individuals and gives these species an evolutionary advantage in environments where populations are frequently destroyed (*93*). This is well illustrated by the behavior of members of the complex in agricultural areas.

MORPHOLOGY

Habit and Growth

All four species are herbs or subshrubs, which generally do not exceed 1 m in height. Individual plants with branching axes of over 2 m in length have been observed, and fully mature individuals less than 10 cm tall are common. *S. pty-*

canthum and *S. americanum* are usually erect, and the other two species are commonly low growing (fig. 1).

The borderline between annual and perennial lifespan is not well marked in *S. americanum*, *S. ptycanthum*, and *S. nigrum*. They are variously described as annual, short-lived perennial, or perennial in taxonomic treatments. Observations by the authors confirm that these species may survive for long periods in the greenhouse. In northern climates, they do not survive cold temperatures and are annual. In southern climates, they may become perennial (*2*, *42*). *S. sarrachoides* is the only species which is strictly annual. Termination of growth in this species seems to be more closely related to age than to any environmental factor. All four species display the sympodial growth pattern typical of black nightshade (*14*) with leaves and flowers being produced along the branching axes throughout the lifespan of the plant.

Vegetative Characteristics

As previously discussed, most vegetative structures of these plants are highly plastic and may vary greatly in size and shape when grown under different conditions.

All four species have a fibrous root system. Burgert and Burnside (*9*) found that, compared with a variety of crop and weed species, black nightshade (UNK) had a relatively high shoot-to-root ratio, indicating a relatively small root system. Significant differences in root and biomass between species have been found in growth chamber studies (*64*).

Stems of the four species are slender and herbaceous or woody with age. They may be round, angular, ridged, or ridged with small teeth. The type of stem architecture seems to be highly controlled by environmental conditions.

Leaves are extremely variable in size (for example, 2 to 18 cm for *S. nodiflorum* (AM) (*42*)) and shape. The leaf margins may be entire to sinuate or dentate.

Stomates are similar to those of other species of *Solanum* (fig. 2) (*4*). Both anomocytic and anisocytic stoma are present (*54*). *S. nigrum* has larger stoma than the other three species because it is polyploid (*27*). Stoma are about two or three times more numerous on the lower leaf surface than on the upper surface. Mukherjee and Das (*61*) found 20 to 30 stoma per square millimeter on the upper surface and 90 to 100 per square millimeter on the lower surface in *S. nigrum* (UNK). Sen (*85*) found approximately 80 per square millimeter on the upper surface and 170 per square millimeter on the lower surface in *S. nigrum* (UNK).

Three types of hairs are found on the four species--gland-tipped finger hairs, finger hairs, and multicellular glands (*84*) (fig. 3). All four species have multicellular glands and finger hairs. Only *S. sarrachoides* has gland-tipped finger hairs, which give this species its viscid or sticky texture. Landré (*54*) discussed development of these hairs and noted that multicellular glands have a high ploidy level compared with other somatic cells.

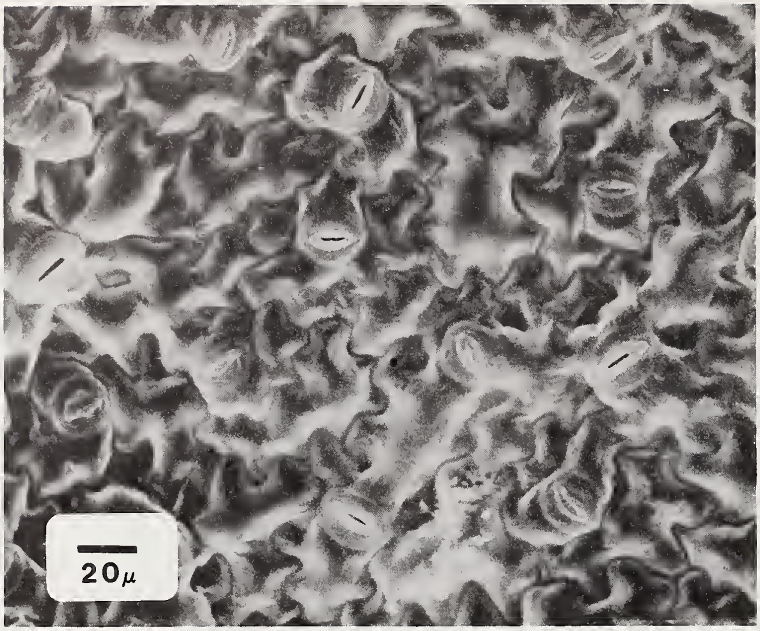

Figure 2.--Scanning electron micrograph of stomates of the lower leaf surface of *S. sarrachoides* (X400).

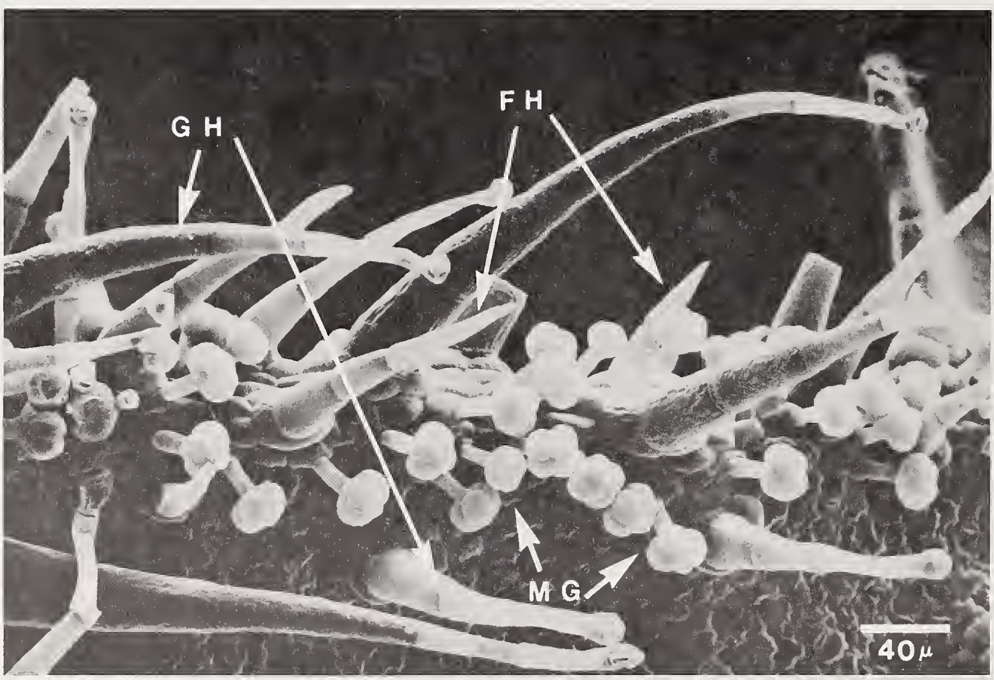

Figure 3.--Scanning electron micrograph of margin of young leaf of *S. sarrachoides* showing three types of trichomes found on North American members of the complex. (FH = finger hairs, GH = gland tipped finger hairs, MG = multicellular glands) (X300).

Floral and Fruiting Structures

Inflorescences are usually simple, extra axillary cymes which grade from a compressed (umbelliform) type frequently found in *S. nigrum* and *S. sarrachoides* to an elongated (racemiform) type, which is common in the other two species. The number of flowers per inflorescence may vary from as few as 3 or 4 to over 20.

Flowers are five-merous and vary from 4 to 10 mm in diameter (fig. 4). The corolla is generally white but may be tinted or striped purple especially in *S. ptycanthum*. The central portion near the anthers (corolla star) is usually greenish yellow. It may have purple flecks in *S. sarrachoides*.

The five stamens are epipetalous and open by both apical pores and longitudinal slits. The style is usually straight or may be slightly bent. The stigma may be variously globose or flattened.

Pollen is granular, hyaline, smooth, prolate when dry, and usually with three germ pores (fig. 5). Pollen grain size frequently varies among species (*42*, *67*, *80*). *S. nigrum* has large pollen (26 to 35 μm in diameter), *S. sarrachoides* has intermediate size pollen, and the other two species have small pollen (15 to 25 μm in diameter).

Fruits are berries which vary in color, size, presence of sclerotic granules, and number of seed (fig. 6). Berries may be brown, green, yellow-green, brown-green, or black. Size may vary from 5 mm to over 10 mm in diameter. Sclerotic granules, a fraction the size of seed, are present in berries of some species and are seldom more than six per berry. The number of seed per berry may be as few as 15 in the large seeded species (*S. sarrachoides*) and as many as 110 in the smaller seeded species (*S. ptycanthum*) (*67*).

Seeds are strongly flattened, white, yellowish, or tan. The seedcoat is reticulate with many small hairlike structures, which are strands of epidermal wall thickening (fig. 7) (23; also, see footnote 7). The hilum is inconspicuous, marginal, near the seed base, and linear. The embryo is linear and imbricate (*35*). Seed varies in length from 1.4 to 2.1 mm, depending upon the species. Estimates of the production of seed per plant vary from 8,000 to 178,000 (*43*, *50*, *105*).

PLANT-ENVIRONMENT RELATIONSHIPS

Responses of these species to environmental factors are not well known. Only general observations can be extracted from the studies which have been published.

These species are notorious for colonizing disturbed habitats and agricultural lands (*42*, *47*). They are particularly well adapted to moist conditions with fertile soil, such as irrigated farmland (*43*). Weller and Phipps (*105*) noted that black nightshade is well suited to soils with high nitrogen levels.

These species are not generally well adapted to dry conditions. Singh (*89*) noted that *S. nigrum* (UNK) avoids open areas in warmer months. Sen (*85*) found that it (UNK) does not control stomatal aperture effectively under moisture stress. Burgert and Burnside (*8*) found that black nightshade (UNK) is

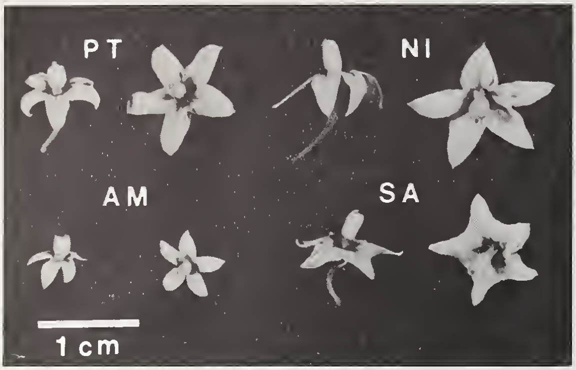

Figure 4.--Flowers of the four North American species

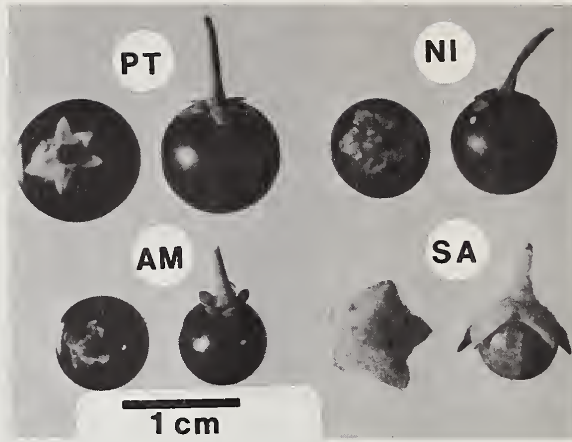

Figure 6.--Fruits of the four North American species.

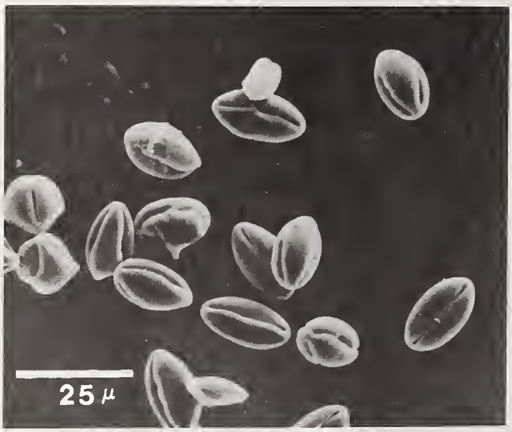

Figure 5.--Scanning electron micrograph of pollen grains of *S. sarrachoides* (X600).

generally less tolerant of moisture stress than a variety of common crop and weed species. Sharma and Sen (*86*) and Singh (*89*) found that growth and seed production were generally favored by long photoperiods or relatively high light intensity, although plants acted as sciophytes (shade loving) during the tropical hot season. Sen (*86*) noted that stomatal movements of *S. nigrum* (UNK) were not correlated with exposure to light.

GERMINATION

These species are similar to each other in general germination behavior; however, subtle differences between species are numerous and have been recently studied (*65*, *101*).

Seeds are adapted for germination within a year or two of production, but seed more than 10 years old may still be viable (*76*, *99*). In temperate areas, germination begins in the spring and may continue through September with heaviest germination during the first months (*63*, *76*). Black nightshade (UNK) may frequently germinate long after vegetable crops have emerged, making it difficult to control (*105*).

Most investigators report optimal germination under conditions of alternating temperatures with a high temperature in the range of 20° to 30°C.

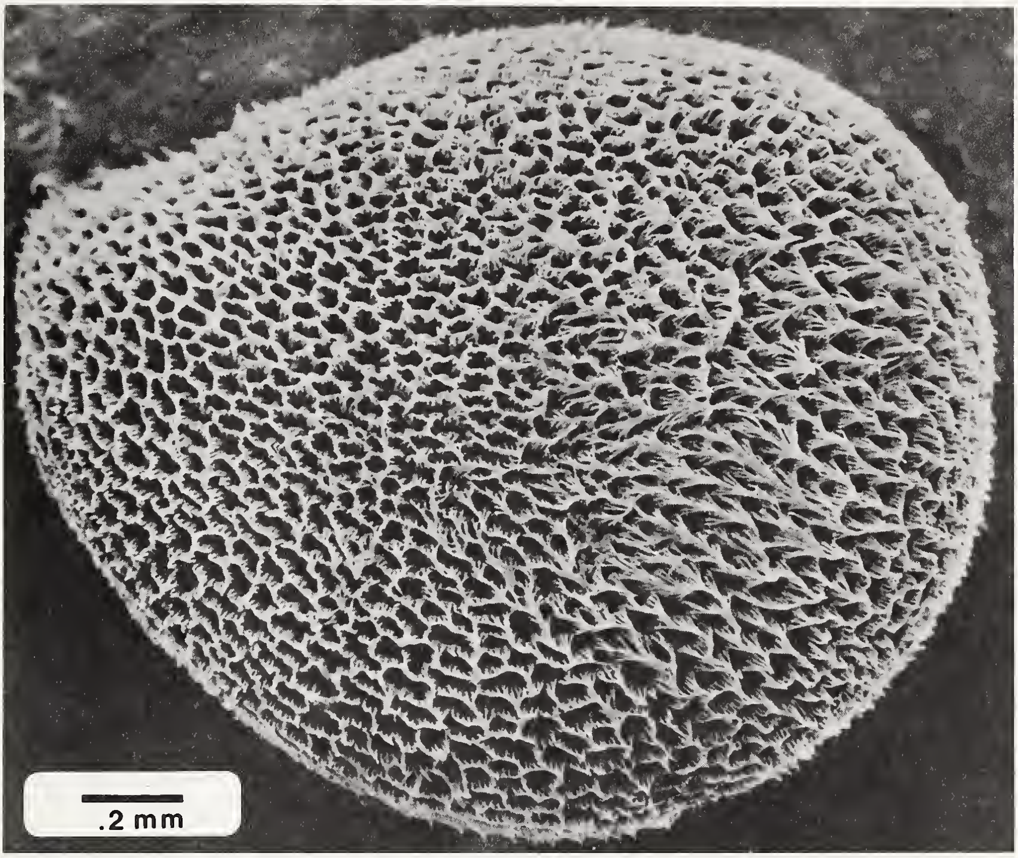

Figure 7.--Scanning electron micrograph of a seed of *S. sarrachoides*.

Generally, constant temperatures have been found to inhibit germination except by Burgert and Burnside (*10*) who reported high germination at a constant 30°C.[8] Other solanaceous species germinate well under alternating temperatures (*75*).

Moist storage at cool temperatures and winter storage outdoors have been found to enhance germination of these species (*65*, *76*, *102*). Increases in germination after moist storage at cool temperatures were noticed after as little as 1 week of storage.

Reports vary of the effects of light on germination. Roberts and Lockett (*75*) found that intermittent light enhanced germination at less favorable germination temperatures. Wakhloo (*103*) found that germination was highest in complete darkness and green light, high in intermediate light, low in direct light, and there was no germination under red light. Singh (*90*) found that lower light intensities were generally more favorable for germination.

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[8] Burgert and Burnside (*10*) may have been studying *S. sarrachoides*, which may germinate well at high constant temperatures under certain conditions (*65*).

Rinsing the seed before germination may or may not affect germination percentage. Vandeventer (*101*) found no effect, and Wagenvoort and Van Opstal (*102*) found a decrease in germination after rinsing.

Gibberellic acid is well known as a germination stimulant especially in solanaceous species (*69*, *92*). Seeds of all four North American species germinate well after moist storage of at least 1 month and followed by a pretreatment of at least 1,000 parts per million of gibberellic acid (*65*).

Germination-soil relationships have been little studied. Burgert and Burnside (*11*) found that black nightshade (UNK) seed germinated better when planted at one-quarter centimeter deep than deeper. They also found no significant difference in germination percentage between seed sown in silt clay loam and that sown in sandy loam.

CHARACTERIZATION

A detailed taxonomic key and species descriptions are presented in Ogg et al. (*67*) and are not necessary here. As a field identification aid, table 1 is provided to help distinguish among these species, using easily recognizable field characters.

S. americanum Mill., American black nightshade

This is a common species in the more frost-free areas of the Southeast and West near the coasts. It is abundant in California where it is a serious weed in certain places. A number of morphological types have been recognized in the United States by Schilling (*80*, *81*), and subspecies have been named in other countries. It is most similar to eastern black nightshade and may be confused with it in the Southeastern States where they both occur. An annual or short-lived perennial diploid (2n = 24) with native and introduced populations. This species has been frequently called *S. nodiflorum* (*80*, *95*).

S. nigrum L., black nightshade

Locally common in the far western States, but rarely found elsewhere. It occurs together with American black nightshade in California, but is easily distinguishable by its larger seeds and pollen. An annual or short-lived perennial hexaploid (2n = 72) introduced from Eurasia.

S. ptycanthum Dun., eastern black nightshade

This species is the common black-berried nightshade east of the Rocky Mountains. An annual or short-lived perennial native diploid (2n = 24). This species has been frequently called *S. americanum* (*80*, *95*).

Table 1.--*Characterization of species in the field*

Character	Hairy nightshade	Black nightshade	Eastern black nightshade	American black nightshade
Berries	Brownish to olive green, calyx expanded 1/4 to 1/2 over berry, 2 or 3 sclerotic granules per berry, no white flecks.	Black, rarely yellow green; no sclerotic granules, no white flecks.	Black, rarely yellow green, 4 to 15 sclerotic granules per berry, no white flecks.	Black or sometimes brownish black, 0 to 4 sclerotic granules per berry, white flecks on immature berries.
Seed	Large, 1.8 to 2.3 mm long, 10 to 35 per berry, tan.	Large, 1.8 to 2.2 mm long, 15 to 60 per berry; usually yellow or nearly white.	Small, 1.5 to 1.8 mm long, 50 to 110 per berry; usually yellow or nearly white.	Small, 1.4 to 1.6 mm long, 50 to 110 per berry; usually yellow or nearly white.
Flower	White with greenish yellow star with purple flecks; rotate.	White with greenish yellow star; stellate.	White, sometimes tinted or streaked purple with greenish yellow star; stellate.	White, rarely tinted purple with greenish yellow star; stellate.
Pubescence	Usually obviously hairy; especially young leaves, frequently sticky.	Not obviously hairy.	Not obviously hairy.	Not obviously hairy.
Pollen	24 to 27 µm in diameter.	26 to 35 µm in diameter.	15 to 25 µm in diameter.	15 to 25 µm in diameter.

S. sarrachoides Sendt., hairy nightshade

A widespread species in North America, especially in parts of the Plains States, Pacific Northwest, and adjacent Canada. It is unique in many characters and is relatively uniform morphologically throughout its range. An annual diploid (2n = 24) introduced from South America.

DISCUSSION

These nightshades are currently being recognized as important weeds in areas where they were previously uncommon. Behind their success as weeds are many factors, such as efficient seed dispersal, control of other weeds to lessen competition, resistance to control methods, and variable response to herbicides. We predict that the trend of increasing prevalence will continue and that these species will be the subject of more intensive control research.

The extreme phenotypic and genetic variability among weed species of the complex presents a formidable problem for those involved in control research. Ecological, physiological, and pharmacological properties as well as response to control methods are undoubtedly linked to the morphological variation described in this review.

The limits of taxonomic variation among species have been clarified here and elsewhere (*67*, *81*) and will serve to eliminate much of the variability in reporting results of future control research if widely used by investigators.

Variation below the species level is known to express itself as numerous morphological types and may indicate that variation in control response will be regularly found in infraspecific taxa or among the many unnamed "microspecies" which constitute these species. If so, there will be a need for description of variability below the species level.

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GLOSSARY

Allopolyploid...A polyploid in which the genomes were derived from different sources through hybridization.

Anisocytic stoma... Stoma surrounded by three cells, of which one is smaller than the other two.

Anonomocytic stoma... Stoma surrounded by cells that are indistinguishable from other epidermis cells.

Chemotaxonomy... The study of organisms with regard to their natural relationships as defined by chemical studies.

Dentate... Margins of leaves or other organs with rounded or sharp, coarse teeth that point outwards at right angles to midrib or midvein, cut 1/16 to 1/8 distance to midrib or midvein.

Diploid... The chromosome complement that consists of two complete sets of chromosomes (2n), one from each parental gamete.

Electrophoresis... An electrochemical process in which charged particles or macromolecules, such as proteins, migrate in solution under the influence of electric charge. Sometimes used in chemotaxonomic studies.

Epipetalous... With organ (usually stamens) attached to or inserted upon petals or corolla.

Genome...A complete haploid set of chromosomes. The haploid being the lowest ploidy level (1n) with a complete set of chromosomes.

Hexaploid... The chromosome complement that consists of six complete chromosome sets (6n).

Indumentum...Pubescence or vestiture.

Infraspecific taxa...Categories of classification below the species level, such as subspecies and variety.

Ploidy level...The level of chromosome number.

Polyploid...A chromosome complement which consists of three or more complete sets of chromosomes (3n, 4n, 5n, etc.).

Sclerotic granule...A small hard object found in various organs of plants. In nightshades, they are granular, less than 0.5 mm in diameter, and found in the fruits.

Sinuate...Margins of leaves or other organs, shallowly and smoothly indented, wavy in a horizontal plane, indented 1/16 to 1/8 distance to the midrib or midvein.

Sympodial growth...Branching habit in which there is no distinct main axis.

Tetraploid...The chromosome complement that consists of four complete sets of chromosomes (4n).

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