Descriptive analysis of Montana species of Amaranthus
by Paungpen Sirirugsa

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE in Botany
Montana State University
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Abstract:
The Amaranthus species of Montana, A. albus, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus have been collected and studied. Morphological characteristics of roots, stems, leaves, inflorescences, bracts, flowers (sepals, ovaries, stamens, and pollen), fruits and seeds of all species have been shown by tables and plates.

Herbarium specimens of A. albus, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus of the U. S. National Herbarium, Smithsonian Institution (Washington, D.C.) and of the herbarium of Montana State University have been studied. The distributions, habitats and dates of collections of the specimens were recorded. The distributions of the six Amaranthus species in Montana are shown by maps.

Pollen grains were examined and drawn showing shape and internal morphological characteristics as observed by light microscopy.

Species descriptions and a key, which identifies the species of Amaranthus of Montana, are provided.

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Date May 25, 1973

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A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Botany

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MONTANA STATE UNIVERSITY
Bozeman, Montana

June, 1973

ACKNOWLEDGMENT

The author expresses her sincere appreciation to Dr. J. H. Rumely for his advice, constructive criticism and patience in preparation of this thesis, as well as his kindness throughout this course of work. His consistent devotion to this thesis has been an inspiration to the author.

Also, the author expresses her sincere appreciation to Dr. W. E. Booth for initial guidance, helpful cooperation and encouragement.

Special appreciation is expressed to Dr. Don Mathre and Dr. I. K. Mills for their helpful comments and suggestions.

Special thanks go to Dr. Thomas Carroll for his help concerning the internal morphological study of the pollen grains and to Mrs. Mary Carpenter for the use of the seed germinater.

Sincere appreciation is expressed to the herbarium curators of Montana State University and the Smithsonian Institution of Washington, D.C.

Also, the author acknowledges, with thanks, the help and instruction received from: Professor H. N. Metcalf, Dr. Chaitat Pairintra, Mrs. Bertha Gillam, Mrs. Karen Worden, Lt. Nick Menasuta and Mr. and Mrs. J. F. Reagan.

Finally, the author extends her special thanks to the AID training program for the grant which made this study possible.

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ABSTRACT

The Amaranthus species of Montana, A. albus, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus have been collected and studied. Morphological characteristics of roots, stems, leaves, inflorescences, bracts, flowers (sepals, ovaries, stamens, and pollen), fruits and seeds of all species have been shown by tables and plates.

Herbarium specimens of A. albus, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus of the U. S. National Herbarium, Smithsonian Institution (Washington, D.C.) and of the herbarium of Montana State University have been studied. The distributions, habitats and dates of collections of the specimens were recorded. The distributions of the six Amaranthus species in Montana are shown by maps.

Pollen grains were examined and drawn showing shape and internal morphological characteristics as observed by light microscopy.

Species descriptions and a key, which identifies the species of Amaranthus of Montana, are provided.

INTRODUCTION

Amaranthus is a genus of the subfamily Amaranthoideae Schintz ex Engler and Prantl (1960) of the family Amaranthaceae. The family is represented by approximately 50 genera of which four are recorded as being in the Rocky Mountains by Rydberg (1917), but Amaranthus is the only one recorded for Montana (Booth and Wright, 1966).

Within the genus Amaranthus, distinct morphological features on which separation of species can be made are few and the general habit within most species is variably influenced by diverse environments. Sauer (1950) lists important factors that have contributed to confusion in classifying Amaranthus species. First is the wide dispersal of many species which have only subtle differences among them. The problem is compounded because, through the course of botanical history different binomials have been applied in different regions to these widespread species. Second, most of the early species descriptions are minimally brief and the characteristics cited are common to several species or else they emphasize trivial features such as pigmentation. Although the species have been described and named according to rules, a description may apply equally well to different species, or only partially to the original species as now known.

A desire to find recognizable morphological features for use in positive species separation of the many ecological forms prompted the present study of the Montana species of Amaranthus. An interest

has also been developed this genus because it is widely represented in the author's home of Thailand.

The present investigation has been oriented toward the study of field collections from Montana, field observations, and herbarium specimens mostly of Montana plants; although an examination was also made of the worldwide collection in the National Herbarium of the Smithsonian Institution of Washington, D.C.

The objectives of this study were:

1. To study the morphological characteristics of the species of the genus Amaranthus of Montana.

2. To construct an easily usable key to the species of this region.

3. To study the ecological variations in the Montana species of Amaranthus from field observations and from examination of specimens in herbaria of this area and in the National Herbarium in Washington, D.C. with the hope of being able to account for specimen variation that may at times be interpreted as species variation.

REVIEW OF LITERATURE

Linnaeus (1753) included 11 species of the genus Amaranthus in "Species Plantarum". Three of them, A. graecizans, A. hybridus and A. retroflexus have been found in the northern Rocky Mountains of the United States.

Studies by several taxonomists of the northern Rocky Mountain species of Amaranthus began in the last century. Coulter (1885) described 5 species from the Rocky Mountain region between New Mexico and the Canadian border, although he used the spelling "Amarantus" instead of "Amaranthus". Two of the species listed by Coulter were A. albus and A. retroflexus, both of which are of interest in this study.

Uline and Bray (1894) described 32 species in North America. Five of them, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus are included in this study. The species were identified by number of sepals and stamens. A. powellii is in the group with 5 sepals and 3 stamens. A. hybridus and A. retroflexus are in the group with 5 sepals and 5 stamens. A. graecizans is in the group with 3 sepals and 3 stamens. A. californicus is in the group with sepals fewer than 3 and 3 stamens.

Howell (1903) listed 5 species in northwest America, of which A. californicus, A. graecizans and A. hybridus are in the northern Rocky Mountains of the United States and are discussed in this study.

Howell tried to distinguish among the species by the numbers of sepals and bracts.

Rydberg (1917) described and provided a key to 11 species of Amaranthus found in the North American Rocky Mountains and adjacent plains. Five of the species listed by Rydberg are included in this study.

Stanley (1917) described and provided a key to 42 species of Amaranthus in North America. Five of the species listed by Stanley, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus are included in this study.

Ashton (1933) cited A. retroflexus as being in the Rocky Mountain National Park of Colorado growing along roadsides and on other disturbed ground and referred to it as "rough pigweed".

Stevens (1950) listed, with a key, 4 species that occur in North Dakota; these species are A. albus, A. graecizans, A. hybridus and A. retroflexus.

Davis (1952) described 6 species of Amaranthus in Idaho and presented a key to these species. Only one of the Idaho species is not included in the area of this study.

Harrington (1954) named 8 species, but three of these are of questionable occurrence in Colorado. The remaining 5 are present in the study area of this thesis.

Tucker and Sauer (1958) described aberrant characteristics of sepals, bracts, fruits and inflorescences of 5 species of Amaranthus that occur in California. Three of these species, A. hybridus, A. powellii and A. retroflexus are included in this study.

Hitchcock et al. (1964) listed 5 species of Amaranthus as being in the Pacific Northwest, all of which are present in the Rocky Mountain area and are included in this study.

Booth and Wright (1966) listed 6 Montana species and provided a key to these species. All of these, A. albus, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus are of importance in this study.

Sauer (1967) characterized A. retroflexus as a native riverbank pioneer of the central and eastern United States and adjacent regions of southeastern Canada and northeastern Mexico. A. powellii is a pioneer of canyons, desert washes, and other open habitats ranging through the western Cordilleras of North and South America. It appeared as an uncommon adventive in eastern North America about 1900. Since 1940 it has been regarded as a widespread and troublesome weed there. A. hybridus is evidently a native riverbank pioneer of mild and moist regions from eastern North America through Mexico and Central America to northernmost South America. Its earliest and most successful historically documented emigration was to the Mediterranean

region where it arrived by the 18th century. A. hybridus was also recorded by Hanelt (1968) as a cultivated crop of American origin. It is among the oldest cultivated plants of American agriculture.

There are only indirect evidences of the prehistoric range of Amaranthus as a recognizable taxon. Sauer (1950) recorded that evidence of the use of Amaranthus as crop plants occurs very faintly among the Indians of the southwestern United States, is more distinct in northwestern Mexico and in a central Mexican stronghold of the crop, but is indistinct in southern Mexico. A small isolated center of use is found in Guatemala and a large one in the Andes including Peru, Bolivia and northwestern Argentina. On the western side of the Pacific, indistinct evidence of crop use occurs in Manchuria and interior China. There once was a major center in the Himalayas and indistinct use in Afghanistan and Persia. There was a small outpost in southern India and Ceylon. There are vague traces of the use of Amaranthus as a crop in Africa.

Wodehouse (1935) studied pollen and recorded that all species of Amaranthus are wind pollinated, and that several are troublesome hay fever weeds. A. retroflexus flowers from August to October, does not shed much pollen but occasionally becomes a factor in hay fever, particularly in Arizona, Oklahoma, California and Oregon. A. hybridus flowers at the same time as A. retroflexus. It probably is an

important cause of hay fever. A. graecizans sheds much less pollen than most other members of the genus and is not important in hay fever.

Erdtman (1952) documented that pollen grains of amaranthoid type testify to the close relationship between Amaranthaceae and Chenopodiaceae, supporting the opinion that Amaranthaceae and Chenopodiaceae, because of many natural affinities, actually may be considered to comprise a single family.

Seeds of the genus Amaranthus were studied by Martin and Barkley (1961). They described the gross structure of the seeds of this genus as: circular-lenticular, with edge narrowed into a thin rim; notched on margin; usually shiny black or dark reddish brown; mostly 1-1.5 mm. in diameter. Also they reported that the embryo is curved around a firm and starchy endosperm.

Wiese and Davis (1967) reported that the emergence of A. retroflexus from soil in a growth chamber was best with an 8-hr. night temperature of 65° F and a 16-hr. day temperature of 80° F, at a 1/2 in. depth of planting, and using a coarse-textured soil rather than on a fine-textured soil. Under dry soil conditions, emergence was reduced by soil crusting.

Experiments of Palmblad (1969) indicated that A. retroflexus often has germination polymorphism (discontinuous germination).

Darlington (1922), Kivilaan and Bandursky (1973) reported from Dr. W. J. Beal's seed viability experiment that A. retroflexus seeds

remain viable for 40 years, but they probably do not remain viable after 50 years.

Goering (1967) reported that the starch in seeds of A. retroflexus is composed of 2 distinct entities: a small amount of very small spherical granules and a large amount of massive starch chunks. These starch chunks were found to have unusual "pasting" characteristics. The Brabender viscosity curve for this starch does not show a cooking maximum; it is different from any other known natural starch. The low solubility and expansion of chunk pigweed starch suggest it has very strong, uniform and extensive forces holding the mass together.

Bamberger and Mayer (1960) reported that kinetin induces formation of red pigments in seedling of A. retroflexus in the dark. The pigment is not an anthocyanin, and its formation is not affected by inhibitors of anthocyanin formation.

The results of Marshall et al.'s experiments (1967) indicated that leaves of A. retroflexus contained 12 to 30% oxalate, expressed as oxalic acid (on a dry weight basis). On the basis of its high oxalate content, they concluded that this species should be classed as potentially toxic to animals. The nitrate content of the A. retroflexus plants analyzed was highly variable. The plant has been shown to be a causative agent of perirenal edema of swine (Marshall et al., 1967). That pigs fed with A. retroflexus developed clinical signs of

perirenal edema was also reported by Osweiler et al. (1969). Certain biochemical values and electrolyte levels of blood were changed in pigs fed A. retroflexus, i.e., large and consistent increases in serum potassium and smaller increases in serum magnesium levels, and marked increase in blood urea nitrogen value.

Grant (1959) reported the chromosome numbers of 30 species of Amaranthus. Five of them, A. albus, A. graecizans, A. hybridus, A. powellii, and A. retroflexus are included in the area of this study. A. albus, A. graecizans and A. hybridus have 2n = 32. A. powellii and A. retroflexus have 2n = 34. A cytological study of A. cruentus x powellii x retroflexus showed that this hybrid has a somatic chromosome number of 32. Another hybrid between A. cruentus (2n = 34) and A. hybridus (2n = 32) has a somatic chromosome number of 34. The investigated species of Amaranthus may be organized into two groups upon the basis of haploid chromosome numbers, i.e., one group in which n = 16 and another in which n = 17.

MATERIALS AND METHODS

Herbarium Study

Herbarium specimen sheets of *Amaranthus albus*, *A. californicus*, *A. graecizans*, *A. hybridus*, *A. powellii*, and *A. retroflexus* of the world collection of the U. S. National Herbarium (Smithsonian Institution, Washington, D.C.) and of the Herbarium of Montana State University were studied to obtain information about habitats, morphological variation, phenology and distribution.

Field Collection

Specimens of *A. albus*, *A. californicus*, *A. graecizans*, *A. hybridus*, *A. powellii*, and *A. retroflexus* were collected in Montana during July and September of 1972. These specimens were used for analysis of morphological characters. The location, habitat, and the collection date of each specimen were recorded.

Morphological Character Study

Roots, stems, leaves, inflorescences, flowers, and seeds of each species were examined, measured, drawn and photographed, as described below:

Roots: The color and system of roots were determined by gross inspection. The depth of the roots was measured with a metric ruler.

Stems. The colors, textures and branching patterns of the stems were determined by gross inspection. The statures of the stems were measured with a metric ruler.

Leaves. The colors, textures and the shapes of the leaves of each species were determined by gross inspection. The sizes of the leaves were measured with a metric ruler.

The leaves were cleared for study of venation. Leaves were first immersed in a beaker of hot water, and then chlorophyll was removed by placing the leaves in hot 70% alcohol. Then the leaves were placed in petri dishes containing approximately a 2.5% aqueous NaOH solution for a week until all parts appeared translucent. The clearing solution was poured off and the leaves were rinsed several times in tap water. A strong aqueous solution of chloral hydrate (250 gm chloral hydrate in 100 ml water) was added to the petri dishes. After a few days, the materials became nearly transparent. They were very cautiously washed in several changes of distilled water. The materials were passed through the following dehydration series:

a. 50% alcohol for 5 min.

b. 70% alcohol for 5 min.

c. 95% alcohol for 5 min.

d. 100% alcohol for 5 min.

e. 100% alcohol for 10 min.

f. 100% alcohol for 10 min.

g. 1:1 absolute alcohol and xylene for 10 min.

h. 1:1 absolute alcohol and xylene for 10 min.

The cleared leaves were mounted on microscope slides with clove oil and were studied unstained under the dissection microscope at 25X. The number of paired major veins in the leaves were counted and patterns of venation were drawn.

Inflorescences and flowers. The inflorescences of the species were examined and measured in the metric system.

The flowers of each species were examined with optical aid of a dissection microscope. The number of bracts, sepals, ovaries and stigmas of the pistillate flowers and stamens of the staminate flowers were counted. The pistillate flowers, staminate flowers, bracts, sepals, ovaries and stamens were measured in the metric system and were drawn. The floral diagram of the pistillate flowers and the staminate flowers were constructed for each species.

Pollen grains. Raw pollen grains of each species were mounted in water, examined under the compound microscope, measured with a calibrated ocular-micrometer and drawn.

Seeds. Mature seeds were collected separately for each species during July and September of 1972. They were examined by gross

inspection and measured with a metric ruler under a dissection microscope and then drawn.

Seed Germination

After all seeds were stored for nine months, fifty seeds each of A. albus, A. californicus, A. graecizans, A. hybridus, A. powellii and A. retroflexus were placed on square towel papers and moistened with distilled water in square boxes (13 x 13 cm). The boxes were placed in the refrigerator at the temperature about 40° F for five days. Then the boxes were moved to the seed germinater alternating conditions of 8 hours light (at 59° F) and 16 hours dark (at 77° F).

RESULTS

Herbarium Study

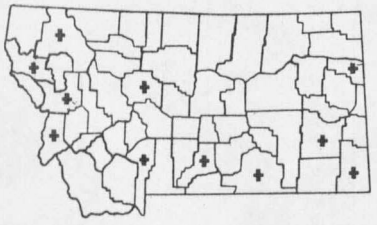
The genus *Amaranthus* grows throughout the United States and many countries in the world. *A. albus*, *A. californicus*, *A. graecizans*, *A. hybridus*, *A. powellii*, and *A. retroflexus* have been collected from 22, 7, 28, 17, 6, and 36 states of the United States, respectively. The distribution of collections in Montana is shown by maps (see Fig. 1). The maps are based upon both the accessioned herbarium collections studied and the personal observation and collection of the author.

The habitats of *Amaranthus* plants are usually waste places or cultivated fields. As they have been found, *A. albus*, *A. graecizans*, *A. hybridus*, *A. powellii*, and *A. retroflexus* grow at altitudes of about 732-2227 meters (2400-7300 feet), 348-1830 meters (1440-6000 feet), 336-2715 meters (1100-8900 feet), 1235-1983 meters (4050-6500 feet) and 290-1830 meters (950-6000 feet), respectively.

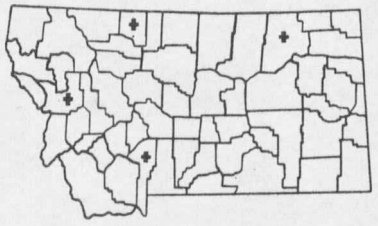
The herbarium specimens of these species collected in the United States were dated between July and November (*A. albus*), July and September (*A. californicus* and *A. powellii*), July and October (*A. graecizans* and *A. hybridus*), May and November (*A. retroflexus*).

Field Collection

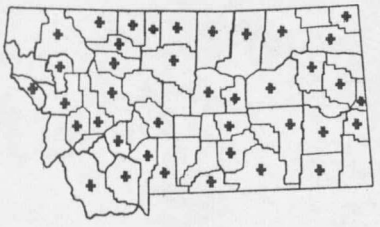
Six species of *Amaranthus* have been found in Montana: *A. albus*, *A. californicus*, *A. graecizans*, *A. hybridus*, *A. powellii*, and



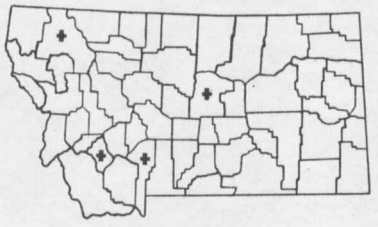
A. albus



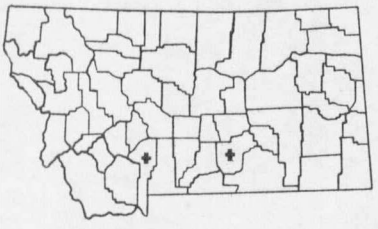
A. californicus



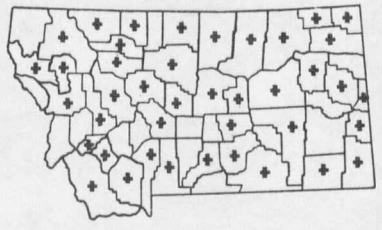
A. graecizans



A. hybridus



A. powellii



A. retroflexus

Fig. 1. Distribution maps of six taxa of Amaranthus occurring in Montana. A "+" symbol within a county indicates a recorded collection from that county.

A. retroflexus. They are found along roadsides, waste areas, and on cultivated lands.

Morphological Character Study

The morphological characteristics of roots, stems, leaves, inflorescences, bracts, flowers, fruits, and seeds of each species are compared in Table 1 and plates (Figs. 2 to 7). Each species is described based on morphological characteristics (see pages 27 to 44). A key has been constructed for separating the six species of Amaranthus of Montana (pages 55 and 56).

Pollen grains. The results of the measurement of the pollen grain of the six species of Amaranthus were that the pollen grains of A. albus and A. powellii range from 0.015-0.020 mm in diameter; of A. californicus, A. graecizans and A. powellii range from 0.018 to 0.022 mm in diameter; of A. retroflexus range from 0.025-0.030 mm in diameter. The average of the sizes of the pollen grains of each species have been illustrated in Table 1.

Seed Germination

After the seeds were placed in the seed germinater for a week, the numbers of seedlings of each species were counted. The percentages of seed germination were shown in Table 2.

Table I. Comparison of Characteristics of Montana Species of *Amaranthus*.

Character	Taxon	
	A. albus	*A. californicus*
Geographic Origin	Tropical America (Munz and Keck, 1959)	California, Nevada and northwestern North America (Munz and Keck, 1959)
Longevity	Annual	Annual
Root System		
Type	Excurrent	Excurrent
Size	About 4-12 cm deep	About 4-8 cm deep
Color	White	White
Stem		
Form	Rigid, branching freely, pyramidal shape	Branching from the base to form mats over the ground
Stature	Erect, to 6 dm tall	Prostrate, forming mats about 1-4 dm wide
Surface	Glabrous	Glabrous
Color	White	White
Leaf		
Outline	Spatulate to obovate	Spatulate
Apex	Mucronate	Mucronate
Margin	Undulate	Entire to undulate
Base	Decurrent	Decurrent
Size	Blade 0.5-2.5 cm long, 0.3-1.2 cm wide, about twice length of petiole	Blades 0.3-2 cm long, 0.1-0.7 cm wide, about 4 times as long as the petiole
Veins	Mostly 4 pairs	Mostly 2 or 3 pairs
Veinlets	Not prominent	Not prominent

Table I continued

Character	Taxon	
	A. albus	A. californicus
Surface	Glabrous	Glabrous
Color	Pale green	Upper surface green, lower surface and petiole purple
Inflorescences		
Type	Small axillary clusters	Small axillary clusters
Bracts		
Number	1	1
Shape	Lanceolate, acicular	Subulate, acicular
Size	About 2-2.5 mm long, twice as long as the sepals	About 2 mm long, almost twice as long as the sepals
Color	White, translucent, midnerve green	White, translucent, midnerve green
Pistillate Flower		
Sepals:		
Number	3, unequal	3, very unequal, 2 of them reduced as scales
Shape	Lanceolate, acute	Linear-lanceolate, acicular
Size	1-1.5 mm long	The largest one about 1 mm long
Color	White, translucent, midnerve green	White, translucent, midnerve green
Ovary	1 carpel, about 2 mm long, 1-1.3 mm wide, stigmas 3	1 carpel, about 2 mm long, about 0.8-1 mm wide stigmas 3

Table I continued

Character	Taxon	
	A. albus	A. californicus
Staminate Flower		
Sepals:		
Number	3, equal	3, equal
Shape	Lanceolate, acute	Linear-lanceolate, acicular
Size	1-1.5 mm long	About 1 mm long
Color	White, translucent, midnerve green	White, translucent, midnerve green
Anthers:	Versatile	Versatile
Number	3	3
Pollen	Spherical, about 0.017 mm in diameter	Spherical, about 0.020 mm in diameter
Fruit	1 seeded, circumscissile utricle	1 seeded, circumscissile utricle
Seed		
Color	Smooth, shiny, dark brown	Smooth, shiny, dark brown
Shape	Discoid	Discoid
Size	About 1 mm in diameter	About 0.8-1 mm in diameter

Table I continued

Character	Taxon	
	A. graecizans	A. hybridus
Geographic Origin	Eastern North America (Linn, 1753)	Eastern North America, Central America, and northern South America (Sauer, 1967)
Longevity	Annual	Annual
Root System		
Type	Excurrent	Excurrent
Size	About 3-15 cm deep	About 10-15 cm deep
Color	White	White
Stem		
Form	Branching from the base, spreading over the ground	Branching freely, erect, straight, rigid
Stature	Prostrate, mats to 10 dm wide	Erect to 9 dm tall
Surface	Glabrous	Glabrous
Color	Pale green, tinged with red	Pale green, tinged with red
Leaf		
Outline	Spatulate to obovate	Mostly rhombate
Apex	Retuse to mucronate	Acute to mucronate
Margin	Entire to undulate	Undulate
Base	Decurrent	Oblique
Size	Blade 0.5-4 cm long, 0.5-1.8 cm wide, about 4 times as long as the petiole	Blade 1.5-8 cm long, 0.7-3.5 cm wide, less than twice as long as the petiole
Veins	Mostly 5 pairs	Mostly 8 pairs

Table I continued

Character	Taxon	
	A. graecizans	A. hybridus
Veinlets	Not prominent	Visible but not prominent
Surface	Glabrous	Glabrous
Color	Pale green	Dark green
Inflorescence		
Type	Small axillary clusters	Terminal or axillary cylindrical spikelike panicle
Bract		
Number	1	1
Shape	Lanceolate, acicular	Lanceolate, tapering to spine tip
Size	About 1.5-2.5 mm long, about half as long as sepal	About 4-5 mm long, about twice or more as long as sepal
Color	White, translucent, midnerve green	White, translucent, midnerve green
Pistillate Flower		
Sepals:		
Number	5, unequal	5, about equal
Shape	Lanceolate, spine tip	Lanceolate, acute
Size	About 2.5-3.5 mm long	About 2 mm long
Color	White, translucent, midnerve green	White, translucent, midnerve green
Ovary	1 carpel, about 3 mm long, about 1.5-2 mm wide, stigmas 3	1 carpel, about 2 mm long and 0.8-1 mm wide, stigmas 3

Table I continued

Character	Taxon	
	A. graecizans	A. hybridus
Staminate Flower		
Sepals:		
Number	5, unequal	4-5 equal
Shape	Lanceolate, spine tip	Lanceolate, acute
Size	About 2.5-3.5 mm long	About 2 mm long
Color	White, translucent, midnerve green	White, translucent, midnerve green
Anther:	Versatile	Versatile
Number	3 or 4	3 or 4
Pollen	Spherical, about 0.020 mm in diameter	Spherical, about 0.020 mm in diameter
Fruit	1 seeded, circumscissile utricle	1 seeded, circumscissile utricle
Seed		
Color	Smooth, shiny, black	Smooth, shiny, black
Shape	Discoid	Discoid
Size	About 1.7 mm long	About 1.3 mm long

Table I continued

Character	Taxon	
	A. powellii	A. retroflexus
Geographic Origin	Eastern North America (Sauer, 1967)	Eastern North America (Sauer, 1967)
Longevity	Annual	Annual
Root System		
Type	Excurrent	Excurrent
Size	About 6-10 cm deep	About 6-15 cm deep
Color	Red	Red
Stem		
Form	Branching freely, straight	Branching freely, straight
Stature	Erect to 6 dm tall	Erect to 10 dm tall
Texture	Glabrous or lightly puberulent, rigid	Hairy, rough, rigid
Color	Pale green	Pale green
Leaf		
Outline	Ovate to rhombate	Ovate or oblanceolate
Apex	Acute to mucronate	Obtuse to retuse
Margin	Undulate	Denticulate to undulate
Base	Cuneate	Cuneate
Size	Blade 1-6.5 cm long, 0.5-3 cm wide, about twice as long as the petiole	Blade 1-10 cm long, 1-6 cm wide, about twice as long as the petiole
Veins	Mostly 8-12 pairs	9-12 pairs
Veinlets	Prominent	Prominent
Surface	Almost glabrous	Hairy
Color	Pale green	Pale green to dark green

Table I continued

Character	Taxon	
	A. powellii	A. retroflexus
Inflorescence		
Type	Terminal or axillary cylindrical spikelike panicle	Terminal or axillary conical spikelike panicle
Bract		
Number	1	1
Shape	Linear-lanceolate, truncate at the base, spine tip	Lanceolate, spine tip
Size	About 5-6 mm long, about twice or more as long as sepals	About 4-5 mm long, about twice as long as sepals
Color	White, translucent, midnerve green	White, translucent, midnerve green
Pistillate Flower		
Sepal:		
Number	5, unequal	5, equal
Shape	Lanceolate, acute	Oblong, rounded-emarginate with a very shortly excurrent midnerve
Size	About 2-3 mm long	About 2 mm long
Color	White, translucent, midnerve green	White, translucent, midnerve green
Ovary	1 carpel, about 3 mm long and 1-1.2 mm wide, stigmas 3	1 carpel, about 2-2.5 mm long, 1-1.4 mm wide, stigmas 3
Staminate Flower		
Sepal:		
Number	3-5, unequal	5, equal

Table I continued

Character	Taxon	
	A. powellii	*A. retroflexus*
Shape	Lanceolate, acute	Oblong, rounded-emarginate with a very shortly excurrent midnerve
Size	About 2-3 mm long	About 2 mm long
Color	White, translucent, midnerve green	White, translucent, midnerve green
Anther:	Versatile	Versatile
Number	3 or 4	5
Pollen	Spherical, about 0.017 mm in diameter	Spherical, about 0.027 mm in diameter
Fruit	1 seeded, circumscissile utricle	1 seeded, circumscissile utricle
Seed		
Color	Smooth, shiny, black	Smooth, shiny, black
Shape	Oval	Oval
Size	About 1.4 mm long	About 1.3 mm long

Table II. Percentage of Seed Germination

Taxon	No. of seed	No. of seedlings	Percentage of germination
A. albus	50	20	40
A. californicus	50	22	44
A. graecizans	50	1	2
A. hybridus	50	13	26
A. powellii	50	14	28
A. retroflexus	50	38	76

SPECIES DESCRIPTIONS

Amaranthus albus L. Sp. Pl. 2nd. 1404. 1763

A. graecizans of auth. not of L.

Annual of pyramidal shape; taproot 4-12 cm long, white; stems rigid, glabrous, erect, freely branched, about 6 dm tall, whitish green; leaves usually numerous, pale green, the blades spatulate or obovate, about 0.5-2.5 cm long, 0.3-1.2 cm wide, apex mucronate, base decurrent, margin undulate, veins mostly 4 pairs, veinlets not prominent, the petioles 0.5-2.5 cm long; monoecious; flowers in small axillary clusters; bracts lanceolate, acute, about 2-2.5 mm long; sepals of the staminate flowers 3, all about 1-2 mm long, lanceolate, acute; sepals of the pistillate flowers 3, unequal, about 1-1.5 mm long; stamens 3, anthers versatile; ovary 1, stigmas 3; fruits greenish or purple; circumscissile, 1 seeded about 2 mm long and 1-1.3 mm wide; seeds discoid, about 1 mm in diameter, notched, smooth, shiny, dark brown.

Amaranthus californicus (Moq.)S. Wats. Bot. Calif. 2:42. 1880

Mengea californica Moq. in D.C. Prodr. 132:270. 1849

Amaranthus carneus Greene, Pittonia 2:105. 1890

Amaranthus albomarginatus Uline and Bray, Bot. Gaz. 19:318. 1894

Annual; taproot 4-8 cm long, white; stems not rigid, glabrous, prostrate, much branched from the base, usually slender, forming mat up to 4 dm wide, pale green and tinged with red; leaves numerous, pale

Fig. 2. Amaranthus albus

A. Pistillate flower, X 15

B. Staminate flower, X 15

C. Sepal, X 15

D. Bract, X 15

E. Leaf, X 1.5

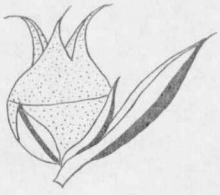
F. Seed in front view, X 15

G. Seed in side view, X 15

H. Floral diagram of a pistillate flower

I. Floral diagram of a staminate flower

J. Plant of A. albus, X 1/6



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B



C



D



E



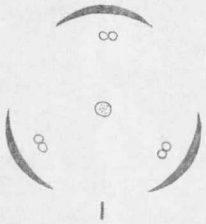
F



G



H



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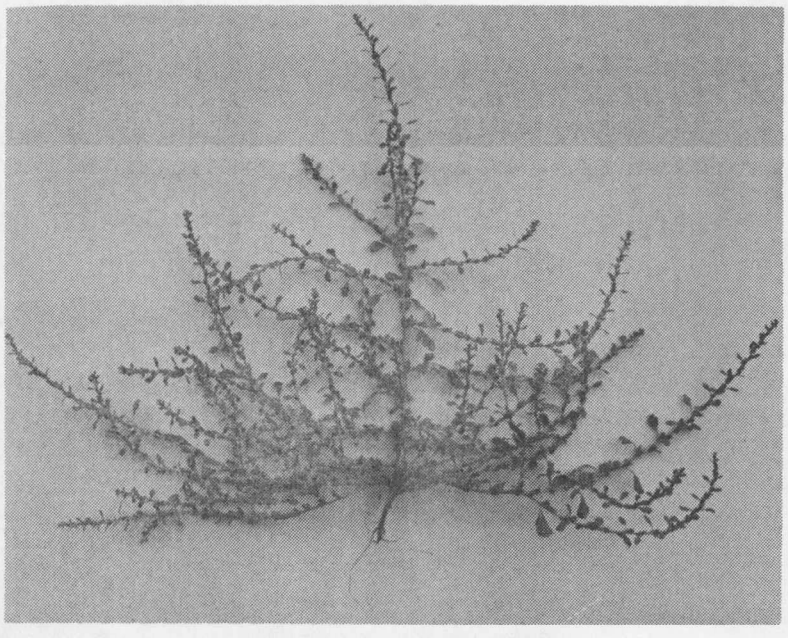


J

green, usually with purple under-surface, glabrous, the blades spatulate, 0.3-2 cm long, 0.1-0.7 cm wide, apex obtuse, midnerve exceeded, base decurrent, margin usually undulate, veins mostly 3 pairs, veinlets not prominent, the petioles about 0.2-1.5 cm long; monoecious; flowers in small axillary clusters; bracts lanceolate, acute, subulate-tipped, about 2 mm long; sepals of the staminate flowers 3, about equal, lanceolate, about 1 mm long; sepals of the pistillate flowers 3, unequal, one narrowly lanceolate, the others usually reduced or absent; stamens 3, anthers versatile; ovary 1, stigmas 3; fruits greenish or purple, circumscissile, 1 seeded about 2 mm long and 1 mm wide; seeds flat; discoid, about 0.8 mm in diameter, notched, smooth, shiny, dark brown.

Amaranthus graecizans L. Sp. Pl. 990. 1753

A. albus L. Syst. ed. 10. 2:1268. 1759

Pyxidium graecizans Moench, Meth. 359. 1794

A. leucanthus Raf. Fl. Ludov. 32. 1817

A. oleraceus Eaton, Man. ed. 2 152. 1818 (Not A. oleraceus L. 1753)

A. Blitum nanus Moq. in D.C. Prodr. 13^2:263. 1849

A. Blitum graecizans Moq. in D.C. Prodr. 13^2:263. 1849

A. albus paviflorus Moq. in D.C. Prodr. 13^2:264. 1849

Dimeiandra graecizans Raf. Moq. in D.C. Prodr. 13^2:264, as synonym. 1849

Galliaria albida Bubani Fl. Pyren. 1:185. 1897

Fig. 3. *Amaranthus californicus*

A. Pistillate flower, X 15

B. Staminate flower, X 15

C. Sepal, X 15

D. Bract, X 15

E. Leaf, X 1.5

F. Seed in front view, X 15

G. Seed in side view, X 15

H. Floral diagram of a pistillate flower

I. Floral diagram of a staminate flower

J. Plant of *A. californicus*, X 1/6



A



B



C



D



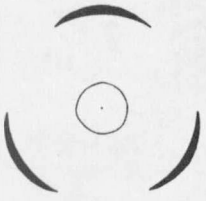
E



F



G



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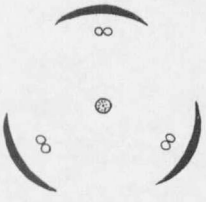

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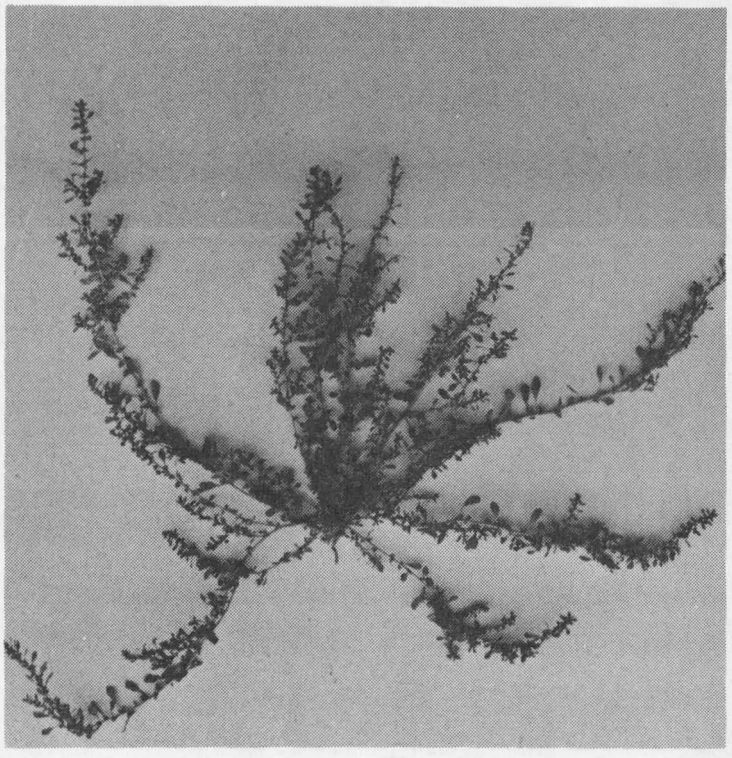

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A. albus puberurus Thellung in Asch. and Graebn. Syn. Fl. Mittel-Eur. 5:287. 1914

A. albus rubicundus Thellung in Asch. and Graebn. Syn. Fl. Mittel-Eur. 5:287. 1914

A. albus monosepalus Thellung, in Asch. and Graebn. Syn Fl. Mittel-Eur. 5:287. 1914

Galliaria graecizans Nieuwl. Am. Midl. Nat. 3:278. 1914

Annual; taproot 3-15 cm long, white; stems not rigid, glabrous, prostrate, much branched from the base, forming a mat up to 10 dm wide, greenish white sometimes tinged with red; leaves pale green, glabrous, spatulate or obovate, 0.5-4 cm long, 0.5-1.8 cm wide, apex varying from retuse to mucronate, base decurrent, margin varying from entire to undulate, veins mostly 5 pairs, veinlets rare; petioles slender, about 0.2-2 cm long; monoecious; flowers in small axillary clusters; bracts lanceolate, acute, about 1.5-2.5 mm long; sepals 5, unequal, lanceolate, spine tipped, the longest ones about 2.5-3 mm. long; stamens 5, anthers versatile; ovary 1, stigmas 3; fruits pale green, circumscissile, 1 seeded about 2.3 mm long and 2 mm wide; seeds lenticular-discoid, about 1.7 mm in diameter, notched, smooth, shiny, black.

Amaranthus hybridus L. Sp. Pl. 990. 1753

A. hypochondriacus L. Sp. Pl. 991. 1753

A. hecticus Willd. Hist. Amaranth. 25. 1790

A. strictus Willd. Hist. Amaranth. 27. 1790

A. laetus Willd. Hist. Amaranth. 28. 1790

Fig. 4. Amaranthus graecizans.

A. Pistillate flower, X 15

B. Staminate flower, X 15

C. Sepal, X 15

D. Bract, X 15

E. Leaf, X 1.5

F. Seed in front view, X 15

G. Seed in side view, X 15

H. Floral diagram of a pistillate flower

I. Floral diagram of a staminate flower

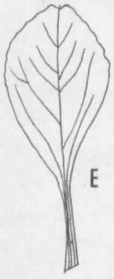
J. Plant of A. graecizans, X 1/6


A


B


C


D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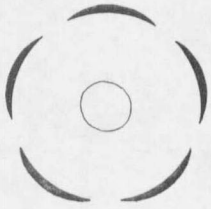
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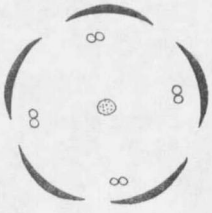
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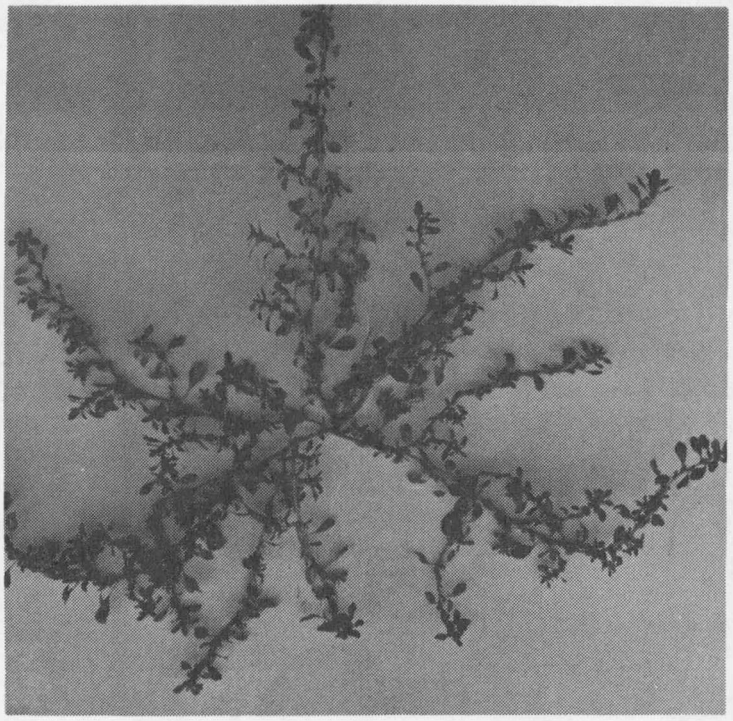
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A. chlorostachys Willd. Hist. Amaranth. 34. 1790

A. retroflexus hybridus A. Gray, Man. ed. 5. 421. 1867

A. retroflexus chlorostachys A. Gray, Man. ed. 5 422. 1867

A. chlorostachys hybridus S. Wats in A. Gray. Man. ed. 6. 428. 1890

A. hybridus hypochondriacus B. L. Robinson, Rhodora 10:32. 1908

A. hybridus chlorostachys G. Beck, in Reichenb. Ic. Fl. Germ. 24:175. 1908

Galliaria hybridus Nieuwl. Am. Midl. Nat. 3:278. 1914

Annual; taproot 10-15 cm long, white; stems rigid, glabrous, erect, freely branched, about 9 dm tall, pale green, frequently tinged with red; leaves usually numerous, dark green, glabrous, the blades mostly rhombate, about 1.5-8 cm long, 0.7-3.5 cm wide, apex varying from acute to mucronate, base oblique, margin undulate, veins mostly 8 pairs, the petioles slender about 1-6 cm long; monoecious; flowers in terminal or axillary cylindrical spikelike panicles which are about 2-10 cm long; bracts lanceolate, tapering to a spine tip, about 4-5 mm long; sepals 5, about equal, lanceolate, acute, about 2 mm long; stamens 3 or 4, anthers versatile; ovary 1, stigmas 3, fruits pale green or brown, circumscissile, 1 seeded 1.5-2 mm long and 1 mm wide; seeds oval, about 1.3 mm long, notched, smooth, shiny, black.

Amaranthus powellii S. Wats. Proc. Am. Acad. 10:347. 1875

A. obovatus S. Wats. Proc. Am. Acad. 12:275. 1877

Fig. 5. *Amaranthus hybridus*

A. Pistillate flower, X 15

B. Staminate flower, X 15

C. Sepal, X 15

D. Bract, X 15

E. Leaf, X 1.5

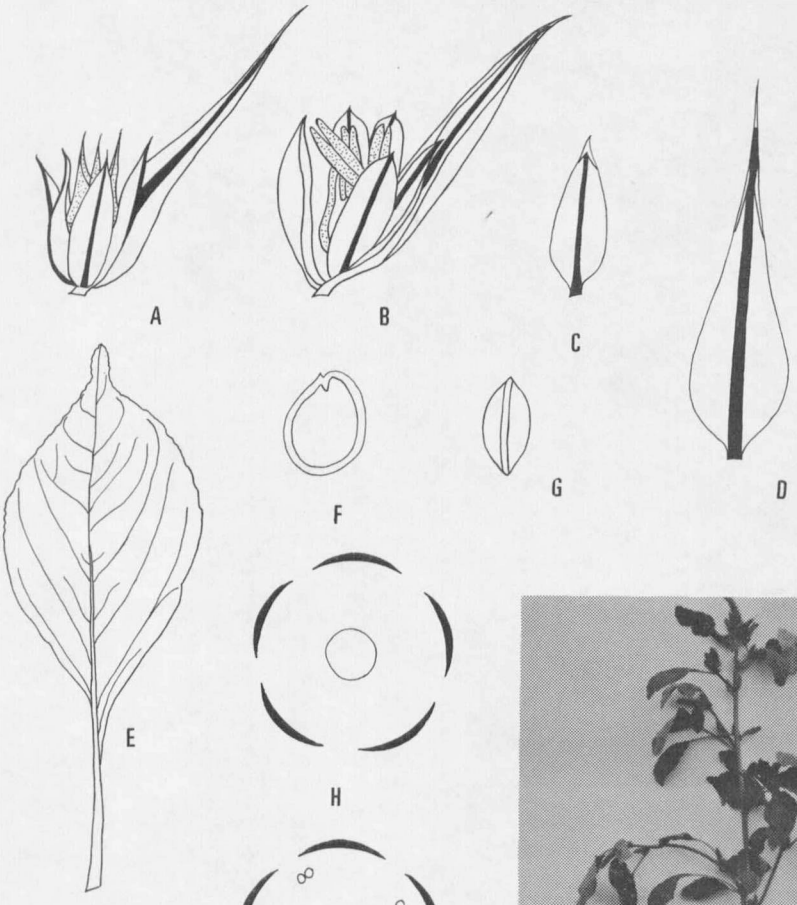
F. Seed in front view, X 15

G. Seed in side view, X 15

H. Floral diagram of a pistillate flower

I. Floral diagram of a staminate flower

J. Plant of *A. hybridus*, X 1/6





J

A. chlorostachys pseudoretroflexus Thellung, Viert. Nat. Ges. Zurich 52:443. 1970

Annual; taproot 6-10 cm long, red; stems rigid, glabrous or lightly puberulent, erect, simple or freely branched, stout, frequently ridged, about 2-6 cm tall, pale green often tinged with red; leaves pale green, glabrous or puberulent, the blades ovate or rhombate, about 1-7 cm long, 0.5-3.5 cm wide, apex acute or mucronate, base cuneate, margin undulate, veins mostly 8 or 9 pairs, veinlets prominent, the petioles 1-4 cm long; monoecious; flowers in terminal or axillary cylindrical spikelike panicles which are about 2-10 cm long; bracts linear-lanceolate, truncate at the base, spine-tipped, about 5-6 mm long; sepals of staminate flowers 4, about equal, lanceolate, acute, about 2-3 mm long; sepals of the pistillate flowers 5, unequal, some as long as the ovary and some longer; stamens 3 or 4, anthers versatile; ovary 1, stigmas 3; fruits pale green, circumscissile, 1 seeded about 3 mm long and 1-1.2 mm wide; seeds oval about 1.4 mm long, notched, smooth, shiny, black.

Amaranthus retroflexus L. Sp. Pl. 991. 1753

A. spicatus Lam. Fl. Fr. 3:192. 1778

A. recurvatus Desf. Gat. Hort. Par. ed. 3. 309. 1829

A. Delilei Richt. and Loret, Bull. Soc. Bot. Fr. 13:316. 1866

Galliaria scabra Bubani, Fl. Pyren. 1:187. 1897

Fig. 6. Amaranthus powellii

A. Pistillate flower, X 15

B. Staminate flower, X 15

C. Sepal, X 15

D. Bract, X 15

E. Leaf, X 1.5

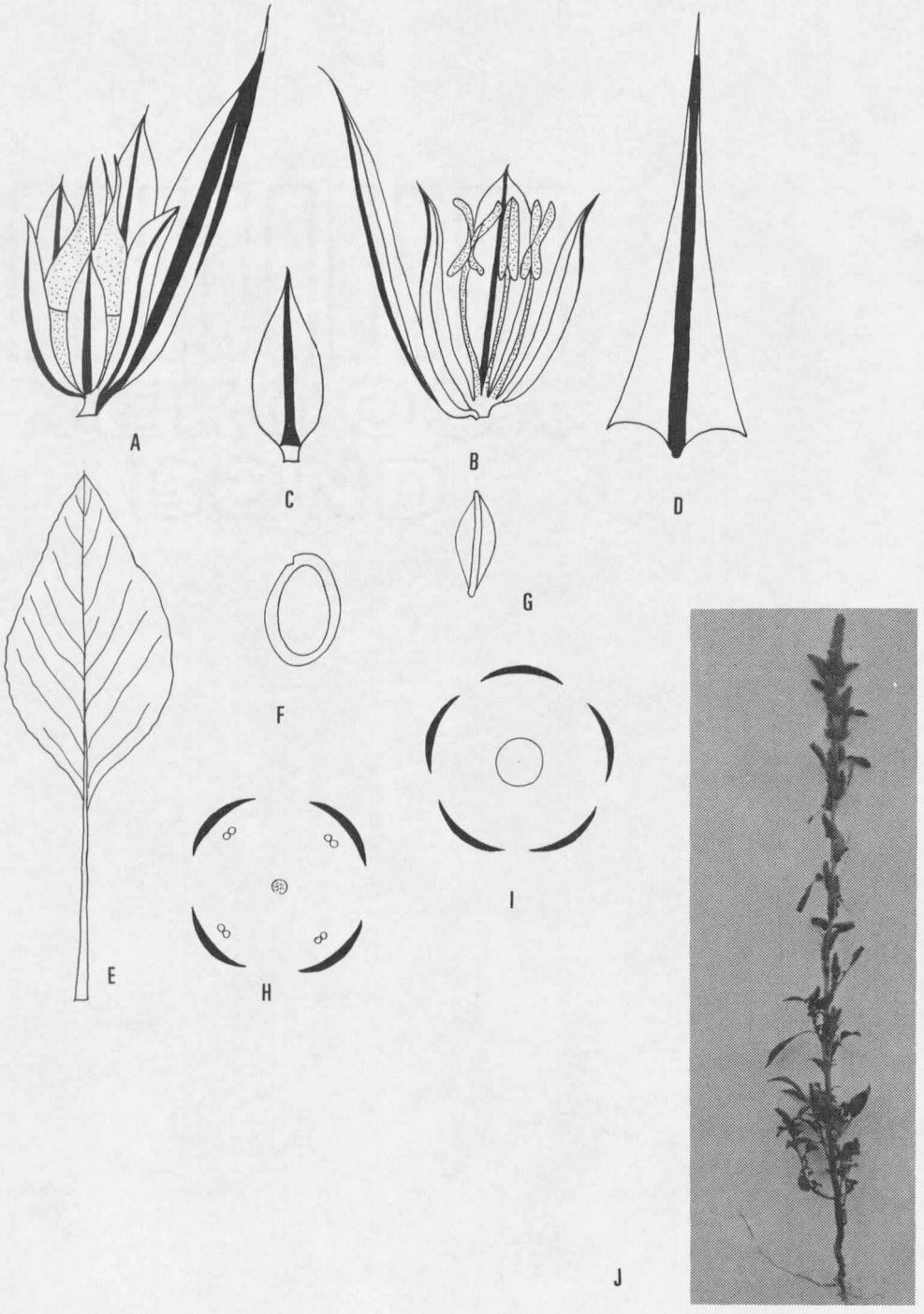
F. Seed in front view, X 15

G. Fruit in side view, X 15

H. Floral diagram of a pistillate flower

I. Floral diagram of a staminate flower

J. Plant of A. powellii, X 1/6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Galliaria retroflexus Nieuwl. Am. Midl. Nat. 3:278. 1914

Annual; taproot 6-15 cm long, red; stems rigid, hairy, erect, freely branched, stout, about 3-10 dm tall, pale green, leaves pale green, hairy, the blades ovate or oblanceolate, about 1-10 cm long, 1-6 cm wide, apex obtuse or retuse, base cuneate, margin varying from denticulate to undulate, veins mostly 9 pairs, veinlets prominent, the petioles about 1-8 cm long, hairy; monoecious; flowers in terminal or axillary conical spikelike panicles which are about 2-10 cm long; bracts lanceolate, spine-tipped, about 4-5 mm long; sepals 5, about equal, ovate-oblong to lanceolate, rounded to emarginate with a very shortly excurrent midnerve, about 2-3 mm long; stamens 5, anthers versatile; ovary 1, stigmas 3; fruits greenish, circumscissile, 1 seeded about 2 mm long and 1-1.4 mm wide; seeds oval, about 1.3 mm long, notched, smooth, shiny, black.

Fig. 7. *Amaranthus retroflexus*

A. Pistillate flower, X 15

B. Staminate flower, X 15

C. Sepal, X 15

D. Bract, X 15

E. Leaf, X 1.5

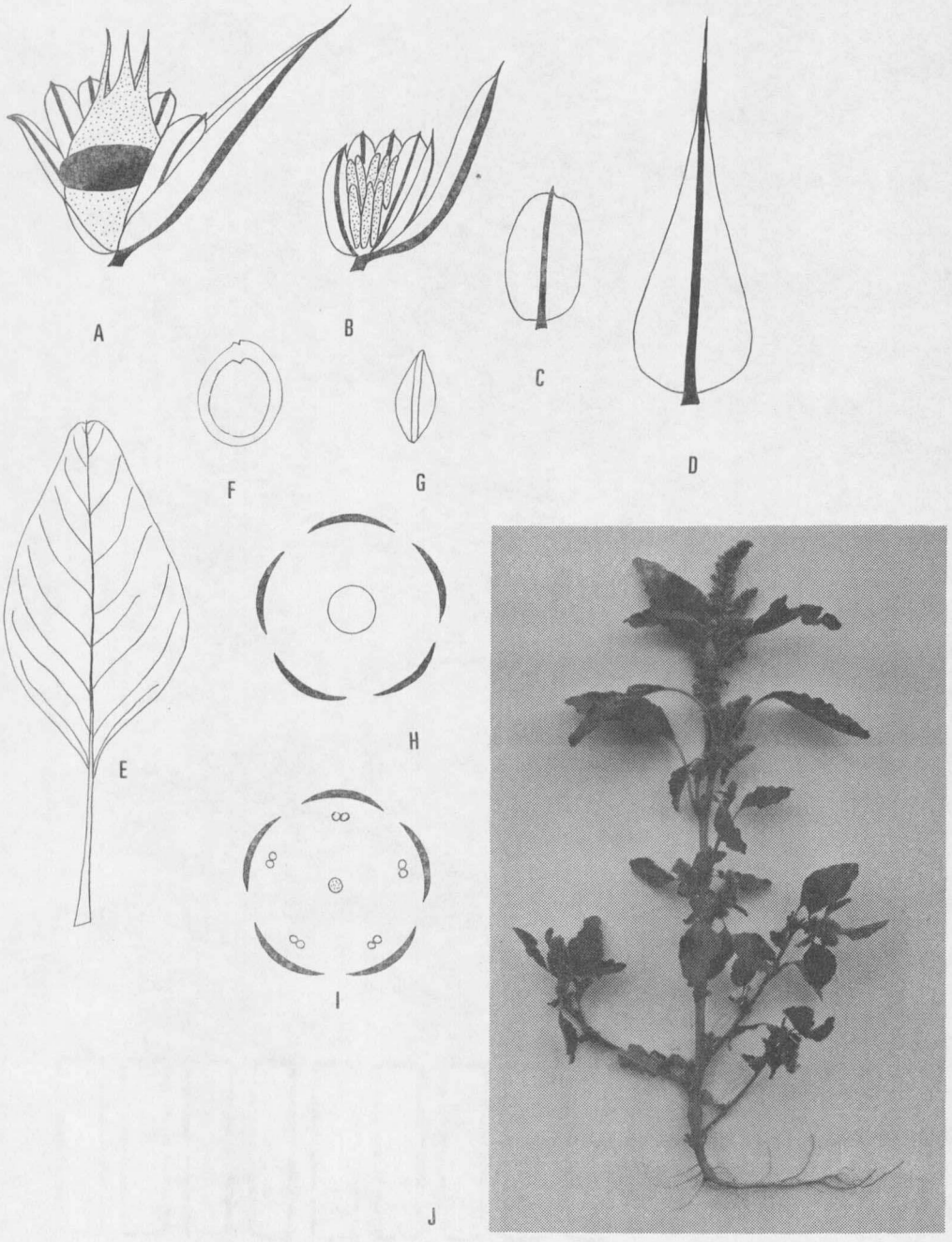
F. Seed in front view, X 15

G. Seed in side view, X 15

H. Floral diagram of a pistillate flower

I. Floral diagram of a staminate flower

J. Plant of *A. retroflexus*, X 1/6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DISCUSSION

Herbarium Study and Field Collection

An inventory of collection locations of herbarium specimens of the six studied species of *Amaranthus* was not available, so this was undertaken as a part of this study. According to the location of collections of herbarium specimens of the six studied species from the National Herbarium of the Smithsonian Institution of Washington, D.C. and from the herbarium of Montana State University, *Amaranthus retroflexus* is the most widely collected in the United States and in Montana. These data suggest that *A. retroflexus* is conspicuous and probably grows most abundantly and has the widest distribution of the six species here in the United States, and that *A. powellii* probably is uncommon in the United States.

A. powellii had never been collected before in Montana. It was found in Bozeman (Gallatin County) and in Laurel (Yellowstone County) in this study. Voucher Specimens (P. Sirirugsa No.'s 33,42) are deposited in the herbarium of Montana State University.

Based on the location of collections of herbarium specimens of *Amaranthus* species of Montana, *A. graecizans* and *A. retroflexus* are the most widely collected species in Montana, and therefore appear to occur throughout the state (see distribution maps, Figure 1).

Dates of Collection

Herbarium specimens of A. retroflexus in flowering or fruiting stage represent the widest range of time, from May to November in the United States. Although most specimens of the various species in Montana have been collected in July and August, the author has observed mature plants from June to October.

Morphological Characteristics

The statures of the stems of the genus Amaranthus in Montana represent two types: those with erect stems (A. albus, up to 6 dm tall; A. hybridus, up to 9 dm tall; A. powellii, up to 6 dm tall and A. retroflexus, up to 10 dm tall) and those with prostrate stems (A. californicus, 1-4 dm wide; A. graecizans, 10 dm wide). These results are approximately the same as the record of Booth and Wright (1966). However, Hitchcock (1964) recorded that A. albus is up to 10 dm tall, A. powellii is up to 2 m tall, A. retroflexus is up to 5-10 (20) dm tall, A. californicus is up to 6 dm broad and A. graecizans is up to 1 m broad.

All erect stemmed plants are relatively large leaved with leaf blades usually more than 3 cm long, except A. albus which is small-leaved with leaf blades less than 3 cm long. The leaves of A. hybridus A. powellii and A. retroflexus are similar to each other in being rhombate or obovate in shape and in having approximately the same number of dominant veins, about 8-10 pairs. The shapes of the leaves of these

three species in Montana have been recorded as lanceolate to ovate (A. hybridus), lanceolate or ovate (A. powellii) and ovate (A. retroflexus) (Booth and Wright, 1966). The dominant veins of the leaves had never been recorded before. The leaves of A. retroflexus are prominent hairy and can be distinguished from those of the other species by this character.

Three species, A. albus, A. californicus and A. graecizans are small leaved with leaf blades less than 4 cm long. The blade of A. californicus is the smallest one in this group, about 0.3-2 cm long; of A. albus is about 0.5-2.5 cm long; of A. graecizans is about 0.5-4 cm long. These results are different from the publication of Booth and Wright (1966) that published that the blades of A. albus are 1 to 2 cm long, of A. californicus are 1 to 3 cm long and of A. graecizans are 0.5-2.5 cm long. This showed that A. albus has the smallest leaf blades. The leaves of these three species are similar to each other in having spatulate shapes and not prominent dominant veins. However, sometimes A. albus and A. graecizans have obovate leaves. Booth and Wright (1966) described the shapes of the leaves of A. albus as obovate to spatulate-oblong, A. californicus as ovate or spatulate, and A. graecizans as obovate to spatulate that are different from this study. These data suggest that the leaves are variable in shape.

The inflorescences of the genus Amaranthus of Montana represent two types. One is small terminal or axillary cluster (A. albus,

A. californicus and A. graecizans). The other is terminal or axillary spikelike panicle that can be divided into two types: the thick conically shaped (broad at base), 1-10 cm long, inflorescence of A. retroflexus and the slender cylindrical, 2-10 cm long, inflorescences of A. hybridus and A. powellii. In the Flora of Montana by Booth and Wright (1966), A. hybridus was reported to have a dense spike inflorescence, up to 15 cm long; and A. retroflexus dense spikes, 5-10 cm long.

All Montana species of Amaranthus are monoecious. Both pistillate and staminate flowers lack petals. All ovaries are hypogynous, one-carpellate and three-styled. These results are the same as Booth and Wright (1966) recorded in Flora of Montana.

Each flower of every species is subtended by one bract. Two small flowers are found each with its own bract, attached to the central flowers (see Figure 8). Formerly these lateral flowers were thought to be merely bracts of the central flower (Bailey, 1949; Rydberg, 1917).

The shapes of the bracts of A. californicus and A. powellii are the same, linear-lanceolate, of A. albus, A. graecizans, A. hybridus and A. retroflexus are the same, lanceolate. The bract of A. powellii is the longest one of all species, about 5-6 mm long. However, Booth and Wright's publication (1966) indicated that A. retroflexus has the longest bract, about 5-8 mm long.

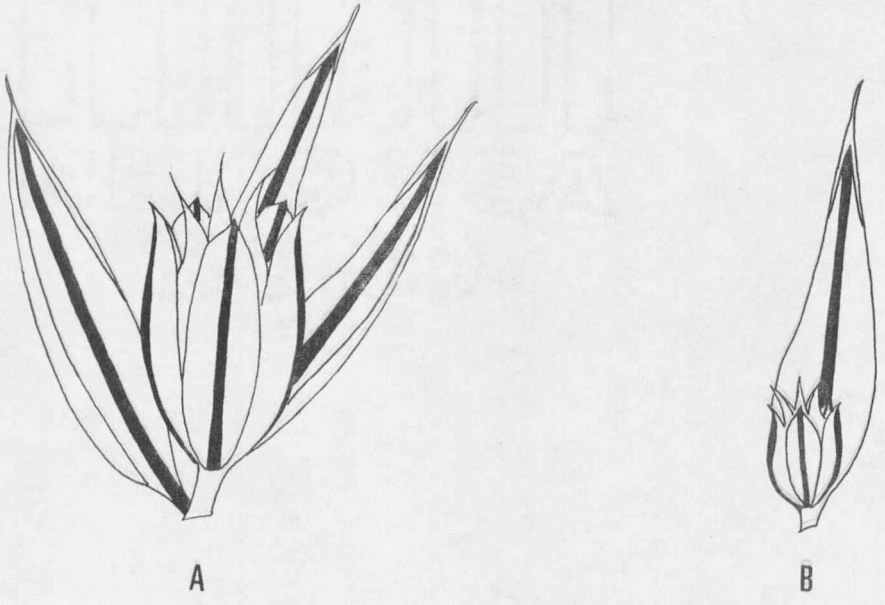

Fig. 8. Pistillate flowers of Amaranthus

A. Large central flower, X 15

B. Small attached flower, X 15

The sepals of the flowers of all species are shorter than the bracts except the sepals of A. graecizans which are about twice as long as the bract. The bract of A. graecizans is the shortest one of all species, about 1 mm long. The flower of A. graecizans have five unequal sepals. Two of the five sepals of each flower are larger than the other three and look like bracts. The bract itself is shorter than these sepals. The two larger sepals of the flower were thought to be bracts of the flower by some taxonomists (Uline and Bray, 1894; Harrington, 1954).

The pistillate flowers of A. californicus have three unequal sepals. Two of the three sepals are reduced to scales. However, it was recorded that sometimes the two reduced scalelike sepals are not present (Booth and Wright, 1966; Hitchcock et al., 1964). Three anthers of each staminate flower of A. californicus have been found. However, Booth and Wright (1966) recorded that there are 1-2 stamens, Hitchcock et al. (1964) recorded that there are 1-3 stamens.

The flowers of A. retroflexus have five equal sepals, and the staminate flowers have five stamens. These results have been recorded by Booth and Wright (1966) and Uline and Bray (1894) before. The pistillate flowers of A. hybridus have five equal sepals, the staminate flowers have five unequal sepals and three or four stamens. However, Uline and Bray (1894) recorded that the staminate flowers of A. hybridus

have 5 stamens. The pistillate flowers of A. powellii have five unequal sepals, but the sepals of the staminate flowers vary from three to five. The numbers of sepals of this species have not been mentioned in the previous work on Amaranthus in Montana (Booth and Wright, 1966).

The pollen grains of A. retroflexus are the largest ones of all six species, about 0.027 mm in diameter. Those of A. californicus A. graecizans and A. hybridus are about 0.020 mm in diameter and the pollen grains of A. albus and A. powellii are about 0.017 mm in diameter. Wodehouse (1935) recorded that the pollen grains of A. graecizans are about 24.2 μ (0.0242 mm) in diameter, of A. hybridus are 26.8-28.5 μ (0.0268-0.285 mm) in diameter and of A. retroflexus are 23-25 μ (0.023-0.025 mm) in diameter. He did not mention the source of the specimens he examined. On observation under the light microscope, the internal morphological characteristics of the pollen grains of each species are alike (Figure 9). Pollen of Amaranthus retroflexus stained with a 5% acetocarmine solution revealed a generative nucleus and a vegetative nucleus. After staining with an IKI solution, starch grains were found, interpreted by an affinity for the stain. Sudan IV staining resulted in stain accumulation into discrete vacuolar areas. On the basis of this observation, it is believed that these vacuoles contained some lipids.

The shapes (oval) and sizes (about 1.3-1.4 mm long) of the seeds of A. hybridus, A. powellii and A. retroflexus are almost the

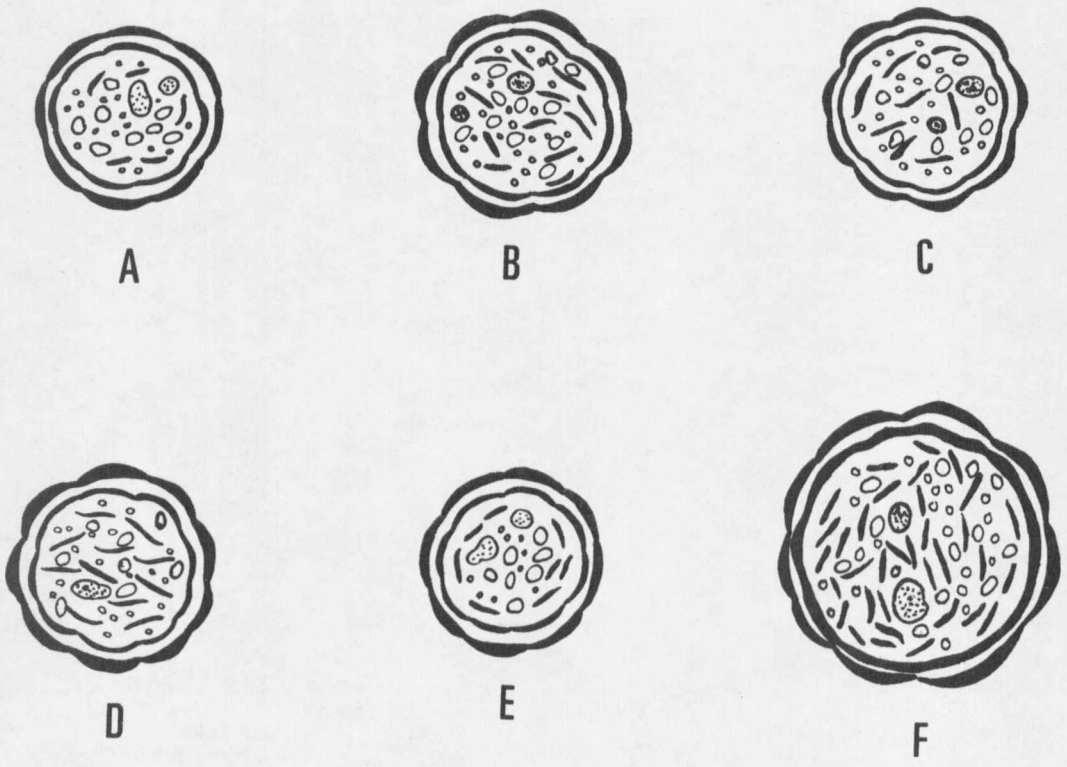

Fig. 9. Amaranthus pollen grains, median sect, X 1500

A. A. albus
B. A. californicus
C. A. graecizans
D. A. hybridus
E. A. powellii
F. A. retroflexus

same. The different sizes of the seeds of A. californicus (0.8-1 mm in diameter) and A. graecizans (about 1.7 mm in diameter), make it easy to distinguish between these two species if mature seeds are available. By Booth and Wright's measurement (1966), the seeds of A. californicus are 0.8 mm in diameter and of A. graecizans are 1.3 to 1.5 mm broad.

Previous keys to the Montana Species of Amaranthus (Booth and Wright, 1966) require plants in flowering condition for identification. The key to Montana species of Amaranthus of this study has been developed to try to use prominent vegetative characters as well as floral features, to separate the species. For example, A. hybridus and A. powellii are separable upon the basis of leaf texture as well as upon the floral bract shape and length. Therefore, both of these features are used in the present key. It is pertinent to point out that Booth and Wright (1966) used the length of sepals to separate A. retroflexus "sepals 2.5-4 mm long" and A. powellii "sepals 2-3 mm long" in their key. The length of the sepals of A. retroflexus that they reported is more than twice as great as the length of the sepals (about 2 mm) of A. retroflexus that has been found in this study.

Seed Germination

The seeds of A. retroflexus showed the highest percentage of germination, 76%. This indicates that the seeds of this species

germinate in this condition better than the others. The seed of A. graecizans exhibited only 2% germination under the same conditions.

KEY TO MONTANA SPECIES OF AMARANTHUS

1. Stem with a single erect central axis

   2. Flowers in short axillary clusters; leaf blades small, usually shorter than 3 cm long; stems slender, white, smooth . . . . A. albus

   2. Flowers in terminal or axillary spikelike panicles; leaf blades usually more than 3 cm long; stems slender or stout, pale green often red tinged, ridged.

      3. Stems and leaves hairy; panicle thick, conical, broad at base; sepals oblong, rounded-emarginate with a very shortly excurrent midnerve . . . . A. retroflexus

      3. Stems and leaves glabrous or lightly puberulent; panicles slender, cylindrical, not broad at base; sepals lanceolate, acicular

         4. Leaves lightly puberulent, (ovate or rhombate; sepals 3-5, unequal); floral bracts linear lanceolate, truncate at the base, 5-6 mm long . . . . A. powellii

         4. Leaves glabrous, (mostly rhombate; sepals 4 or 5, almost equal); floral bracts lanceolate, rounded at the base, 4-5 mm long . . . . A. hybridus

1. Stem with several nearly equal prostrate branches from the base, (no erect central stem)

5. Sepals 3; mature leaves generally short (2-3 cm long); seeds less than 1 mm in diameter (0.6-0.8 mm) . . . . A. californicus

5. Sepals 5; mature leaves generally long (4-6 cm long); seeds more than 1 mm in diameter (1.5-1.8 mm) . . . . A. graecizans

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