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Some Factors Affecting the Response of Spiny Aster to Herbicide Sprays

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METRIC UNITS — ENGLISH EQUIVALENTS

Metric Unit	*English Equivalent*
Centimeter	0.4 inch
Gram	0.035 ounce (weight)
Hectare	2.47 acres
Kilogram per hectare	0.89 pounds per acre
Kilometer	0.62 statute mile
Liter	0.26 gallon
Meter	3.28 feet
Microgram per gram	One part per million
Milliliter	0.034 ounce (volume)
Millimeter	0.04 inch
Degrees Celsius × 9/5 + 32	Degrees Fahrenheit

KEYWORDS: spiny aster/herbicide sprays/herbicide penetration/ecology/anatomy.

Contents

Summary

Spiny aster occurs as an incidental species on fertile bottomland range sites throughout most of Texas. However, on portions of the Coastal Prairie, spiny aster eliminates forage production on substantial areas of native rangeland. After initial invasion of rangelands, seed production does not appear to be important in development of spiny aster stands. Reproduction is primarily through vegetative propagation by rhizomes which allows spiny aster to tolerate top removal. Since spiny aster cannot be controlled with conventional mechanical treatments used on range and pastures, several herbicides and herbicide combinations were evaluated as broadcast foliar sprays applied to both shredded and undisturbed stands.

Applied in the fall, broadcast sprays of 2,4-D, dicamba, or picloram, alone or in combination at rates of 2.24 kilograms per hectare or less, did not effectively control spiny aster. Applied in spring when leaves were present on spiny aster stems, only picloram at 2.24 kilograms per hectare satisfactorily reduced spiny aster stem densities. Glyphosate, atrazine, paraquat, 2,4-D, or dicamba applied in spring at 2.24 kilograms per hectare or less did not control spiny aster. Shredding during the winter prior to application of herbicidal sprays in the spring substantially improved the initial response of spiny aster to all herbicides. However, control with sprays in combination with shredding was short-lived except where an established perennial grass was present to compete with the weed.

The apparent low susceptibility of spiny aster to foliar sprays is attributed to the low degree of penetration of topgrowth by herbicides. Herbicide translocation is also slow in spiny aster. Neither picloram nor 2,4-D could be detected in rhizomes up to 5 days after foliar application. Herbicide uptake by leaves and stems may be limited by small stomatal size and number, compared to other plants, but cuticle thickness is apparently not a factor.

Herbicide penetration of rapidly growing stems 2.5 months after shredding was slightly greater than that of live undisturbed stems. Stomatal densities of regrowth stem tips were about 10 percent greater than those of undisturbed stem tips, but stomatal aperture size did not differ. Increased initial control of spiny aster regrowth with herbicide sprays, compared to undisturbed growth, probably results from increased herbicide penetration and improved spray deposition and interception. Dead plant material accounts for about 50 percent of undisturbed spiny aster canopy; shredding removes the standing dead stems without substantially reducing the number of live stems in regrowth. Thus, spray effectiveness is not reduced by deposition on dead plant material.

Some Factors Affecting the Response of Spiny Aster to Herbicide Sprays

H. S. Mayeux, Jr., C. J. Scifres, and R. E. Meyer*

Botanical Description

Spiny aster (*Aster spinosus* Benth.), also called wolfweed or Mexican devil-weed, is a perennial plant that spreads by rhizomes and, consequently, occurs primarily in clumps or continuous stands rather than as individuals. Stems of spiny aster are slender, erect, and bright green (Figure 1). Stem height ranges from 0.5 to 2 meters, but usually averages about 1 meter. Dense stands develop in which stem densities exceed 100 stems per square meter. Short thorns, variable in size and number, occur on mature stems. The stems are apparently responsible for photosynthetic activity, since leaves are present for only a brief period in the spring (Figure 2). The oblong leaves are as long as 8 centimeters near the base of stems, but smaller, tapered leaves occur in the upper canopy.

Little is known about sexual reproduction of spiny aster. The flower heads are small, measuring about 1 centimeter across, and contain white ray and yellow disk florets. The flower heads occur throughout the summer and fall months. The seed (2500 per gram) is an achene equipped with a persistent pappus (tuft of hairs).

Distribution and Status as a Weed

Spiny aster occurs throughout the American Southwest and is common on roadsides and irrigated areas of northern Mexico. Correll and Johnston (5) describe the species as "locally very abundant" in the south and west half of Texas.

Spiny aster occasionally invades upland sites with clay soils of high water-holding capacity. More commonly, spiny aster occurs in small stands along waterways, lake shores, and other wet sites, even if periodically flooded. On portions of the Texas Coastal Prairie, however, spiny aster occurs in dense, continuous stands over extensive areas, excluding almost all other vegetation (Figure 3). Infested areas are primarily native rangeland. Sites dominated by spiny aster often are fertile bottomlands which receive additional water as runoff from surrounding upland sites. Thus, the impact of spiny aster as a weed is significant, even though the geographical area affected is relatively limited in size.

Spiny aster is a tenacious weed on sites where it is well adapted. Shredding several times a year for many years in succession or tillage associated with production of grain sorghum (*Sorghum vulgare* Pers.) has not eliminated spiny aster[1].

Although spiny aster is not considered an important forage plant, cattle occasionally graze succulent new growth. The authors have often observed browsing of spiny aster stem tips by white-tailed deer (*Odocoileus virginianus* Bod.).

Specific objectives of this research included investigations of aspects of spiny aster ecology and anatomy that are pertinent to its control with herbicidal sprays and the evaluation of selected herbicides and mixtures, alone and in combination with a mechanical pretreatment, for control of spiny aster.

METHODS AND MATERIALS

Study Area

Field studies were conducted near Bloomington in Calhoun County, Texas. All experiments were positioned within a level swale encompassing about 90 hectares. The swale receives runoff from surrounding areas of slightly higher elevation, but standing water does not persist during years of normal rainfall.

Vegetation in the swale consists of an almost pure stand of undisturbed spiny aster. Peripheral areas of the depression support sea oxeye daisy [*Borrichia frutescens* (L.) DC.] and Carolina wolfberry (*Lycium carolinianum* Walt.) in association with spiny aster. Although not common, a few herbaceous plants grow where spiny aster stem densities are low. These include an annual groundsel

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[1]Phillips, Tommy. 1975. Personal communication. Ranch manager, Greenlake Ranch, Victoria, TX 77015.

(*Senecio imparipinnatus* Klatt.), Missouri ironweed (*Vernonia missurica* Raf.), and barnyardgrass [*Echinochloa crusgalli* (L.) Beauv.]. A portion of the swale was plowed and seeded to kleingrass (*Panicum coloratum* L.) about 5 years prior to initiation of this research. A good stand resulted, but the grass is now heavily infested with spiny aster.

Soils of the swale are clays of the Victoria series (Typic Pellustert). Clay content is about 60 percent in the upper horizons. Soil reaction is basic, and the soil is slightly saline, with 2,180 parts per million of salts near the surface, increasing to 2,700 parts per million at 45 centimeters. Less than 3 percent organic matter occurs in the A horizon. No B horizon is apparent. The soil is calcareous throughout and very dark in color. Soils of this series are typically fertile.

Annual rainfall of the area averages 93.5 centimeters (Figure 4). The precipitation pattern is characterized by slight rainfall peaks in spring and fall. The mean maximum temperature for July is 33.3° Celsius, and the mean minimum temperature in January is 8.3° Celsius (2).

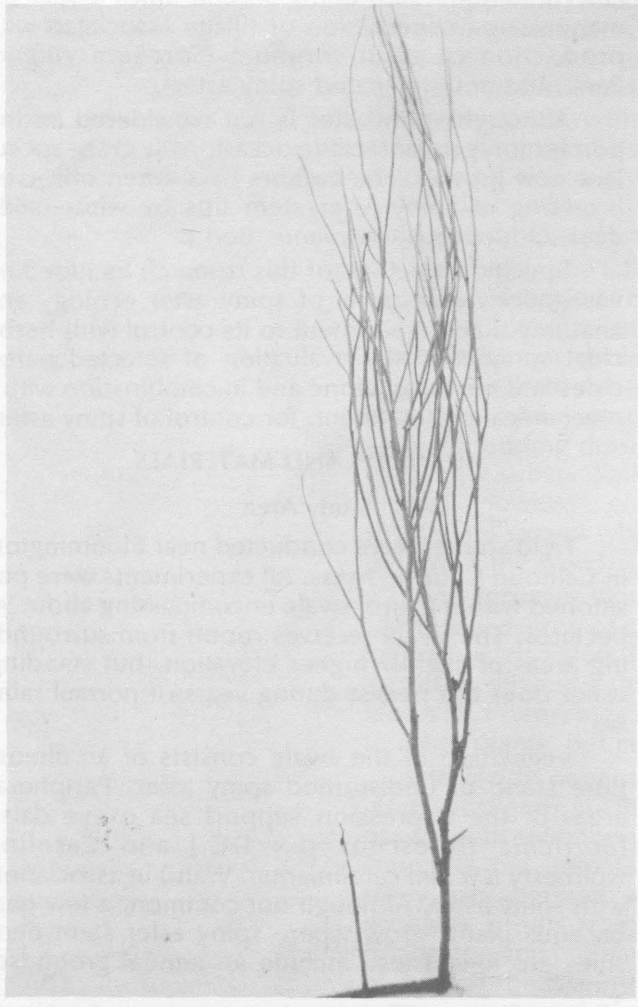

Figure 1. A leafless spiny aster shoot with rhizome and newly initiated stem.

Figure 2. Spiny aster stems photographed near Bloomington, Texas, in April, while leaves are present.

Autecological Observations

Although growth and phenology of spiny aster were not studied in detail, time and duration of leaf presence and stem growth were observed periodically during 1975 and 1976. During June of each year, numbers of new stems, overwintered stems, and standing dead stems were counted in 0.25-square-meter quadrats on both undisturbed and previously shredded stands.

The relative importance of sexual and vegetative reproduction was also evaluated. Flower heads on main stems and numbers of achenes per head were counted on plants in the field and in a greenhouse at College Station. Mature, filled achenes from both locations were tested for germinability at 20° Celsius for 16 hours and 30° Celsius for 8 hours with light. In March, 100 rhizome sections 10 to 20 centimeters long with at least two nodes were transplanted to the greenhouse. These were planted in 20-centimeter diameter pots with Victoria clay soil. Numbers of new stems and the time required for resprouting were recorded. Regrowth plants were maintained in a slathouse to provide leaves and stems for subsequent experiments.

Leaf and Stem Anatomy

Potted plants grown outdoors were the source of organs and tissues for study. Impressions of upper and lower leaf surfaces were obtained by the plastic stripping method (24). Impressions were also made of main stem and fine terminal stem surfaces. Numbers of stomata were counted within ten 0.05-square-millimeter areas on at least five leaves o stems with a light microscope. A filar micrometer eyepiece mounted on a light microscope was used to measure stomatal apertures.

Figure 3. A dense stand of spiny aster covering about 100 hectares near Bloomington, Texas; the stake in the foreground is 1.5 meters tall.

In general, the procedures of Johanson (11) and Sass (22) were followed in the preparation of permanent slide mounts of leaf and stem transections. Organs were fixed in a Craf solution and dehydrated in an ethanol-*tert*-butyl alcohol series. Tissues were embedded in Paraplast and 12- or 14-micrometer sections were cut with a rotary microtome. Tissue sections were stained for 30 minutes in safranin-0 and then for 5 minutes in fast green FCF. Transections were photographed with a 10- by 12.7-centimeter camera using transmitted light. To obtain micrographs of upper and lower leaf surfaces, samples were dehydrated, coated with gold, and photographed at 10 kilovolts in a Cambridge S-4 Stereoscan electron microscope.

Herbicide Penetration and Translocation

Leaves and stems of spiny aster were exposed to aqueous solutions of picloram (4-amino-3,5,6-trichloropicolinic acid) and 2,4-D [(2,4-dichlorophenoxy)acetic acid] to evaluate rate and extent of herbicide uptake (3). Leaves of sunflower (*Helianthus annuus* L.) were included as a reference, since sunflower is easily controlled with these herbicides. The objective of these experiments was to investigate potential morphological barriers to herbicide uptake by spiny aster.

Undamaged leaves of uniform size and maturity were removed from the same location on stems, between 4 and 10 centimeters from the growing tip. Spiny aster stems were collected from plants in the field during June. Stem sections, 20 centimeters long, were cut from the large, main portion of current-year shoots. Similar stem samples were collected from an undisturbed stand and from regrowth following shredding to a 4-centimeter stubble height 90 days previously. All stems were kept moist and transported over ice (but not frozen) to the laboratory.

Cut ends of spiny aster stem sections were dipped in paraffin wax and coated with stopcock grease to prevent herbicide movement through the open end. Six leaves of sunflower or spiny aster, two spiny aster main stem sections, or five spiny aster stem tips were suspended around the inside edges of 20-centimeter diameter culture dishes. Leaves or stems were adjusted so that the acropetal halves were immersed in herbicide solutions. The solutions (10^{-3} molar) were prepared with analytical grade picloram or 2,4-D acid in distilled water with pH ad-

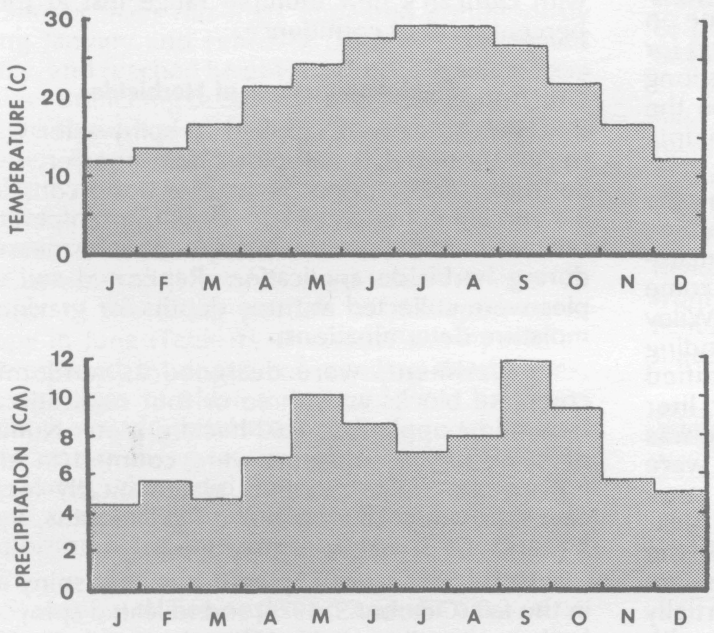

Figure 4. Average monthly temperature and precipitation at Victoria, about 22 kilometers from the spiny aster research area near Bloomington, Texas (1).

justed to 11 with potassium hydroxide. The herbicide solutions were then adjusted to pH 6.8 with hydrochloric acid. The solutions were slowly swirled and care was taken to maintain the immersed organs freely suspended in the solutions. After 2, 4, or 6 hours, the organs were washed in a stream of acidified acetone. Leaves and stem sections were cut at the solution line, and the immersed portions were blotted dry, weighed, and stored frozen.

Comparisons included herbicide uptake by leaves of the two species, and uptake by leaves, main stems, undisturbed stem tips, and stem tips from regrowth of spiny aster only. Each treatment was triplicated in each of two experiments. Hierarchical analyses of variance were conducted with herbicide as main effects, plant part as subplot effects, and time as the sub-subplot effects (25). Means were compared with Duncan's new multiple range test at the 95-percent level of confidence.

Rate of foliar herbicide uptake and extent of translocation to rhizomes were investigated at the Bloomington study site on March 12, 1976, when spiny aster was in full leaf, and again on June 24, 1976, when stems were leafless. Herbicide treatments consisted of either 1.12 kilograms per hectare of the potassium salt of picloram or 2.24 kilograms per hectare of diethylamine salt of 2,4-D applied in water with 0.5 percent (volume basis) commercial surfactant (containing sodium dodecyl, benzene sulfonate, trimethyl nonylether, and ethylene glycols). Treatments were applied in early morning to 16-square-meter plots with a back-pack sprayer.

In March, herbicide uptake was determined by removing four separate, random samples of 10 leaves each. Each sample was rinsed in 0.1 normal ammonium hydroxide (NH_4OH), blotted dry, and placed in plastic bags. Leaf rinses were also kept for analysis. Sampling was conducted immediately after herbicide application, after 8 hours, and then daily for 5 days. Terminal stems were collected in June on the same time schedule and rinsed as described for leaves. Rhizome samples, about 10 centimeters long and with large aerial stems, were collected on the same schedule. All samples were stored frozen until extraction and analysis.

Established techniques were followed for the extraction and preparation of samples containing picloram (4) and 2,4-D (10, 12) and for chromatographic determinations (12, 16). Stems and rhizome samples were cleaned of soil and ground in a Wiley mill. Picloram and 2,4-D were extracted by blending tissue samples with 30 or 60 milliliters acidified acetone (4 milliliters hydrochloric acid per liter acetone) for 2 minutes. The resulting macerate was filtered under vacuum, tissue and filter paper were blended a second time, and the filtrates were combined. After the acetone was evaporated to near dryness and 10 milliliters water were added, the aqueous solution was made basic with potassium hydroxide. Interfering compounds were partially removed by shaking in a separatory funnel with three, 30-milliliter diethylether washes. After acidification with hydrochloric acid, herbicides were extracted by shaking three times with 30-milliliter aliquots of ether. Extracts were combined and the ether evaporated.

Both herbicides were esterified with 8 milliliters boron trifloride-methanol solution (10 to 12 percent). Samples containing 2,4-D were briefly heated during methylation, but picloram samples were heated on an oscillating hotplate to near dryness (26). After cooling, herbicides were dissolved in 10 milliliters of distilled hexane.

Herbicide concentrations were determined with a Barber Coleman Model 5360 gas chromatograph with a radium-226 electron-capture detector and a column packed with 1.5 percent SE 30 Chromasorb 'W'. Prepurified nitrogen gas was used as carrier at a flow rate of 70 milliliters per minute. Injector, column, and detector temperatures for picloram were 260, 200, and 230° Celsius, respectively. Injector and detector temperatures were unchanged for 2,4-D determinations, but column temperature was adjusted to 185° Celsius.

Two microliters of the herbicide methyl ester-hexane solution were injected onto the column. Herbicide concentrations were determined by comparing peak heights to those of fortified samples. Recovery percentages of picloram and 2,4-D extracted from leaves and rinses were 96 and 86 percent, respectively. Herbicide recovery from rhizomes was about 70 percent.

Foliar herbicide uptake was expressed as the ratio of herbicide concentration in leaf tissue divided by the total herbicide concentration in tissue and rinse. Hierarchical analysis of herbicide uptake data included herbicide treatments or mechanical pretreatment as main plot effect and time periods as subplot effects. Mean differences were compared with Duncan's new multiple range test at the 95-percent level of confidence.

Field Applications of Herbicides

Herbicides were applied to spiny aster with a tractor-mounted, small-plot boom sprayer, which delivered 200 liters per hectare of water containing 0.5 percent commercial surfactant. Air temperature, relative humidity, and wind speed were measured during herbicide application. Replicated soil samples were collected at three depths for gravimetric moisture determinations.

Experiments were designed as randomized complete blocks with three or four replications of treatments applied to 0.02-hectare plots. Numbers of live spiny aster stems were counted in eight, 0.25-square-meter quadrats systematically located down the center of each plot at 7 to 9 months, 1 year, 2 years, and 3 years after treatment.

Herbicides were applied to leafless spiny aster in the fall (October 5, 1974) and to leafed spiny aster in the spring (March 20, 1975, and March 16, 1976).

Fall treatments included the dimethylamine salt of dicamba (3,6-dichloro-*o*-anisic acid), butoxyethanol ester of 2,4-D, and the potassium salt of picloram applied alone at 0.5, 1.12, and 2.24 kilograms per hectare. Also, dicamba or 2,4-D was combined with picloram at 1.12 and 2.24 kilograms per hectare total herbicide. Treatments applied in the fall, and atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-*s*-triazine], glyphosate [*N*-(phosphonomethyl)glycine], and paraquat (1,1'-dimethyl-4,4'-bipyridinium ion) were applied in the spring. Glyphosate, atrazine, and paraquat were applied at 1.12 and 2.24 kilograms per hectare.

A portion of the spiny aster stand was shredded to a height of 4 centimeters in March 1975. Leafless regrowth had reached 40 centimeters on June 2, 1975, when herbicides were applied. Dicamba, 2,4-D, glyphosate, and atrazine were applied individually at 1.12 and 2.24 kilograms per hectare. Picloram was applied at the lower rate only.

On June 17, 1976, herbicide treatments were applied to spiny aster regrowth following shredding during the previous winter within the portion of the swale seeded to kleingrass. Broadcast sprays were repeated on the same day in an adjacent area covered with dense, undisturbed spiny aster.

RESULTS AND DISCUSSION

Autecological Observations

Leaves appeared on spiny aster in the field during late January in both 1975 and 1976 and were present until mid-April. Overwintered stems bore widely scattered groups of leaves that resembled rosettes and occurred only in the upper portions of the canopy. Leaves on developing stems occurred singly, alternately, and were uniformly distributed from stem base to tip.

Shoots from rhizomes appeared continuously during January and February (Figure 5), elongated rapidly, and reached heights of about 50 centimeters by June. Branching occurred during this period, and a single shoot had as many as 20 stem tips by midsummer. Progressive narrowing of diameter as upward growth and branching progressed transformed the stems from thick and fleshy to a fine, flexible appearance.

Current year's growth accounted for over 75 percent of the living portion of the spiny aster canopy in June (Table 1). Live stem density was almost equaled by density of standing dead stems. Although ages of older stems could not be determined, it was doubtful that many survived beyond the second growing season. Top removal by shredding during winter did not substantially alter numbers of new stems. In June, stem density on a shredded portion of the study area averaged 92 per square meter.

Stem growth first appeared 2 weeks after transplanting spiny aster rhizomes into pots during March and 86 percent of the rhizomes ultimately developed aerial stems. Most pots contained two to four individual shoots which grew to a height of 80 centimeters by August when growth ceased. The appearance of stems of potted plants did not outwardly differ from that of plants in the field. Leaves of potted spiny aster appeared soon after growth began and lasted through May.

Figure 5. Spiny aster shoot about 8 centimeters tall, which developed from a rhizome, photographed in early March at the study site near Bloomington, Texas.

A few flower heads formed on spiny aster in the field site and in pots during the summer. Flower head numbers reached a maximum in October, and blooming ceased in late November. Flower heads ranged from 5 and 25 per stem and averaged 17 in the field. Counts of achenes in undamaged flower heads collected in the field averaged 63 and ranged from 44 to 84. Potted spiny aster plants averaged 60 achenes per head, ranging from 40 to 84. Approximately one-third of all flower heads inspected,

Table 1. Average density of new, overwintered, and dead stems of spiny aster in June near Bloomington, Texas

Stem numbers/m^2			
Live stem age			
<1 yr	>1 yr	Total	Dead stems
113	35	148	139

whether on potted or field-grown plants, contained a small, unidentified insect larva that fed on the developing seeds.

Few spiny aster seeds germinated at alternating temperatures of 20° and 30° Celsius with light. Average germination of well-filled achenes collected in the field was 1.4 percent, whereas 5.7 percent of the achenes produced by potted plants germinated. Experiments were initiated shortly after achenes were collected so that aging and storage did not affect viability. A dormancy mechanism may be involved, however, and temperature or light conditions other than those employed may be required for high germination of spiny aster seed.

Leaf and Stem Anatomy

Stomatal concentrations on upper leaf surfaces are about twice those on lower leaf surfaces of spiny aster (Table 2). Most plants have highest stomatal densities on lower surfaces (8), and spiny aster leaves have few stomata relative to other species. For example, stomatal densities of honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) are about twice those of spiny aster (17).

The epidermis of terminal stems contains more and larger stomata than do leaves (Table 2). Also, mechanical pretreatment increased stomatal density in the upper spiny aster canopy. Stomatal densities averaged 344 per square millimeter on regrowth stems 12 weeks after top removal. Densities on terminal stems collected from undisturbed top-growth were lower, averaging 309 per square millimeter.

Stomatal densities on main stems located in the middle portion of the spiny aster canopy were lower than on stem tips. Densities of stomata increased from the main stem outward to the shoot tip. Although stomatal apertures of main stems were not measured, they appeared to be larger than terminal stem stomata.

A few uniseriate papillae (hairs) occurred on the upper surface of spiny aster leaves, but none were noted on the lower epidermis (Figure 6). Epidermal cells of both leaf surfaces are irregular in shape and size, especially those of the lower surface.

According to the classification of Martens (13), the cuticular structure of the upper surface is strongly ridged, while that of the lower leaf surface is an intergrade between ridged and smooth. Subsidiary cells of the lower surface are more noticeably ridged than ordinary epidermal cells.

Table 2. Average stomatal densities and aperture lengths of upper and lower leaf surfaces and stems of spiny aster

Location	Density (stomata/mm^2)	Aperture length (μm)
Upper leaf surface	109	15
Lower leaf surface	53	17
Undisturbed stem tip	309	39
Regrowth stem tip	344	38
Main stem	78	

Spiny aster does not have heavy leaf cuticle (Figure 7). Cuticle development does not appear to differ on upper and lower leaf surfaces, and cuticle thickness is uniform across epidermal layers of both surfaces.

Leaf mesophyll of spiny aster is relatively dense, with little intercellular space (Figure 7). The mesophyll consists of a single layer of palisade parenchyma cells and a well-developed spongy parenchyma. A resin canal (oil duct) is associated with each vascular bundle. Similar structures have been reported in western ironweed and other weedy members of the Composite family (15).

Both larger main stems and fine, terminal stems of spiny aster are herbaceous in cross section. Terminal stems are somewhat costate (ridged) (Figure 8), but main stems are rounded (Figure 9). Fiber bundles and resin canals are located at the ridges of terminal stems, separated by dense cortex. Resin canals in main stems are not associated with fiber bundles, however. Large, thin-walled cortical parenchyma cells, possibly epithelial oil cells, are grouped adjacent to the xylem in the terminal stem and between the fiber bundles in the main stem.

Pith constitutes a large portion of spiny aster stem volume, especially in the main stem. Xylem occurs as a continuous ring adjacent to the pith in both spiny aster stem types, while phloem occurs only adjacent to fiber bundles. Stomates occur on the epidermis of both terminal and main stems.

Herbicide Penetration and Translocation

Leaves of spiny aster absorbed little herbicide relative to that in annual sunflower (Table 3). Concentrations of 2,4-D and picloram in leaves of annual sunflower were substantially higher than concentrations reported in live oak (3) and honey mesquite (14) leaves exposed to 2,4,5-T using the same experimental method. After 2 hours, for instance, sunflower leaves contained about 24 micrograms 2,4-D per gram of leaf tissue, while less than 2 micrograms per gram was detected in spiny aster leaves. Picloram was not detected in spiny aster leaves until after 4 hours (Table 3). Therefore, foliar absorption may be the limiting factor in response of spiny aster to broadcast applications of 2,4-D or picloram.

Leaves of both spiny aster and sunflower generally had absorbed more of the potassium salt of 2,4-D than picloram after 4 and 6 hours but not after 2 hours in the laboratory. Increased uptake of 2,4-D with time was pronounced in leaves of annual sunflower. However, significant differences in the concentrations of the two herbicides in spiny aster leaves occurred only after the longest exposure time, 6 hours.

The various organs of spiny aster clearly differed in regard to rate of herbicide penetration (Table 4).

Initially, leaves and main stems absorbed either herbicide rather slowly under laboratory conditions. Picloram content of leaves after 2 hours was below the limit of detection (0.01 microgram picloram per gram leaf tissue). Terminal stems, whether from undisturbed growth or previously shredded spiny aster, apparently absorbed at least three times more herbicide than did leaves and main stems during the initial 2-hour period. Picloram accumulation in leaves equaled or exceeded that in terminal and main stems at 4 and 6 hours, however.

The accumulation of high amounts of either herbicide in terminal stems early in the experiments without continued accumulation of comparatively high concentrations compared to other organs seems questionable. Epidermal surfaces of terminal and main stems do not visibly differ. These results suggest mass flow of the herbicide solutions into the terminal stems upon immersion rather than actual passage of herbicides through morphological barriers. A possible route of herbicide entry may be through the meristematic tips of the fine stems, which abort when growth ceases. A small, irregularly-shaped callus forms, which may readily admit solutions. However, stems of regrowth spiny aster appeared to be actively growing when collected in June. Terminal tips were soft, pale green, and rounded; those of undisturbed shoots were inflexible, dark green, and callused. If herbicide solutions easily entered through aborted tips, terminal stems from spiny aster shoots without mechanical pretreatment should have absorbed more herbicide than those from regrowth. However, the reverse occurred, although differences were not always significant. The higher stomatal concentrations observed on regrowth stem tips may be responsible for the differential absorption. A relationship between stomatal abundance and herbicide uptake has been noted in foliage of several woody species (6).

No portion of the spiny aster canopy is readily penetrated by 2,4-D or picloram, relative to foliage of annual sunflower. Apparently, spiny aster leaf presence is not an important consideration in timing of broadcast sprays, since leaf uptake of herbicide is only slightly greater than stem uptake. However, leaf presence would increase the total absorptive area of the spiny aster canopy and thus improve spray interception.

In the first field experiment, penetration of spiny aster leaves by 2,4-D and picloram proceeded at the same rate until 96 hours after treatment (Table 5). At 96 and 120 hours after treatment, absorption ratios for 2,4-D were significantly higher than those for picloram.

Absorption ratios for spiny aster leaves are comparable to some previously reported for other species. For instance, blackberry (*Rubus procerus* P.J. Muell.) absorbed only 38 to 59 percent of applied 2,4,5-T (21). Blackberry is not controlled by a single application of 2,4,5-T (21). On the other hand, honey mesquite leaves absorbed about 40 percent of available 2,4,5-T after 1 day and 90 percent after 5 days (23). Que Hee and Sutherland (20) found that 65 to 70 percent of the dimethylamine salt of 2,4-D penetrated sunflower leaves within 13 hours of

Table 3. Herbicide concentrations (micrograms per gram fresh weight) in detached leaves of sunflower and spiny aster after exposure to 10^{-3} molar aqueous solutions of 2,4-D or picloram for 2, 4, or 6 hours[a]

Species	Time elapsed (hr)					
	2		4		6	
	2,4-D	Picloram	2,4-D	Picloram	2,4-D	Picloram
Sunflower	24.4 d	21.5 d	54.3 g	28.3 e	77.2 h	33.1 f
Spiny aster	1.7 a	ND[b]	10.3 b	9.8 b	16.2 c	11.7 b

[a]Means followed by the same letter do not differ significantly at the 95-percent confidence level using Duncan's multiple range test.
[b]ND denotes no detectable herbicide.

Table 4. Herbicide concentrations (micrograms per gram fresh weight) in detached leaves, terminal stems of undisturbed growth, terminal stems of regrowth following shredding, and main stems of spiny aster exposed to 10^{-3} molar aqueous solutions of 2,4-D or picloram for 2, 4, or 6 hours[a]

Organ	Time elapsed (hr)					
	2		4		6	
	2,4-D	Picloram	2,4-D	Picloram	2,4-D	Picloram
Leaves	1.7 b	ND[b]	10.3 g	9.8 fg	16.2 i	11.7 gh
Undisturbed stem tips	6.9 de	4.9 c	11.5 gh	7.2 de	12.8 h	9.6 fg
Regrowth stem tips	9.7 fg	7.0 de	13.4 h	8.5 ef	15.8 i	10.9 g
Main stems	2.0 b	1.9 b	6.6 cde	5.3 cd	11.4 gh	9.8 fg

[a]Means followed by the same letter do not differ significantly at the 95-percent confidence level using Duncan's multiple range test.
[b]ND denotes no detectable herbicide.

spraying; penetration of long-chain amine formulations reached 90 percent in only 4 hours. Leaf absorption of the dimethylamine salt of 2,4-D by spiny aster in the field was only 20 percent (absorption ratio × 100 = percent) after 1 day and 49 percent after 5 days (Table 5).

Herbicide concentrations within leaves of spiny aster sprayed with 2.24 kilograms per hectare of 2,4-D reached a maximum of about 15 micrograms per gram fresh weight at 24 and 48 hours after application (Table 5). Thereafter, 2,4-D concentrations were reduced by about half. Picloram concentrations in leaves of spiny aster treated with 1.12 kilograms per hectare were also greatest at 24 hours and declined rapidly at subsequent samplings. The rapid decrease in picloram concentration in spiny aster leaves may be attributed to greater mobility and more rapid export, compared to 2,4-D. Picloram is more mobile than 2,4,5-T in certain woody species (7) but less mobile than 2,4-D in skeleton weed (*Chondrilla juncea* L.) (9). The comparative extent of degradation of the two herbicides in spiny aster leaves may also be a factor.

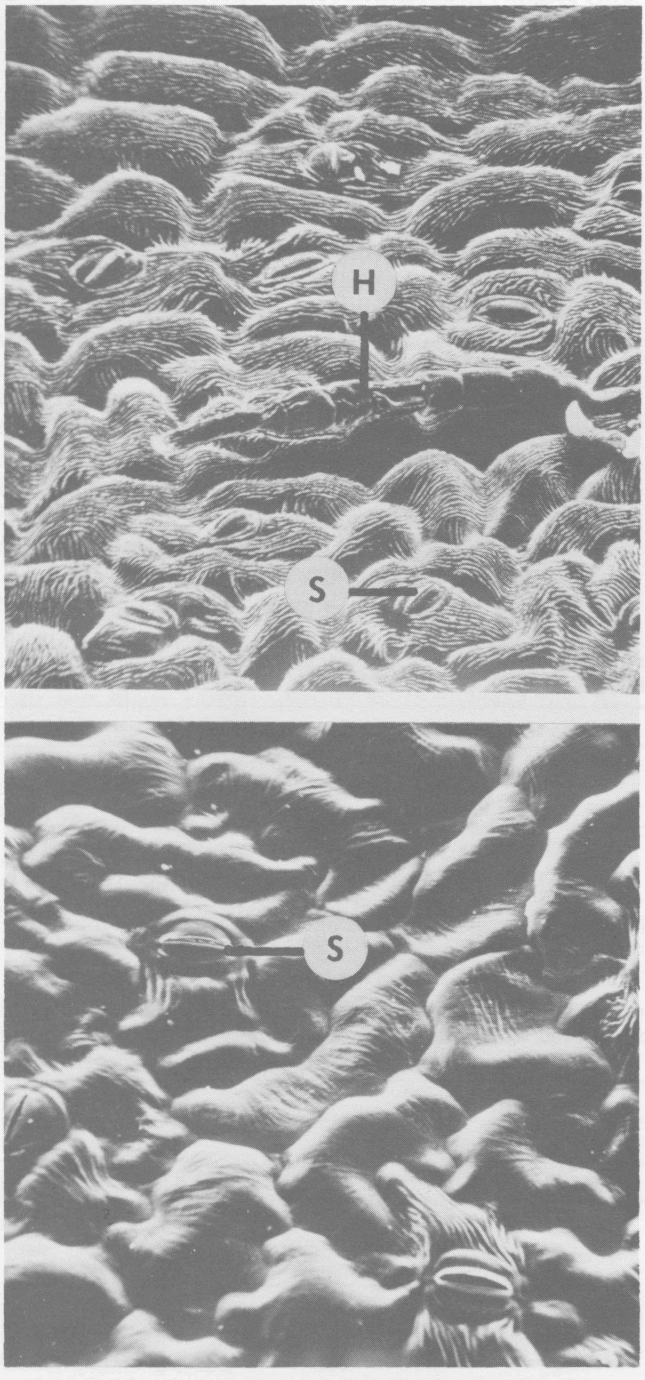

Figure 6. Spiny aster upper leaf surface, X620 (upper). Note ridged surfaces. Lower leaf surface, X620 (lower), with relatively smooth cuticle. Symbols are H, hair; S, stomate.

In general, 2,4-D behaved similarly when applied to leafless spiny aster in June (Table 6) and to leafy spiny aster in March (Table 5). Concentrations of 2,4-D in terminal stems of regrowth 74 days after shredding rose rapidly to almost 19 micrograms per gram at 24 hours after application and fell gradually to about 5 micrograms per gram after 120 hours. Maximum 2,4-D concentration in terminal stems of undisturbed spiny aster was less than 14 micrograms per gram. Picloram concentrations in terminal stems were highly variable.

There were usually no significant differences between herbicide concentrations in shredded and nonshredded terminal stems. However, herbicide concentrations averaged across time tended to be greater in regrowth stems than in undisturbed plants (Table 6). Elapsed time was significant for 2,4-D penetration but not for picloram.

No 2,4-D or picloram was detected in rhizomes of spiny aster in either field experiment. Apparently, downward translocation of these herbicides by spiny aster is slight. Least detectable limits, determined with fortified samples of rhizomes, were 0.025 microgram per gram for 2,4-D and 0.01 microgram per gram for picloram.

Table 5. Herbicide absorption ratios and concentrations (micrograms per gram fresh weight) in spiny aster leaves at various intervals after broadcast sprays of 2.24 kilograms per hectare 2,4-D or 1.12 kilograms per hectare picloram in March[a]

Time elapsed (hr)	Absorption ratio[b]		Herbicide concentration	
	2,4-D	Picloram	2,4-D	Picloram
1	0.01 a	0.01 a	0.5 a	0.5 a
8	0.07 a	0.07 a	6.9 c-e	6.4 c-e
24	0.20 b	0.22 b	15.1 f	16.9 f
48	0.22 b	0.19 b	14.8 f	9.8 e
72	0.26 b	0.21 b	6.4 c-e	6.2 b-e
96	0.40 cd	0.23 b	7.4 de	3.0 a-c
120	0.49 d	0.31 bc	5.1 b-d	2.3 ab

[a]Means beneath a major heading (absorption ratio or herbicide concentration) followed by the same letter do not differ significantly at the 95-percent level using Duncan's multiple range test.

[b]Absorption ratio = micrograms herbicide in leaves/(micrograms herbicide in leaves + micrograms herbicide in leaf rinses).

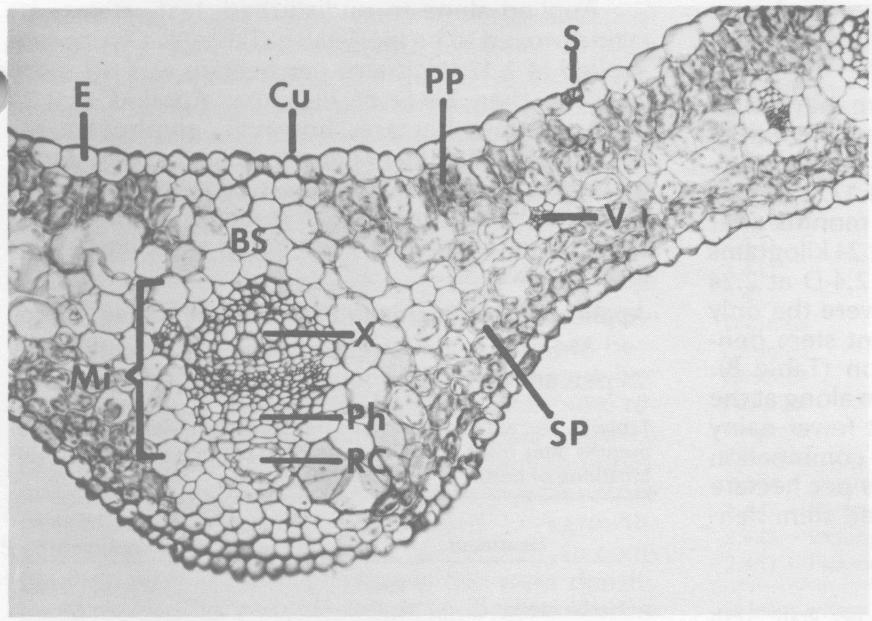

Figure 7. Transection of midrib area of spiny aster leaf, X170. Symbols are BS, bundle sheath; Cu, cuticle; E, epidermis; Mi, midrib; Ph, phloem; PP, palisade parenchyma; RC, resin canal; S, stomate; SP, spongy parenchyma; V, vein; X, xylem.

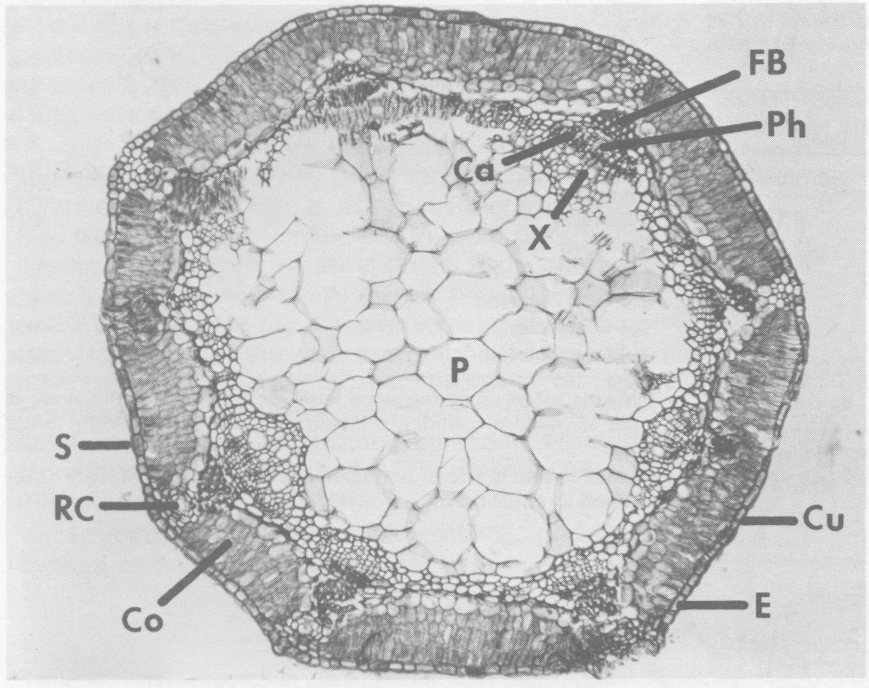

Figure 8. Transection of terminal portion of spiny aster stem, 2 centimeters from tip, X90. Symbols are Ca, cambium; Co, cortex; Cu, cuticle; E, epidermis; FB, fiber bundle; P, pith; Ph, phloem; RC, resin canal; S, stomate; X, xylem.

Response to Herbicides

Conditions of drought or excessive moisture did not occur when herbicides were applied. Soil water content ranged from 26 to 32 percent in the upper 45 centimeters of the soil profile when sprays were applied.

Fall and Spring Applications

When herbicides were applied on October 4, 1974, spiny aster stems were leafless, stem elongation had ceased, and most stems were in full bloom. Few stems were completely killed, regardless of herbicide or rate applied, in May of the following year (Table 7). Lower portions of main stems were green, and new stems were growing from old stem bases and rhizomes. Only 2,4-D plus picloram applied at 2.24 kilograms per hectare significantly reduced live spiny aster stem numbers. Three years after fall applications, spiny aster stem densities in treated plots were essentially equal to those of untreated plots (Table 7).

Spiny aster leaves were fully expanded and stems were elongating rapidly when herbicides were applied in March. Control from spring applications was substantially higher than that obtained in the fall. Seven months after treatment, 2,4-D or dicamba significantly reduced stem densities only at the highest rate, 2.24 kilograms per hectare (Table 8). In combination, 2,4-D and dicamba tended to be more effective, reducing stems by 50 percent at 2.24 kilo-

grams per hectare, but the increases in control were not significantly greater than where the herbicides were applied alone.

Picloram was the most effective herbicide applied in the spring to leafy spiny aster. Stem densities were reduced by 72, 86, and 95 percent following picloram applications of 0.56, 1.12, and 2.24 kilograms per hectare, respectively, 7 months after applications. Picloram alone at 1.12 or 2.24 kilograms per hectare and in combination with 2,4-D at 2.24 kilograms per hectare total herbicide were the only treatments which maintained significant stem density reductions 1 year after application (Table 8). After 3 years, plots treated with picloram alone at the highest rate still supported 63 percent fewer spiny aster stems than untreated plots. The combination of 2,4-D and picloram at 2.24 kilograms per hectare total herbicide also significantly reduced stem density at the final evaluation.

Table 6. Herbicide concentrations (micrograms per gram fresh weight) in terminal stems from shred regrowth or undisturbed spiny aster at various time intervals after broadcast sprays of 2.24 kilograms per hectare 2,4-D or 1.12 kilograms per hectare picloram in June[a]

Time elapsed (hr)	2,4-D		Picloram	
	Shredded	Undisturbed	Shredded	Nonshredded
1	0.1 a	0.2 a	0.5 a	0.1 a
8	12.3 d	13.6 d	10.0 c	11.5 cd
24	18.7 e	13.2 d	9.2 bc	9.1 bc
48	12.0 d	9.7 cd	7.6 bc	7.4 bc
72	8.7 bcd	7.7 bcd	14.2 d	11.1 cd
96	7.7 bcd	7.6 bcd	14.5 d	6.0 b
120	5.2 b	6.8 bc	14.8 d	9.3 bc
Avg	9.2	8.4	10.1	7.8

[a]Means beneath a major heading (2,4-D or picloram) followed by the same letter do not differ significantly at the 95-percent level using Duncan's multiple range test.

Applied alone to undisturbed, leafy stems, atrazine proved to be ineffective (Table 9). Glyphosate applied at 1.12 kilograms per hectare was no more effective than 2,4-D or dicamba. Applied at 2.24 kilograms per hectare, however, glyphosate reduced spiny aster stem density by 62 percent, about twice the reduction obtained by applications of 2,4-D or dicamba at the same rate, 9 months after application. Glyphosate was not as effective as picloram, however.

Applications to Regrowth Following Shredding

Shredding alone reduced live stem numbers by 24 percent on the previously undisturbed spiny aster

Table 7. Percent reduction of spiny aster stem density 7 and 36 months after foliar applications of selected herbicides and combinations of herbicides in October 1974

Treatment		Months after treatment[a]	
Herbicide(s)	Rate[b] (kg/ha)	7	36
None	—	0 a	0 a
2,4-D	0.56	7 a	0 a
2,4-D	1.12	6 a	0 a
2,4-D	2.24	17 ab	6 a
Dicamba	0.56	3 a	0 a
Dicamba	1.12	3 a	0 a
Dicamba	2.24	1 a	0 a
Picloram	0.56	8 a	0 a
Picloram	1.12	8 a	0 a
Picloram	2.24	28 ab	11 a
2,4-D + Dicamba	1.12	10 a	0 a
2,4-D + Dicamba	2.24	10 a	1 a
2,4-D + Picloram	1.12	11 a	0 a
2,4-D + Picloram	2.24	35 b	10 a

[a]Means followed by the same letter do not differ significantly at the 95-percent confidence level using Duncan's multiple range test.

[b]Rates shown are total herbicide applied; herbicides were combined in equal ratios.

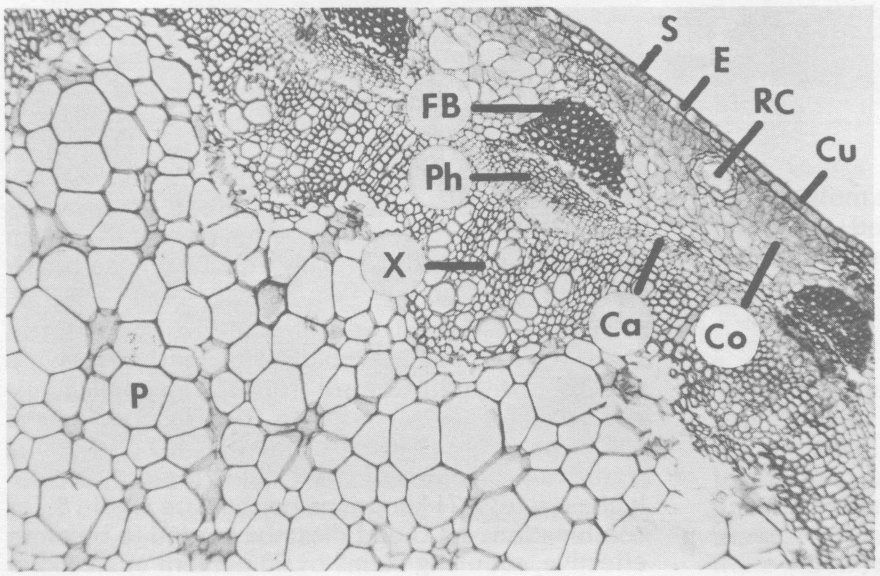

Figure 9. Transection of main stem from midcanopy of spiny aster, X90. Symbols are Ca, cambium; Co, cortex; Cu, cuticle; E, epidermis; FB, fiber bundle; P, pith; Ph, phloem; RC, resin canal; S, stomate; X, xylem.

stand (Table 9) and by 58 percent on the seeded area (Table 10). As a pretreatment, shredding at least doubled the effectiveness of most herbicide applications in both experiments. While differences between responses to spraying only and to shredding plus spraying were significant for each herbicide and rate, responses to rates of the same herbicide applied with or without pretreatment were not significantly different. The major factor, then, was pretreatment versus no pretreatment rather than rate of herbicide, within the narrow range of rates applied.

Glyphosate applied at 1.12 kilograms per hectare in March without pretreatment reduced live stem density by 24 percent, which was the same response obtained by shredding alone (Table 9). Twice that rate of glyphosate reduced live stems of undisturbed spiny aster by 62 percent, which was no more effective than the lower rate applied to regrowth. The higher rate, 2.24 kilograms per hectare, in combination with shredding reduced live stem density by 93 percent at 9 months after application. In the 1976 experiment, spiny aster responded similarly when glyphosate was applied without the shredding pretreatment (Table 10). However, after 1 year, responses to glyphosate applied to regrowth at 1 or 2 kilograms per hectare did not differ.

Of the herbicides compared, atrazine responded most positively from the mechanical pretreatment. Spiny aster control was increased from less than 10 percent reduction in stem density following applications of atrazine to leafy plants in March to 54 and 68 percent, respectively, when 1.12 and 2.24 kilograms per hectare were applied to regrowth (Table 9). Either the pretreatment resulted in increased foliar uptake of the herbicide, or rapid stem regrowth following shredding contributed to greater root uptake of atrazine. Applied to regrowth, atrazine was as effective as 2,4-D or dicamba but was not as effective as picloram.

In combination with shredding, picloram applied at 1.12 kilograms per hectare in 1975 com-

Table 8. Percent reduction of spiny aster stem density 7, 12, and 36 months after foliar applications of selected herbicides and combinations of herbicides in March 1975 and 1976

Treatment		Months after treatment[a]		
Herbicide(s)	Rate[b] (kg/ha)	7	12	36
None		0 a	0 a	0 a
2,4-D	0.56	10 ab	7 a	5 a
2,4-D	1.12	22 ab	20 ab	5 a
2,4-D	2.24	31 b	25 ab	9 a
Dicamba	0.56	6 a	10 a	4 a
Dicamba	1.12	24 ab	24 ab	3 a
Dicamba	2.24	34 b	25 ab	6 a
Picloram	0.56	72 cd	24 ab	14 a
Picloram	1.12	86 d	39 b	21 ab
Picloram	2.24	95 d	77 c	63 c
2,4-D + Dicamba	1.12	21 ab	28 ab	7 a
2,4-D + Dicamba	2.24	50 bc	31 ab	10 a
2,4-D + Picloram	1.12	70 cd	19 ab	12 a
2,4-D + Picloram	2.24	91 d	33 b	30 b

[a]Means within a column followed by the same letter do not differ significantly at the 95-percent confidence level using Duncan's multiple range test.

[b]Rates shown are total herbicide applied; herbicides were combined in equal ratios.

Table 9. Percent reduction of spiny aster stem density 9 months after foliar applications of selected herbicides to undisturbed stands in March 1975 or to shred regrowth in June 1975

Treatment		Stem density reduction[a]	
Herbicide	Rate (kg/ha)	Spray alone	Shred + spray
None		0 a	24 ab
2,4-D	1.12	22 ab	58 cd
2,4-D	2.24	31 bc	78 def
Dicamba	1.12	19 ab	55 cd
Dicamba	2.24	34 bc	68 de
Atrazine	1.12	7 ab	54 cd
Atrazine	2.24	4 ab	68 de
Glyphosate	1.12	24 ab	63 d
Glyphosate	2.24	62 d	93 ef
Picloram	1.12	86 def	100 f

[a]Means followed by the same letter do not differ significantly at the 95-percent level using Duncan's multiple range test.

Table 10. Percent reduction of spiny aster stem density 1 and 2 years after foliar applications of selected herbicides in June 1976 to undisturbed stands or to shred regrowth in an area previously seeded to kleingrass

Treatment		Years after treatment[a]			
		1		2	
Herbicide	Rate (kg/ha)	Spray alone	Shred + spray	Spray alone	Shred + spray
None		0 a	58 cd	0 a	43 c
2,4-D	1.12	36 bc	80 e	12 a	69 ef
2,4-D	2.24	35 b	77 e	7 a	71 ef
Glyphosate	1.12	33 b	66 de	5 a	65 def
Glyphosate	2.24	54 cd	67 de	19 ab	37 bc
Picloram	0.56	28 b	64 de	1 a	67 ef
Picloram	1.12	27 b	76 e	0 a	79 f
Paraquat	1.12	31 b	63 de	9 a	46 cd
Paraquat	2.24	42 bc	63 de	20 ab	57 cde

[a]Means within a time after treatment subheading (1 year or 2 years) followed by the same letter do not differ significantly at the 95-percent confidence level using Duncan's multiple range test.

pletely eliminated spiny aster by the first evaluation (Table 9). Picloram was not as effective in 1976 (Table 10), whether applied with or without pretreatment on the area seeded to kleingrass. Subsequent evaluations of plots shredded and sprayed in the dense, grassless spiny aster stand indicated rapid reestablishment of the weed. Three years after treatment, stem density reductions averaged 38 percent in plots shredded and sprayed with 1.12 kilograms per hectare of picloram and 39 percent in plots shredded and sprayed with 2.24 kilograms per hectare of glyphosate (data not shown). Live stem densities in plots receiving other treatments in 1975 did not differ from those in untreated plots 3 years after herbicide application.

Spiny aster control remained high in plots shredded and sprayed where kleingrass was established, however. After 2 years, all herbicides applied to regrowth maintained significantly greater stem reductions than shredding alone except for the higher rate of glyphosate and plots treated with paraquat (Table 10). Picloram or 2,4-D, applied to regrowth in 1976, removed 70 to 80 percent of the spiny aster stems after 2 years. Applied to plots without mechanical pretreatment or grass seeding, no herbicidal treatment significantly reduced the density of live spiny aster stems for 2 years.

Natural Revegetation Following Control

Revegetation following effective control of spiny aster had not occurred by the end of the second growing season after spraying (Figure 10), except where kleingrass was already established. The herbaceous plants that invaded treated plots during the third and subsequent years were barnyardgrass, bushy bluestem [*Andropogon glomeratus* (Walt.) B.S.P.], common bermudagrass [*Cynodon dactylon* (L.) Pers.], and diamond-leaf frogfruit [*Phyla strigulosa* (Mart. & Gal.) Moldenke]. Substantial forage production occurred on only a single nonshredded plot. It had been treated with 2.24 kilograms per hectare picloram in March 1975. The equivalent of 4215 kilograms per hectare of oven-dry standing forage occurred on the plot 40 months after treatment.

Several conditions may have been responsible for the general lack of natural revegetation of denuded plots. The complete dominance of a site for prolonged periods by spiny aster may eliminate the seed sources required for establishment of forage plants or other weeds. Dead stems from the dense spiny aster growth may provide a physical or chemical hindrance to seed germination of other species. Depth of the weed stem litter on bare plots was about 2 centimeters, and decomposition was slow, requiring about 2 years.

Herbicide residues may be suspected of suppressing seedling establishment, but plots treated with the same herbicides and rates in several other studies revegetated naturally within a few months. Mutz et al. (18) reported excellent forage responses after treatment of spiny aster with pelleted picloram if the weed infestation had not eliminated the residual forage seed source. However, in areas where competition from dense stands of spiny aster had eliminated the forage plants, control did not give an equally favorable forage response. Artificial revegetation by seeding with adapted grasses will probably

Figure 10. Spiny aster plot sprayed with 1.12 kilograms per hectare picloram in June 1975, 74 days after shredding, in Calhoun County, Texas (photographed in summer 1976). Note the heavy accumulation of dead stems on the soil surface and the absence of grasses and forbs.

be required on such sites where spiny aster is successfully controlled.

CONCLUSIONS

Clonal increase by rhizome growth is apparently the primary method of spiny aster reproduction. Seed viability appears to be extremely low under standard laboratory seed testing conditions. However, spiny aster seed may have rather unique germination requirements.

Shredding does not effectively control spiny aster. Vigorous resprouting by rhizomes quickly replaces the canopy after either mechanical or ineffective chemical top removal. Control of spiny aster was not obtained with fall applications of several herbicides and mixtures. Susceptibility to herbicides is probably lowered by physiological inactivity during the fall. Applications of 2,4-D, dicamba, atrazine, or glyphosate at 1.12 or 2.24 kilograms per hectare during the brief spring period when leaves are present are more successful than in the fall, but control levels are not satisfactory. Picloram applied during the spring gives temporary control of spiny aster, but 2.24 kilograms per hectare are required.

Shredding spiny aster during early spring prior to spraying greatly increases the effectiveness of herbicides. Picloram or glyphosate applied at 1.12 or 2.24 kilograms per hectare, respectively, to regrowth effectively controlled spiny aster for a single year, but revegetation by other species rarely occurred. Density of live stems was reduced 70 to 80 percent during the second year after treatment where combinations of shredding and spraying were applied to a mixture of spiny aster and kleingrass. Apparently, the competitive influence of an established, perennial grass contributes to the success of the weed control treatments. However, even with mechanical pretreatment, most broadcast sprays did not effectively control spiny aster.

The effectiveness of hormone-like herbicides is limited by poor herbicide uptake by spiny aster topgrowth. Herbicide translocation to rhizomes, required for control of spiny aster, could not be demonstrated in the field. Although epicuticular waxes or other barriers may be important, the relatively low accumulations of 2,4-D and picloram by foliar organs in the laboratory are not adequately explained by cuticle thickness. Chemical characteristics of the epidermal covering may be more responsible for high resistance to herbicide penetration than thickness (19).

Comparatively low stomatal densities on leaves may limit herbicide uptake from aqueous solutions. However, high densities of stomata with relatively large apertures do not substantially enhance herbicide uptake by fine terminal stems. As a mechanical pretreatment, shredding slightly decreases resistance to herbicide penetration of the terminal stems. Furthermore, shredding removes older living stems and standing dead shoots without reducing densities of current-year stems. This contributes to improved herbicide effectiveness by providing a greater proportion of aerial plant surface which is more easily penetrated. Since about half of the undisturbed spiny aster canopy consists of dead stems, herbicide interception by living tissues is substantially reduced in undisturbed stands.

The stimulation of stem initiation and rapid elongation which results from top removal may promote root uptake of herbicides. In view of the latter and the inherent resistance of spiny aster topgrowth to herbicide penetration, further efforts to develop methods for control of spiny aster should stress the evaluation of soil-applied herbicides (18). Greater spiny aster responses to picloram may be attributed to the relatively high soil activity of this herbicide (9), even though the clay and organic matter content of the soils which generally support dense stands of spiny aster have high herbicide-binding potential.

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