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SUBSPECIES SPECIFICITY OF GALL FORMS ON *CHRYSOTHAMNUS NAUSEOSUS*

E. Durant McArthur,¹ Charles F. Tiernan,¹ and Bruce L. Welch¹

ABSTRACT.—Galls induced by tephritid flies (Diptera: Tephritidae) on *Chrysothamnus nauseosus* ssp. *albicaulis*, *consimilis*, *graveolens*, and *salicifolius* are useful in taxonomic identification of these subspecies in Utah. In this study, "callus" galls were found almost exclusively on ssp. *albicaulis*. "Cotton" galls were more frequent on ssp. *consimilis* and *graveolens*. "Mace" galls occurred on all four subspecies but were the only gall found on naturally occurring populations of ssp. *salicifolius*. Gall form specificity is not as well correlated with *C. nauseosus* subspecies in peripheral areas of the species range as in Utah. This decrease in specificity may be due to decreased competition for the host plant in outlying areas.

Chrysothamnus nauseosus, rubber rabbitbrush, is a shrub that is widely distributed in western North America. The shrub occurs from British Columbia and Saskatchewan south to west Texas and Baja California on plains, valleys, and foothills (Hall and Clements 1923). It is most abundant in the central portion of its range, the intermountain area, including all of Utah, most of Nevada, eastern California, southeastern Oregon, southern Idaho, southwestern Wyoming, and western Colorado (Cronquist et al. 1972, Hanks et al. 1975). *Chrysothamnus nauseosus* is often associated with *Artemisia tridentata*, big sagebrush, and is also a frequent component of salt desert shrub communities (Branson et al. 1976, McArthur et al. 1979).

Chrysothamnus nauseosus includes 15 subspecies (Anderson 1966, 1971, Anderson et al. 1974). In Utah, four common subspecies are *albicaulis*, *consimilis*, *graveolens*, and *salicifolius* (Hanks et al. 1975). Each of these subspecies has preferred habitats (Plummer 1977), but occasionally two or more subspecies may be found together in the same area. Some introgression occurs at these sites (Hanks et al. 1975), but hybridization and introgression are minimized because self-pollination is prevalent in *Chrysothamnus* (Anderson 1966, McArthur et al. 1978). The various subspecies of *C. nauseosus* have different forage values in natural stands and different uses in revegetation efforts (McArthur et al. 1974, Hanks et al. 1975, Plummer 1977). There is considerable intraspecific variation in plant

morphology (Hall and Clements 1923, Cronquist 1975), which makes subspecific taxonomic identification of individual plants sometimes difficult.

During the winter of 1975–76, we noted that in some Utah areas tephritid-induced galls of different forms had absolute *C. nauseosus* subspecies specificity. This study was undertaken to see how widespread and how absolute the gall form specificity was on *C. nauseosus* ssp. *albicaulis*, *consimilis*, *graveolens*, and *salicifolius*. It was thought that if these gall forms were subspecies-specific, they could help in subspecies identification, and in the management of the various subspecies. In the course of our data collection we learned that J. K. Wangberg was studying the biology of tephritid gall formers on *Chrysothamnus* (Wangberg 1976), and we compared our results with his.

MATERIALS AND METHODS

Gall form specificity was measured (1) at five sites where two subspecies naturally grow together (Table 1); (2) at the Snow Field Station, Ephraim, Utah, where *Chrysothamnus nauseosus* ssp. *albicaulis*, *consimilis*, *graveolens*, and *salicifolius* are growing in a uniform garden; and (3) in more or less pure natural stands of the four subspecies (Table 2). In addition, gall types were observed at more than 30 other sites in Utah and northern Arizona.

We looked at three gall forms (Fig. 1):

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TABLE 1. Gall frequencies from mixed populations at five Utah localities.

Collection information		
Subspecies ¹	Authors' number	Site
Chna ^a	759	Big Rock Candy Mountain, Sevier Co. ^{3,4}
Chna ^c	760	Big Rock Candy Mountain, Sevier Co. ⁴
Chna ^a	770	3 km S Fountain Green, Sanpete Co. ¹
Chna ^c	979	3 km S Fountain Green, Sanpete Co. ⁴
Chna ^a	791	3 km W Goshen, Utah Co. ⁴
Chna ^c	790	3 km W Goshen, Utah Co. ⁴
Chna ^a	811	1 km W Paragonah, Iron Co.
Chna ^a	812 ⁵	1 km W Paragonah, Iron Co.
Chna ^a	818	Gould Wash, Washington Co. ⁴
Chna ^a	817	Gould Wash, Washington Co. ⁴

¹Subspecies symbols: Chna^a = *Chrysothamnus nauseosus* ssp. *albicaulis*; Chna^c = *C. n. ssp. consimilis*; Chna^b = *C. n. ssp. graveolens*.

² $\bar{x} \pm sd$ = mean (\bar{x}) \pm standard deviation (sd) of number of galls on terminal 15 cm of a random branch/plant.

³Some plants of intermediate morphology were found.

⁴Browsing preference for ssp. *albicaulis* noted. Browsers were deer at Big Rock Candy Mountain, sheep at Fountain Green, horses and cattle at Goshen, and cattle and deer at Gould Wash.

⁵Gall frequencies significantly different with $p < 0.01$.

1. The "callus" gall, which is more or less glabrous, round to ovoid, 0.3 to 1.2 cm in diameter, and persistent up to two years on the plant.

2. The "cotton" gall, which is covered with a thick, white tomentum, round to ovoid, 0.7 to 1.4 cm in diameter, and generally not as persistent as the callus gall, although some galls persist for two years.

3. The "mace" gall, which is usually glabrous, round to ovoid, 0.5 to 1.2 cm in diameter, and covered with small bracts. Persistence of the mace gall past the first year is unknown.

Active galls are those containing larvae; whereas inactive galls are those from which the flies have emerged.

Gall frequencies were scored at collection sites by counting the galls (active and inactive) on the terminal 15 cm of a randomly selected branch of each mature shrub (>30 cm tall) on more or less straight line transects through *C. nauseosus* populations. Fifty plants were scored in each of the pure stands. At the mixed sites 50 plants of each subspecies were scored as the plants occurred on the transects. All data collection and observations were made in the winter and early spring of 1976-77.

Chrysothamnus nauseosus subspecies were identified using Anderson's (1973) key at the time of data collection or during the following summer when leaves were present on the plants. Herbarium vouchers have been deposited at the Shrub Sciences Laboratory Herbarium (SSLP) in Provo, Utah. Flies were reared to maturity from a few galls, and were identified using Wangberg's (1976) key.

A paired *t* test (Woolf 1968) was used to test the significance of gall form frequency differences where two gall types occurred on the same subspecies (Table 1).

RESULTS AND DISCUSSION

CORRELATION OF GALL MORPHOLOGY WITH *Chrysothamnus nauseosus* SUBSPECIES.—The five study areas of Table 1 reflect almost complete gall form specificity for each subspecies. In each case *C. nauseosus* ssp. *albicaulis* is growing with either *C. nauseosus* ssp. *consimilis* or ssp. *graveolens*. The cotton gall was found only on ssp. *consimilis* and ssp. *graveolens*. The callus gall, except for a single plant at the Paragonah site, was found only on ssp. *albicaulis*. Both ssp. *consimilis* and ssp. *graveolens* tend to have greener stems and less leaf and stem tomentum than ssp. *al-*

Gall type					
Callus			Cotton		
$\bar{x} \pm \text{sd}^2$	Range of values	Percent of plants w/galls	$\bar{x} \pm \text{sd}^2$	Range of values	Percent of plants w/galls
7.92 ± 8.55	0-34	80	0	0	0
0	0	0	0	0	0
1.00 ± 1.76	0-9	46	0	0	0
0	0	0	0.70 ± 0.90	0-3	50
4.32 ± 4.83	0-18	80	0	0	0
0	0	0	4.44 ± 6.18	0-23	58
6.02 ± 4.83	0-21	94	0	0	0
0.04 ± 0.28	0-2	2	5.36 ± 2.98	0-11	98
5.56 ± 5.00	0-21	90	0	0	0
0	0	0	3.50 ± 6.45	0-14	80

bicaulis. The exceptional Paragonah plant could well have been an introgressant. At the Big Rock Candy Mountain site galls were not found on the ssp. *consimilis* plants (Table 1). However, a few plants of intermediate morphology were located—they had callus galls.

At the Snow Field Station the four subspecies of *C. nauseosus* are growing in a uniform garden. There callus galls were found on ssp. *albicaulis*, and cotton galls were found, although much less frequently, on the other three subspecies.

In the uniform population studies (Table 2), only callus galls were observed for *C. nauseosus* ssp. *albicaulis*, and only cotton galls were observed for ssp. *consimilis*. Cotton galls were most common on ssp. *graveolens*, although a few mace galls were found on this subspecies at the Hanksville site. Only mace galls were observed on ssp. *salicifolius*.

At sites where observations were made but gall frequency data were not recorded, we rarely found exceptions to the data presented in Table 2. A population of ssp. *albicaulis* (collection number: McArthur, Tiernan, and Welch 769) located 3 km south of Nephi, Juab Co., Utah, had a single plant corresponding to ssp. *consimilis*. Whereas the ssp. *albicaulis* plants had high numbers of callus galls, the aberrant ssp. *consimilis* plant had only a single gall, which was a callus gall.

Galls were much more common in some areas than in others. For example, ssp. *albi-*

caulis plants near Ogden Bay, Weber Co., Utah (McArthur 786), were nearly devoid of galls; whereas a few miles south, on the north end of Antelope Island, Davis Co., Utah, plants of the same subspecies (McArthur 789, Table 2) were heavily infested with galls. In the upper Sevier Valley, ssp. *consimilis* plants lacked galls, but in the lower Sevier Valley and in Sanpete Valley (a Sevier Valley tributary) they had cotton galls. A few mace galls were found with more numerous callus galls on ssp. *albicaulis* in Willow Creek Canyon, north of Richfield, Sevier Co., Utah.

Mace galls were found on all four subspecies in at least one location of our observations. The mace galls were encountered less frequently and had a lower incidence per plant than the other two types of galls.

East of Ephraim, Sanpete County, Utah, we found both ssp. *albicaulis* (McArthur 779) and ssp. *consimilis* (McArthur 780) growing with several plants of intermediate morphology (McArthur 781). There, callus galls were on ssp. *albicaulis* plants; cotton galls were on ssp. *consimilis* plants; and both kinds of galls were found on a few plants of intermediate morphology.

Wangberg (1976) found that the tephritid fly (*Acurina bigeloviae*) was responsible for galls whose descriptions match those of the callus and mace forms discussed in this report. Another tephritid (*A. maculata*) was responsible for galls matching the description

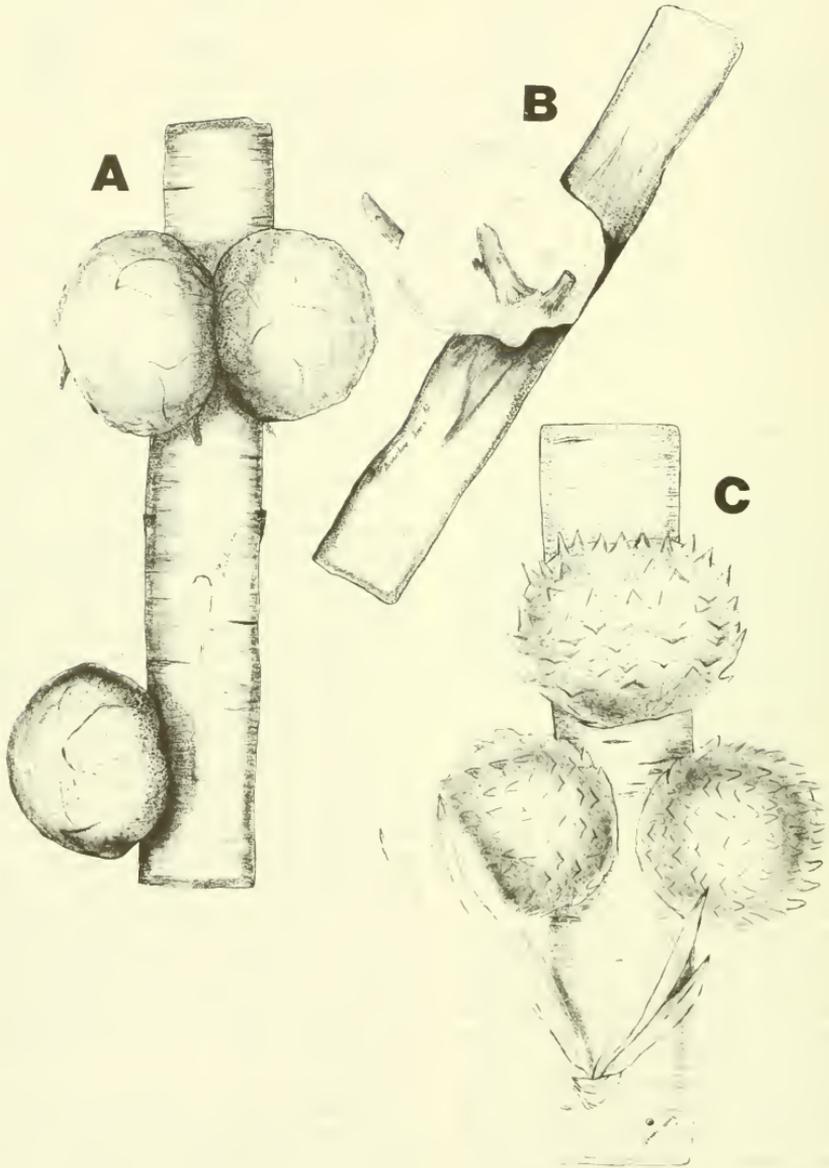


Fig. 1. Drawings of gall forms. A. callus. B. cotton. C. mace. (4X).

of the cotton gall. Wangberg (1976) described the galls but did not use the terms cotton, callus, or mace. He (Wangberg 1976) stated that in Idaho both cotton and callus gall forms were found on *C. nauseosus* ssp. *albicaulis* and ssp. *consimilis*. Observations made during this study in Utah (Tables 1 and 2) and northern Arizona were quite different. The callus gall was very specific for ssp. *albicaulis*. The cotton gall was specific for ssp. *consimilis* and *graveolens* at most locations. Cotton galls were found on ssp. *albicaulis* only where the callus gall was absent. For example, in northeastern Mohave Co., Arizona, and western Kane Co., Utah, ssp. *albicaulis*, *graveolens*, and *consimilis* all had cotton galls (McArthur 819, 820, 832). Mace galls were much rarer than callus or cotton galls in most areas of observation (Tables 1 and 2), but were occasionally found on all four subspecies of *C. nauseosus*.

The relationship between gall tomentum and plant tomentum is perplexing. Glabrous

callus and mace galls have specificity for ssp. *albicaulis* and ssp. *salicifolius*, respectively. These subspecies have looser and more obvious tomentum than ssp. *consimilis* and *graveolens*, which show specificity for the tomentulose cotton gall.

TAXONOMIC INDICATOR VALUE OF GALL FORMS ON *C. nauseosus* SUBSPECIES.—The callus gall form is specific for *C. nauseosus* ssp. *albicaulis* in most of Utah. If a callus gall is present on *C. nauseosus*, the plant is in all likelihood ssp. *albicaulis* (Table 1 and 2). In winter, when leaves are lacking from *C. nauseosus*, callus galls help distinguish ssp. *albicaulis* from ssp. *consimilis* and ssp. *salicifolius*. In Idaho apparently, this specificity does not occur (Wangberg 1976).

The cotton gall, in Utah, is found most commonly on ssp. *consimilis* and *graveolens* (Tables 1 and 2). However, in the few areas where the callus gall is missing the cotton gall may be found on ssp. *albicaulis*. The cotton gall has not been found on naturally

TABLE 2. Gall frequencies in uniform populations at nine Utah localities.

Sub-species ¹	Collection information		Gall type	Frequency		
	Authors' number	Site		$\bar{x} \pm \text{sd}^2$	Range of values	Percent of plants w/galls
Chna ^a	768	Mouth of Chicken Creek Canyon, Juab Co.	Callus	2.03 ± 3.34	0-18	72
Chna ^a	773	3 km S. Bluffdale, Salt Lake Co.	Callus	1.80 ± 2.03	0-8	60
Chna ^a	789	N. end Antelope Island, Davis Co.	Callus	5.10 ± 7.26	0-43	74
Chna ^c	962	Pigeon Hollow, Sanpete Co.	Cotton	1.24 ± 1.41	0-6	68
Chna ^c	976	3 km NE. Ephraim, Sanpete Co.	Cotton	1.06 ± 1.05	0-4	68
Chna ^g	1000	Hanksville, Wayne Co. ¹	Cotton ¹	1.44 ± 1.69	0-7	66
Chna ^s	964	Snowberry Enclosure, Ephraim Canyon, Sanpete Co.	Mace	0.18 ± 0.52	0-3	14
Chna ^s	1061	Red Creek, Duchesne Co.	Mace ¹	0.26 ± 0.49	0-2	24
Chna ^s	1066	Moon Lake, Duchesne Co.	Mace	0.16 ± 0.55	0-3	10

¹Subspecies symbols: Chna^a = *Chrysothamnus nauseosus* ssp. *albicaulis*; Chna^b = *C. n.* ssp. *consimilis*; Chna^g = *C. n.* ssp. *graveolens*; Chna^s = *C. n.* ssp. *salicifolius*.

² $\bar{x} \pm \text{sd}$ = mean (\bar{x}) ± standard deviation (sd) of number of galls on terminal 15 cm of a random branch/plant.

¹Two morphologies of ssp. *graveolens* present. A low incidence of mace galls was observed but not recorded.

⁰One poorly defined cotton gall was observed.

growing populations of ssp. *salicifolius*, but was found on plants of this subspecies transplanted to the Snow Field Station. Subspecies *salicifolius* is ordinarily a mountain taxon, whereas the Snow Field Station is in a valley setting.

The mace gall has been found on all four subspecies but is the only one of the three galls found on naturally occurring populations of ssp. *salicifolius* (Table 2).

RESOURCE PARTITIONING BY THE GALL-FORMING TEPHTRID FLIES.—Wangberg (1976) discussed the problem of niche-sharing by fly species that induce galls on similar parts of the same subspecies of *C. nauseosus* at the same time of the year. Wangberg believed, following Darlington (1972), that tephritid fly species compete in nature and divide the resource. Our studies support such a competitive division of the plant resource. Our study showed more gall-form specificity on *C. nauseosus* subspecies than Wangberg's (1976), perhaps because our study was in the central area of *C. nauseosus*'s range, where there are larger concentrations of the plant than are present where Wangberg studied (Hall and Clements 1923). L. C. Anderson (letter dated 16 February 1978) has data indicating less specificity for gall forms on plants growing outside of Utah than on those growing in Utah. In the central area of the host species' occurrence, the gall formers might be better off to be host specific to avoid competition with large populations of various taxa of gall-forming flies. In outlying areas such host specificity might be a disadvantage because host plants would be rarer. Moreover, gall-forming fly populations would not be as high, so competition would be reduced. MacArthur (1972:17) touched on this problem when he stated that species are more likely to compete in localities where an advantage can be gained.

Another possible explanation for gall-form specificity is that different gall forms are not a response to different fly species but rather a response to the host plant species. We have not reared enough fly specimens to address this possibility. However, we think this explanation is unlikely, because a few individual plants had more than one gall form.

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