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SEASONAL PATTERNS OF ARTHROPOD DIVERSITY AND ABUNDANCE ON BIG SAGEBRUSH, *ARTEMISIA TRIDENTATA*

Monte P. Sanford^{1,2} and Nancy J. Huntly^{1,3}

ABSTRACT.—The sagebrush biotype is the largest in the western United States. This vast sagebrush community is thought to harbor equally vast and diverse arthropod communities, but these remain little explored. Our objective was to examine the diversity, abundance, and seasonal phenology of arthropod taxa found on the dominant shrub of the sagebrush ecosystem, big sagebrush (*Artemisia tridentata*). We wanted to improve understanding of this little-studied arthropod assemblage that may play significant roles in the dynamics of sagebrush populations and the sagebrush ecosystem. We sampled free-living and gall-forming arthropods from a stratified random sample of sagebrush plants at the Barton Road Ecological Research Area, Idaho, resulting in a sample of over 8000 individuals and 232 morphospecies. Species richness and abundance declined from May to August, and abundance of most taxa similarly declined over the summer. A few taxa, including Acari (mites), were notably more abundant in August. Fluid feeders were the most diverse and abundant free-living feeding guild during all months and comprised up to 79% of morphospecies. The gall formers included 4713 individuals of 12 species of gall flies (*Rhopalomyia* spp.), primarily (97%) *R. ampullaria*. Abundance of galls increased from small to large (presumably young to old) plants. Overall, *A. tridentata* was host to a high diversity of arthropods, some of which have potential to cause or mitigate significant damage to their host plant. Arthropods seem likely to have the greatest impact on sagebrush early in the growing season, when they are most diverse and abundant. Documentation of the full diversity of arthropods associated with sagebrush required samples taken throughout the growing season, but a single sample early in the growing season captured a high proportion of taxa.

Key words: *Artemisia tridentata*, big sagebrush, *Rhopalomyia*, arthropod, insect, biodiversity, phenology.

Sagebrush steppe is the largest temperate semidesert ecosystem in North America, comprising an area of about 44.8×10^6 km² (West 1983). The Columbia and Snake River plateaus contain 4.48×10^5 km² of sagebrush communities (West 1983), and the Great Basin desert includes over 2.06×10^5 km² (Brussard et al. 1998). This vast sagebrush community is thought to harbor a similarly vast and diverse arthropod fauna (Horning and Barr 1970, Tingey et al. 1972, Gittins et al. 1976, Jones et al. 1983, Stafford et al. 1986, Stafford 1987, Hampton 2005, Welch 2005). However, little is known about the sagebrush-associated arthropods of the cold-desert regions of North America.

Most research on sagebrush arthropods has focused either on a single taxon known to defoliate sagebrush (e.g., *Aroga* moths; Gates 1964, Hanson et al. 1982) or on the broad biology of a single genus (e.g., gall-forming *Rhopalomyia* flies; Jones et al. 1983). These studies have made significant contributions to our understanding of the life cycles and distributions of the focal taxa, but overall patterns of diversity,

abundance, and seasonal phenology of the arthropods associated with sagebrush are largely unexplored, despite the large spatial extent and economic importance of sagebrush. Welch (2005) reviewed the literature to assemble a list of arthropods associated with sagebrush and reported that 72 spider and 237 insect species are documented associates of sagebrush, including 42 gall-forming insects, 52 aphids, and 23 beetles. However, the typical arthropod fauna of an individual *Artemisia* shrub and the faunal variation over the growing season have not been documented.

Sagebrush steppe is one of North America's endangered ecosystems and is strongly affected by land uses, such as livestock grazing, and by exotic species invasions (Knick and Rotenberry 1997, Dobkin and Sauder 2004, Welch 2005, Bangert and Huntly 2009, Prevey et al. 2010, in press). The arthropods of sagebrush ecosystems are likely to affect the population dynamics of sagebrush because they are major parts of the food webs of sagebrush steppe, they influence ecosystem functioning, and they provide

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ecosystem services, such as pollination and seed dispersal (e.g., Pringle 1960, Banham 1961, Christiansen et al. 1989a, Dobkin and Sauder 2004, Welch 2005, Shiojiri and Karban 2008). Thus, efforts to conserve and restore sagebrush steppe require an understanding of the associated arthropods.

Our research objective was to examine the diversity, abundance, and seasonal phenology of arthropod taxa associated with big sagebrush (*Artemisia tridentata*). We posed 4 questions: (1) What are the patterns of diversity and abundance of arthropods on *A. tridentata* during the spring/summer growing season? (2) What feeding guilds are associated with *A. tridentata*, and how do their diversity and abundance vary over the summer months? (3) What is the taxonomic composition of the fauna of *A. tridentata*? (4) What species comprise the gall-forming guild of *A. tridentata*, and how are galls distributed within the canopy of *A. tridentata*? Our research provides a basis for identifying time frames and target taxa for future research on sagebrush-arthropod interactions and can be used to more fully understand sagebrush ecosystem dynamics.

METHODS

Study Site

This study was conducted in a sagebrush-steppe community at the Barton Road Ecological Research Area. The study site was located at 1450 m elevation in the foothills at the eastern edge of Pocatello, Idaho, at roughly the border of the hydrographic Great Basin and the Snake River Plateau. Soils at the site are deep, well-drained calcareous silt loams that are moderately alkaline near the surface and moderately to strongly alkaline at depths of 20–150 cm (McGrath 1987). Shrub cover on the 27-ha research area ranges from 25% to 35%, perennial grass cover from 20% to 27%, and forb cover from 1% to 3.7% (Inouye 2002). *Artemisia tridentata* is the clear vegetative dominant, comprising more than 95% of total shrub cover and 30% of total cover. Other abundant grasses and shrubs include *Elymus lanceolatus*, *Stipa comata*, several species of *Poa*, and *Bromus tectorum*, a nonnative and invasive grass. Sagebrush density on the plots we sampled averaged 1.02 plants · m⁻² (ranging from 0 to 2.61 plants · m⁻²; Huntly unpublished data).

The progression of summer involves increasing temperature and decreasing precipitation. Annual average precipitation at the Pocatello Airport (17 km from the site and at 1359 m elevation) averages 30.8 cm, with July–October being driest. We calculated average temperature and precipitation for ±5 days from sample dates using weather data from the Pocatello Airport Weather Station. Average high temperatures increased from 78 °F (25.6 °C) in late May to 97 °F (36.1 °C) in late June and dropped to 88 °F (31.1 °C) in late August. Mean precipitation dropped from 3.03 mm in May to 0.04 mm in July and 0.21 mm in August. Evaporation typically exceeds precipitation from late May through early October (Anderson and Inouye 2001).

Free-living Arthropods

We sampled arthropods from sagebrush located on 100 permanent plots that were 10 m × 10 m and separated by 2-m aisles. The *A. tridentata* plant located nearest to the point 4 m north and 6 m east of the southwest corner of each plot was selected to be sampled. Arthropods were sampled in late May (28 May–1 June), late June (28 June), and mid- to late August (23 and 24 August) of 2000. Plants were divided into cardinal quadrants (NE, NW, SE, SW) and one quadrant, selected at random for each shrub, was sampled each month; no quadrant on the same plant was sampled twice. Arthropods were collected by beating sagebrush foliage of a selected quadrant 10 times with a stick and collecting the dislodged arthropods in a 60-cm-diameter sweep net held below the branches. The arthropods were separated from vegetation and kept frozen until processed and identified.

We identified and enumerated arthropods from a randomly selected subset of 50 of the 100 samples from each sample period. Specimens were identified to family using Borror et al. (1989), noted as adult or immature, and further sorted to recognizable taxonomic units (RTUs; Oliver and Beattie 1996, Kerr et al. 2000). Voucher specimens were deposited at Idaho State University. Formicidae were identified to species using Wheeler and Wheeler (1986). Arthropods were assigned to feeding guilds (defoliator [DF], fluid feeder [FF], predator [PD], parasitoid [PT], or gall former [GF]) based on feeding habits according to Borror et

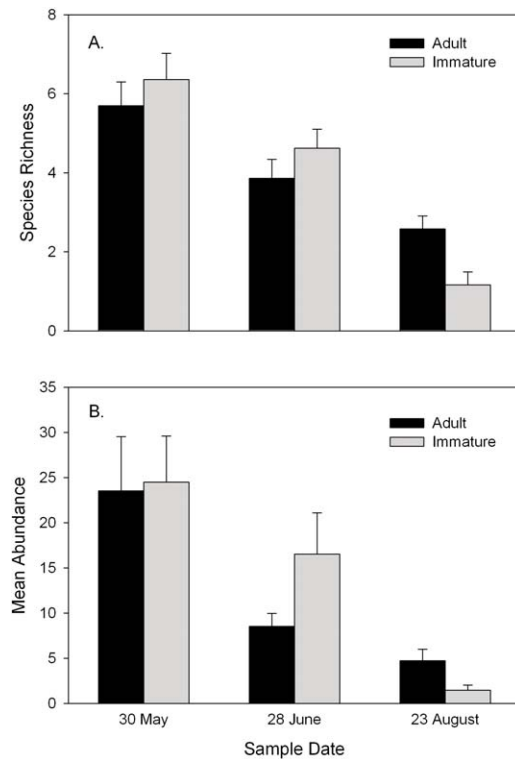


Fig. 1. (A) Species richness (RTUs per sagebrush sample) and (B) abundance (individuals per sagebrush sample) of arthropods on *Artemisia tridentata* shrubs in sagebrush steppe at Barton Research Area, Pocatello, ID. Whisker bars represent 95% confidence intervals.

al. (1989). Arthropod diversity was assessed as the mean number of RTUs (species richness) per sample.

We calculated abundance and diversity (RTU richness) of taxa and feeding groups (mean and 95% confidence intervals) and compared these among the early, mid-, and late summer sampling times. For each taxon that was sufficiently abundant for analysis, we used a chi-square goodness-of-fit test to determine whether abundance was uniform across the summer months. We used one-way ANOVA to test whether abundance and diversity of arthropods differed among sample periods. Repeated-measures ANOVA was not appropriate since we identified arthropods from a randomly selected half of the sagebrush plants from each sample period. We tested whether proportional diversity and abundance of the 5 feeding guilds differed among the sample periods using a chi-square test for association.

Insect Galls

We examined the distribution of *Rhopalomyia* galls within the canopies of 45 *A. tridentata* plants located within 15 plots chosen at random from the total 100 plots. We sampled galls from one small (<50 cm in height), one medium (50–100 cm in height), and one large plant (>100 cm in height) in each plot. Although we had no data on plant age, it is likely that the size categories corresponded to age categories. We sampled galls from each of the 4 cardinal quadrants (NE, NW, SE, SW) of medium and large plants but sampled small plants from only 2 quadrants (N and S) to reduce stress from foliage removal. Galls were sampled only once, in late June, when one 15-cm branch terminus was clipped from each quadrant, bagged, and frozen for later analysis.

We counted and recorded the locations of *Rhopalomyia* galls on these branch termini, placing branches flat on a white surface to help illuminate galls, and identified arthropods to species following Gagne (1989). We used chi-square goodness-of-fit procedures to test whether galls were evenly distributed along the 15-cm *Artemisia* branch tip, among canopy quadrants, and among plant size-age classes. For the last test, small shrubs were analyzed separately from mid- and large shrubs because they were sampled differently. We used the total number of galls for each plant size-age class and quadrant to run 2 chi-square analyses.

RESULTS

Free-living Arthropods

We collected 3991 individuals representing 12 orders and 40 families of free-living arthropods. These were separated into 220 RTUs. A few groups of insects predominated in the samples. Homoptera (65%), Hemiptera (13%), Hymenoptera (4%), and Lepidoptera (6%) were the most commonly collected insects, whereas Collembola, Diptera, Neuroptera, Orthoptera, and Psocoptera each comprised <0.4% of individuals. Sixty-eight percent of all individuals from all sample periods were from 3 insect orders: Aphididae, Cicadellidae, and Miridae. Thirty-seven percent of all individuals were cicadellids (Table 1).

Both arthropod RTU richness and abundance changed significantly from May to August

TABLE 1. Summer phenology (May–August) of arthropod taxa from *Artemisia tridentata* shrubs in sagebrush steppe at Barton Research Area, Pocatello, ID. Values of χ^2 and P are from tests of goodness-of-fit to uniform abundance over the seasonal samples (all $df = 2$). Taxa represented by fewer than 5 individuals were not tested.

Order and family	Total number of arthropods			χ^2	P
	May	June	August		
Acari	22	79	117	62.93	<0.001
Coleoptera	23	10	21	5.44	>0.05
Collembola	0	10	3	12.15	<0.005
Diptera	4	4	6	0.57	0.75
Hemiptera	393	175	14	373.00	<0.001
Miridae	387	128	8	430.44	<0.001
Homoptera	1610	862	70	1399.83	<0.001
Aphididae	330	338	20	286.73	<0.001
Cicadellidae	1218	190	30	1734.16	<0.001
Coccidae	1	10	10	7.71	<0.025
Delphacidae	5	0	0	10.00	<0.01
Issidae	0	0	2	—	—
Margarodidae	9	3	4	3.88	>0.05
Ortheziidae	10	13	3	6.08	>0.05
Psyllidae	38	4	0	62.29	<0.001
Hymenoptera	88	43	36	28.61	<0.001
Formicidae	66	28	5	57.52	<0.001
Lepidoptera	193	21	9	285.13	<0.001
Carposinidae	5	0	0	10.00	<0.01
Cosmopterigidae	40	9	0	53.92	<0.001
Lyonetiidae	113	2	0	218.21	<0.001
Neuroptera	1	0	3	—	—
Orthoptera	3	2	1	1.00	>0.50
Psocoptera	3	0	1	—	—
Thysanoptera	64	36	21	23.62	<0.001
Plaeothripidae	0	34	19	32.87	<0.001
Thripidae	64	2	1	116.63	<0.001

(richness: $F_{2,147} = 84.525$, $P < 0.001$; abundance: $F_{2,147} = 38.194$, $P < 0.001$; Table 1, Fig. 1). Almost 50% of all species and 60% of all individuals were identified in the late-May samples. In contrast, only 16% of taxa and 8% of individuals were in the August samples. Most taxa changed significantly in abundance across the summer months. The great majority of taxa declined significantly in abundance over the summer; only the Acari and Coccidae were significantly more abundant later in the season (Table 1).

Abundance and RTU richness of both adult and immature forms decreased over the summer season (Fig. 1). Immatures and adults were similarly abundant early in the growing season, but adults increasingly became the predominant life stage as summer progressed. We identified similar numbers of taxa in adult and immature form early in the growing season, but more taxa were present as adults later in the summer.

Fluid feeders were the most taxon-rich feeding guild, comprising 87% of taxa in May, 92% in June, and 63% in August (Fig. 2A). Species of Homoptera, Hemiptera, and Thysanoptera

comprised the majority of fluid feeders. Defoliators were the second most diverse guild at the beginning of the season, which was also the time when the highest diversity of defoliators was present. In August, parasitoids were the second most diverse feeding guild, and parasitoid diversity also was highest in August. The most common predators were Hymenoptera, particularly Formicidae; the most common parasitoids were Chalcidoidea; and the predominant gall formers were Cecidomyiidae.

Feeding guilds differed in RTU richness over the growing season ($\chi^2 = 115.54$, $df = 8$, $P < 0.001$; Fig. 2A). The 3 most diverse feeding guilds declined in RTU richness over the summer, but RTU richness of adult galling insects was greatest in August, and that of parasitoids differed little among the seasonal samples.

The relative abundances of feeding guilds also differed over the growing season ($\chi^2 = 421.14$, $df = 8$, $P < 0.001$; Fig. 2B). The abundances of arthropods across feeding guilds showed similar patterns in their diversity, with defoliators, fluid feeders, and predators all declining in abundance over the growing

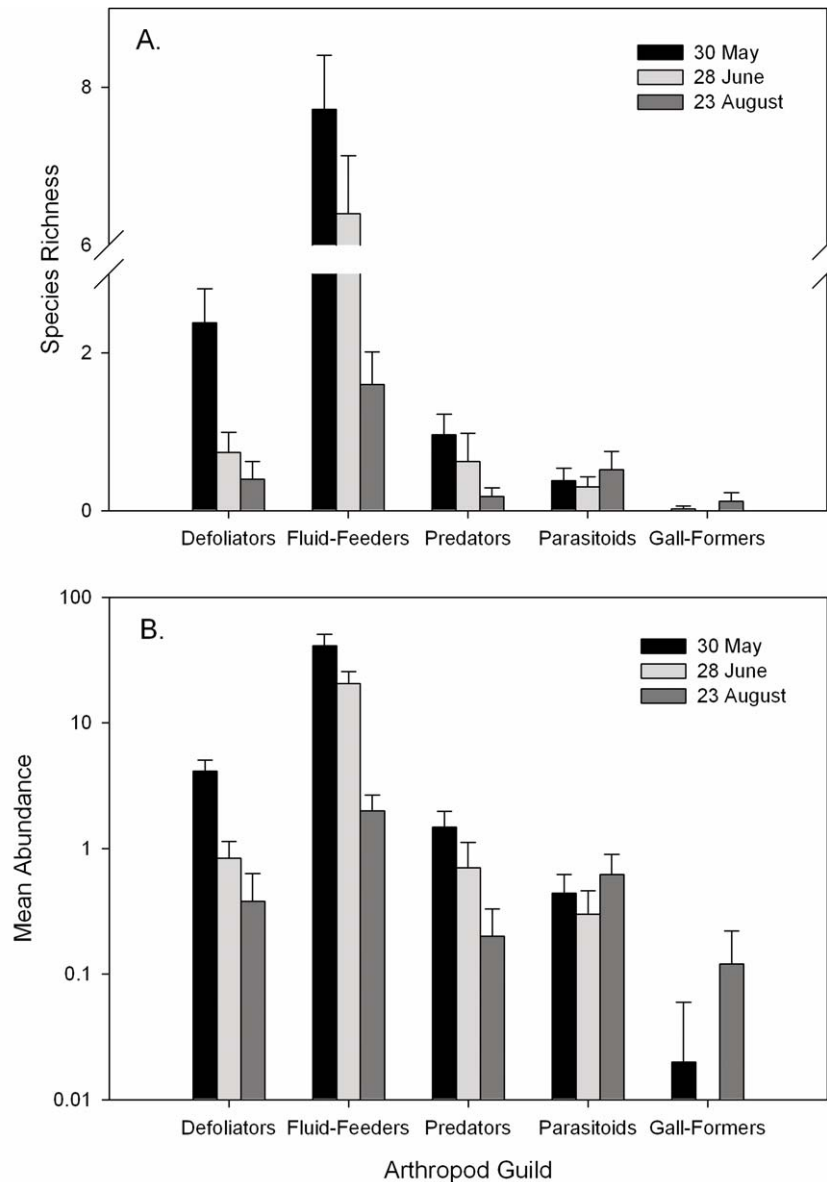


Fig. 2. (A) Species richness (RTUs per sagebrush sample) and (B) abundance (individuals per sagebrush sample) of defoliators, fluid feeders, predators, parasitoids, and gall formers on *Artemisia tridentata* shrubs in sagebrush steppe at Barton Research Area, Pocatello, ID. Whisker bars represent 95% confidence intervals.

season. Parasitoids, in contrast, tended to be more abundant in the late-season sample, and the free-living adult forms of galling insects were most abundant in the August sample.

Insect Galls

There were 4713 individual galls, formed by 12 species of *Rhopalomyia*, in our sample of *A. tridentata* branches (Table 2). Most galls

(97%) were of *R. ampullaria*, indicating strong dominance of a single taxon. Six of the remaining 11 species were roughly equal in abundance, and the other 5 were increasingly rare. Leaf galls (4654 individuals; 98.8%) were the most common gall type, with far fewer stem (55 individuals; 1.1%) and bud (4 individuals; 0.1%) galls. *Rhopalomyia ampullaria* also constituted 55% of stem galls.

TABLE 2. *Rhopalomyia* species and numbers of galls (total) found on 15-cm branch tips from 45 *Artemisia tridentata* shrubs at the Barton Research Area, Pocatello, ID. Descriptions of *Rhopalomyia* (Diptera: Cecidomyiidae) gall species are adapted from Gagne (1989). SAL = similar to *Artemisia* leaf. Gall sizes are recorded as length (L), width (W), and diameter (D).

Gall-forming species	Number	Type	Shape	Surface	Size (mm)	Color
<i>Rhopalomyia ampullaria</i>	4713	Leaf, stem	Conical	SAL	3–5 L	SAL
<i>Rhopalomyia brevibulla</i>	30	Leaf	Hemispherical	Short trichomes	1 L × 1 W	SAL
<i>Rhopalomyia calvipomum</i>	16	Leaf	Globular	Bare	8–20 D	Reddish
<i>Rhopalomyia hirtibulla</i>	1	Leaf	Hemispherical	Long trichomes	1 L × 1 W	Whitish
<i>Rhopalomyia lignitubus</i>	7	Bud	Tubular	Mostly bare	10–19 L	Red-brown
<i>Rhopalomyia medusa</i>	15	Stem	Spherical	Filamentous lvs	8–30 D	Red-green
<i>Rhopalomyia obovata</i>	23	Bud	Spherical	Short vestiges	5–10 D	SAL
<i>Rhopalomyia pomum</i>	7	Leaf	Globular	Short trichomes	8–45 D	Red-green
<i>Rhopalomyia rugosa</i>	20	Leaf	Ovoid	Mostly bare	4–6 L	Brown
<i>Rhopalomyia tubulus</i>	1	Leaf	Cylindrical	SAL	3–6 L	SAL
<i>Rhopalomyia tumidicaulis</i>	17	Stem	Ovoid stem	SAL	5–25 L	SAL
<i>Rhopalomyia tumidibulla</i>	2	Leaf	Hemispherical	SAL	3 D	SAL

TABLE 3. Number (mean with standard error in parentheses) of *Rhopalomyia* (Diptera: Cecidomyiidae) galls found on 15-cm branch tips of *Artemisia tridentata* shrubs at the Barton Research Area, Pocatello, ID. Plants were divided into 3 classes based on relative size. Branches were sampled from the 4 cardinal quadrants of mid- and large-sized plants; small plants had only north and south branches collected.

Size class	Quadrant				Mean number of galls
	NE	NW	SE	SW	
Small	5.96 (1.70)		10.55 (4.85)		7.44 (2.27)
Mid	27.53 (5.49)	38.57 (11.08)	24.80 (4.17)	31.21 (4.70)	30.33 (3.39)
Large	45.07 (7.63)	43.08 (7.08)	48.14 (11.64)	41.50 (8.42)	47.17 (4.37)

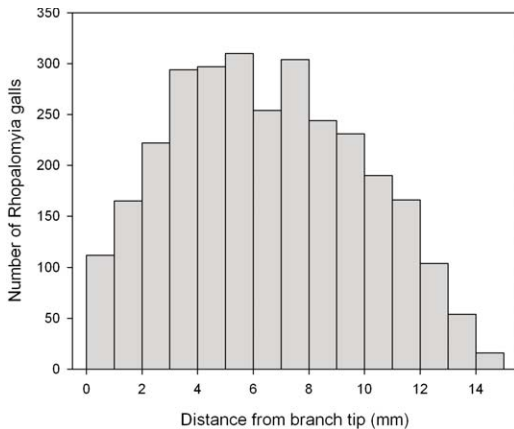


Fig. 3. Frequency distribution of *Rhopalomyia* (Diptera: Cecidomyiidae) galls along 15-cm distal ends of branches from 45 *Artemisia tridentata* shrubs sampled during late June 2000 at the Barton Road Research Area near Pocatello, Idaho.

Gall density varied significantly along branches, among aspects of the canopies of shrubs, and among size classes of sagebrush. Galls were primarily located from 3 to 9 cm from the tips of branches ($\chi^2 = 1052.44$, $df =$

9, $P < 0.001$; Fig. 3) and were more common on the southern sides of small shrubs ($\chi^2 = 15.02$, $df = 1$, $P < 0.001$; Table 3). Galls also were unevenly distributed among quadrants of mid- and large-sized plants ($\chi^2 = 92.47$, $df = 3$, $P < 0.001$, Table 3), but the disproportion was far less than on small plants. Additionally, the number of *Rhopalomyia* galls was greater on larger, presumably older, plants (Table 3).

DISCUSSION

We found a high diversity of arthropods on sagebrush, apparently greater than some previous studies suggest. For instance, Wiens et al. (1991) found 168 distinct arthropod taxa associated with sagebrush in Lake County, Oregon; and Christiansen et al. (1989b) collected 63 foliage-associated and 150 litter-associated taxa from sagebrush-bitterbrush habitat in Carbon County, Wyoming. In contrast, we collected 232 taxa from 50 shrubs sampled 3 times during the growing season.

The higher diversity of arthropods we observed could reflect our sampling strategies, which included dispersing the sample over entire plants and across the primary growing

season and subsampling for sessile galling insects. Our sampling strategy was likely not the most effective, however, for collecting taxa such as the Coccidae (scale insects), which probably remain attached to sagebrush despite vigorous sampling efforts. The sampling strategy also is likely not to have provided a strong index of such large and mobile herbivores as grasshoppers, which can cause significant leaf damage to sagebrush (Takahashi and Huntly unpublished data, Shiojiri and Karban 2008). We did not attempt to discern cryptic species, although we could have counted strongly dimorphic species or unidentified juvenile forms as distinct morphospecies when they were not distinct species. Thus we think our estimates of diversity are conservative. This conclusion is supported by the large pool of arthropod taxa associated with sagebrush (Welch 2005).

Differences between the above-mentioned studies and our study in observed numbers of big sagebrush arthropods could reflect geographic location (Idaho, Wyoming, Oregon) or subspecific differences in *A. tridentata*. Those study sites differ in elevation and other environmental attributes that may affect the composition and abundance of arthropods. They also represent parts of the range of *A. tridentata* that could host different variants of the species. A common garden study of *A. tridentata* subspecies showed that density of *Rhopalomyia* galls varied strongly with environment and *R. ampullaria*, the predominant galling species in our study, varied in density with elevation (Graham et al. 2001). Additionally, at least 6 subspecies of *A. tridentata* are recognized from the western United States, and these subspecies differ in secondary chemistry, which influences the distribution and abundances of many herbivorous insects and their predators (Schultz et al. 1977, Wiens et al. 1991, Schoonhoven et al. 2005). Subspecies of another desert shrub, rubber rabbitbrush (*Chrysothamnus nauseosus*), have distinct assemblages of arthropod species (Floate et al. 1996); in fact, these subspecies are better distinguished by their galls than by their morphology.

Another desert shrub, creosote bush (*Larrea tridentata*), which is a widespread dominant species of the southwestern North American desert, has an arthropod fauna that is regarded as abundant, diverse, and well characterized; nevertheless, it appears to have substantially fewer associated species of arthropods. Sanchez

and Parmenter (2007) reported 91 species associated with creosote bush in New Mexico, and several studies have reported fewer than 60 (Schultz et al. 1977, Lightfoot and Whitford 1987). However, 2 studies that sampled shrubs repeatedly over time, similar to the strategy we used, reported considerably higher diversity of arthropods on creosote bush: 147 (Schowalter et al. 1999) and 150 morphospecies (Rango 2005). These numbers are still well below the 232 taxa we found associated with sagebrush at one Idaho site but add support to the argument that arthropod diversity is only fully revealed by sampling over the growing season of the host plant.

Our study also suggests that the species richness of arthropods on individual shrubs is greater on big sagebrush than on creosote bush. Species richness of arthropods on individual creosote bushes ranged from an average of 3.2 morphospecies for the smallest shrubs to 10.8 for the largest shrubs (Sanchez and Parmenter 2002), based on a single sample of the whole shrub using fumigation with a knock-down insecticide. In contrast, we found 11.5 RTUs on average in a sample of one quadrant of an *A. tridentata* shrub in late May, 8.1 in June, and 2.82 at the end of August.

The density of arthropods on big sagebrush varied greatly over the growing season. Most arthropod groups were most abundant in the first sample period, early in the spring-summer growing season. Similarly, the arthropod communities of creosote bush have been found to be most dense and most species rich in late spring to early summer (Lightfoot and Whitford 1987, Rango 2005). Homopterans were the predominant free-living arthropods on *A. tridentata* at the end of May; and homopterans, especially aphids and cicadellids, declined greatly from May to August, as did ants, moths, and mirids.

Although creosote bush appears to have lower density and diversity of arthropods than documented for big sagebrush in this study, the composition of the arthropod faunas of *A. tridentata* and *L. tridentata* showed taxonomic and feeding-guild similarities. The most abundant taxa associated with creosote bushes in New Mexico were homopterans, especially membracids, followed by Lepidoptera and Hemiptera, especially mirids (Sanchez and Parmenter 2002). Homoptera, especially cicadellids and aphids, also were the most abundant

arthropod group associated with big sagebrush in our study and in studies in Oregon (Wiens et al. 1991) and Wyoming (Christiansen et al. 1989a, 1989b). Similarly, fluid feeders were overall the most diverse and abundant guild in most studies of creosote bush and/or big sagebrush, including our study. Also, like big sagebrush, creosote bush hosts a diverse guild of gall-forming arthropods, especially those of the cecidomyiid genus *Asphondylia* (Schowalter et al. 1999, Waring and Price 2008).

Galls of the cecidomyiid genus *Rhopalomyia* were strikingly abundant in our study, and a relatively high number of *Rhopalomyia* species used *Artemisia*, as also observed by Jones et al. (1983). Although galls of 12 species of *Rhopalomyia* were present, galls of a single species, *R. ampullaria*, greatly predominated. The high abundance of this taxon suggests that the sagebrush-steppe site we sampled was affected by surrounding land use. In another study, *R. ampullaria* was a significant indicator of arthropod samples from *A. tridentata* taken within sagebrush-steppe patches surrounded by dryland agriculture. In comparison, several different species of *Rhopalomyia*, including *R. medusa*, *R. tubulus*, and *R. culmata*, served as indicator species of samples taken from Craters of the Moon National Monument and Preserve—an area that is largely protected from agriculture and other uses by people (Bangert et al. in review).

Rhopalomyia galls were most abundant near the tips of branches. Within the canopies of many trees and shrubs, disproportionate abundances of some insect herbivores are found in areas of the plant where leaves are younger or have higher sun exposure (e.g., Basset 1991, 1992). We also observed that *Rhopalomyia* galls were disproportionately more abundant on the southerly portions of the canopies of small *A. tridentata*. However, as these plants mature, it appears that the differences in gall abundance are size-age related. It is not uncommon for there to be differences in leaf chemistry, leaf morphology, and herbivory among regions of the canopy of trees and shrubs (e.g., Basset 1991, 1992, Stork et al. 2001). For example, Joshua trees (*Yucca brevifolia*) allocate more nitrogen to southerly leaf rosettes (Rasmuson et al. 1994), and desert woodrats disproportionately consume these nitrogen-rich southerly rosettes (Sanford and Huntly 2009). Thus, assessment of potential systematic differences in diversity

and density within the canopy is needed to justify and interpret samples that are restricted to parts of the canopy, such as the branch tips and quadrants used in this study.

The patterns of arthropod diversity and abundance we observed suggest that the effects of arthropods on sagebrush vary over the growing season. Shiojiri and Karban (2008) found that chewing damage to sagebrush was greatest early in the season, following the spring flush of new leaves, in accordance with our observations of the abundance of chewing insects. However, other groups also likely affect *A. tridentata*. For instance, Wiens et al. (1991) found that fluid feeders had more influence on the secondary chemistry of *A. tridentata* than did other guilds. The most abundant taxa and all of the common free-living herbivore taxa were most abundant in late May, so the impact of arthropods on sagebrush seems to be greatest early in the growing season.

In conclusion, the data reported here document high density and diversity of arthropods on big sagebrush and provide a template for determining time frames and target taxa for future studies of arthropod-sagebrush interactions and sagebrush ecosystem dynamics. Both early sampling and repeated sampling over the growing season appear essential to documenting the full diversity and abundance of insects associated with sagebrush. However, if a single sample must suffice, then the maximum density and diversity would be captured by an early season sample.

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