LEAFHOPPER ASSEMBLAGES ON NATIVE AND RESEEDED GRASSLANDS IN SOUTHWESTERN MONTANA

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ABSTRACT.—Using sweep samples, we surveyed leafhoppers (Homoptera: Cicadellidae) on grassland sites in the Gallatin Valley of Montana during 1988 and 1991. We sampled 12 sites representing 2 habitat types defined by their dominant plant species in an undisturbed state (*Stipa comata / Bouteloua gracilis* and *Festuca idahoensis / Agropyron spicatum*). At half of the sites the native plant communities were present, whereas the remainder had been reseeded with either *Agropyron spicatum* (to replace the *S. comata / B. gracilis* assemblage) or *Bromus inermis* (to replace the *F. idahoensis / A. spicatum* assemblage). We found at least 66 species of leafhoppers among 44,428 adults collected. Seven taxa comprised 83% of all individuals collected: *Doratura stylata* (26%), *Ceratagallia* spp. (18%), *Endria inimica* (17%), *Orocastus perpusillus* (7%), *Sorhoanus* spp. (6%), *Athysanella* spp. (5%), and *Psammotettix lividellus* (4%). Sites with similar vegetation had broadly similar leafhopper assemblages, and assemblages differed most between the relatively xeric *Stipa comata / Bouteloua gracilis* sites and the more mesic sites dominated by *Bromus inermis*. The composition of a leafhopper assemblage at a site tended to be more similar to those on noncontiguous sites with the same overall vegetation than to those on contiguous sites with different vegetation. These patterns are likely related to the fact that many Cicadellidae are host specialists. In fact, variation in abundance of some of the most common leafhopper taxa on our sites was correlated with the percent cover of their known host plants. Our analyses of the leafhopper assemblages generally support the contention that terrestrial plant associations are among the more useful indicators of insect community composition.

Key words: biological diversity, grassland, habitat type, prairie, Homoptera, Cicadellidae.

In species richness and density of individuals, leafhoppers (Homoptera: Cicadellidae) are among the dominant herbivorous insects on temperate grasslands (Waloff and Solomon 1972, Cherrill and Rushton 1993, Whitcomb et al. 1994). Many leafhopper species are host-specific. For example, on mixed-grass prairie in Kansas, 54% of the leafhopper species were specialists on a single grass genus or on a small set of grass genera, whereas 7% were specialists on particular forbs (Whitcomb et al. 1986). Thus, many researchers have concluded that the distribution of leafhoppers is correlated with the distribution of their host plants (e.g., Whitcomb et al. 1986, 1987a, Cherrill and Rushton 1993, Hicks and Whitcomb 1993, 1996, Novotny 1994).

Nevertheless, studies of grassland leafhopper assemblages in North America indicate that distributions of many species do not completely encompass that of their host plants (Whitcomb et al. 1986, 1987a, 1987b, 1994, Hicks and Whitcomb 1996). The ability of leafhoppers to colonize sites containing host plants and to maintain populations there may also be influenced by climate (Whitcomb et al. 1987a), plant phenology (Whitcomb et al. 1994), and grazing (Morris 1973, Brown et al. 1992, Kruess and Tscharntke 2002). Plant nitrogen levels, physical structure and age of habitats, and proximity to adjacent grasslands have also been identified as potential correlates of the composition of leafhopper assemblages (Prestidge and McNeill 1983, Denno and Roderick 1990, Morris 1990a, 1990b, Brown et al. 1992). In addition, a plant assemblage variable that is a good predictor of the overall leafhopper assemblage may not predict the distribution of rare species of concern to conservation biologists (Panzer and Schwartz 1998).

The focus of our study was leafhopper assemblages on grasslands of the Gallatin Valley of southwestern Montana. The grasslands in this valley include at least 5 native "habitat types" (Mueggler and Stewart 1980), although many sites have been reseeded with nonnative grasses (Kemp et al. 1990a). Our specific objective was to answer several questions concerning

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the relationship of leafhopper and plant distribution. Do different vegetation assemblages in the valley harbor different leafhopper assemblages? Is the composition of a leafhopper assemblage at a site similar to those on contiguous sites with different vegetation or to those on noncontiguous sites with the same overall vegetation? Does the richness and diversity of leafhopper assemblages vary with corresponding plant variables? Does the abundance of leafhopper species correlate with percent cover of their host plants?

MATERIALS AND METHODS

Study Sites and Vegetation Assemblages

We sampled 12 sites in southwestern Montana, USA, between 45°42′ and 45°56′ north latitude and 111°00′ and 111°37′ west longitude (see map in O'Neill et al. 2001 for area containing sites). At each site we determined percent cover of grasses, forbs, and bare ground (methods and general results described in Kemp et al. 1990a, 1990b; see Table 1 for list of common plant species). The sites represented 2 habitat types named for their dominant plant species in an undisturbed state (Mueggler and Stewart 1980). The 6 sites at the western side of the valley are within the *Stipa comata / Bouteloua gracilis* habitat type, a relatively xeric grassland type occurring where annual precipitation is typically 20–35 cm. The 6 sites at the eastern side of the valley, near the foothills of the Bridger Mountains, are within the *Festuca idahoensis / Agropyron spicatum* habitat type, a relatively mesic grassland type occurring in areas generally receiving 35–50 cm annual precipitation. Half of the sites in each habitat type still have their native plant communities, and so are referred to here as SB (*Stipa / Bouteloua*) and FA (*Festuca / Agropyron*). However, 3 sites in each habitat type were reseeded as part of range management programs in the 1960s. Three SB sites were reseeded with crested wheatgrass (*Agropyron cristatum*) and (at 1 site) alfalfa (*Medicago sativa*), and are referred to here as AM. Three FA sites were reseeded with smooth brome (*Bromus inermis*) and (at 2 sites) alfalfa; these are referred to as BM. We refer to each sampling location as a "site" and sets of sites with similar vegetation as "vegetation assem-

blages." All but one of the native sites were paired with contiguous sites with reseeded vegetation, and so they are given identical numbers to designate adjoining sites: SB1/AM1, SB3/AM3, FA1/BM1, FA2/BM2, and FA3/BM3. Because SB2 and AM4 were 17 km apart, they are given different number designations.

Leafhopper Sampling

To sample leafhoppers with differing seasonal phenologies, we sampled 3 times in 1988 (26 May–2 June, 18–21 July, and 22–25 August) and 4 times in 1991 (18–27 June, 16–18 July, 6–8 August, and 13–16 September). The spread of dates in each sampling period was caused by travel distances between sites (up to 50 km) and the fact that we did not sample on cool, overcast days. Sweep samples taken on each date consisted of a set of 200 sweeps taken with a 40-cm-diameter sweep net along a linear transect, each sweep traversing a horizontal arc of 180° (parallel to the ground). Blocker and Reed (1976) found that suction sampling tended to capture greater numbers of leafhopper individuals than did sweep sampling, but the numbers of leafhopper species collected were similar using the 2 methods. However, it is likely that sweep sampling will underestimate the abundance of species that live close to the soil surface, a bias that we assumed was equal in all vegetation assemblages.

During sorting of samples we identified and counted only adults. When possible, all leafhoppers were identified to species, but a few taxa were difficult to identify beyond genus because of similarities in adult features or because of taxonomic problems. We identified 44 species (Table 2) that included 67.8% of the leafhoppers collected. Another 4 uncommon taxa (<0.2% of the leafhoppers) identified to genus were each apparently represented by a single species: *Dikrella* sp., *Empoasca* sp., *Laevicephalus* sp., and *Lonatura* sp. Nine taxa that included 32.0% of the leafhoppers collected are listed as "unresolved" genera: *Athysanella* spp., *Ceratagallia* spp., *Cloanthanus* spp., *Dikraneura* spp., *Elymana* spp., *Hecalus* spp., *Scleroracus* spp., *Sorhoanus* spp., and *Texananus* spp. In 5 of these genera we identified 14 species from male specimens (Table 2). We do not include species-level counts for these taxa because females were difficult to identify to species and we could not always associate

TABLE 1. Percent cover of the major grass and forb species at each site. Species listed include (1) those that occurred at >5% cover on at least 1 site, (2) less common species that were the most common forb at a site, and (3) several other species referred to in the text. Percent cover values for the most common grass and forb at each site are highlighted in bold.

	Percent cover at each site											
	SB1	SB2	SB3	AM1	AM3	AM4	FA1	FA2	FA3	BM1	BM2	BM3
BARE GROUND	23.9	10.8	13.8	16.3	35.3	34.0	6.8	2.7	10.6	25.1	35.3	34.0
ALL GRASSES	51.0	50.2	62.4	31.7	51.0	30.4	31.3	35.5	35.2	23.5	68.0	79.20
Agropyron cristatum L.	—	—	—	**31.1**	**49.1**	**29.3**	—	—	—	—	—	—
Agropyron intermedium (Host) Beauv.	—	—	—	—	—	—	—	—	—	—	6.4	11.3
Agropyron smithii Rydb.	4.0	0.1	—	—	—	—	3.1	0.4	—	—	—	—
Agropyron spicatum (Pursh)	0.4	—	0.3	—	—	—	4.9	8.2	6.0	—	—	—
Bouteloua gracilis (H.B.K.) Lag.	10.0	3.7	20.4	—	0.4	0.8	—	—	—	—	—	—
Bromis inermis Leyss	—	—	—	—	—	—	—	—	—	**20.1**	**57.3**	26.8
Bromis tectorum L.	—	—	—	—	—	—	0.6	1.25	0.1	—	—	—
Carex filifolia Nutt.	0.4	7.5	4.9	—	—	—	—	—	—	—	—	—
Festuca idahoensis Elmer	1.1	0.7	7.8	1.5	—	1.7	**12.2**	**21.9**	**23.0**	—	—	—
Koeleria cristata L.	—	—	—	—	—	—	0.5	0.03	0.9	2.7	2.2	**41.0**
Poa pratensis L.	—	—	—	—	—	—	0.5	—	—	—	—	0.1
Poa sandbergii Vasey	1.9	2.0	2.1	0.03	0.3	0.4	4.45	1.43	2.1	—	—	—
Stipa comata Trin. & Rupr.	**36.2**	**36.0**	**26.9**	—	0.7	—	2.3	—	—	—	—	—
Stipa viridula Trin.	—	—	—	—	—	—	—	1.6	—	—	—	—
ALL FORBS	20.4	4.4	8.4	1.6	6.3	0.9	30.6	30.6	49.4	18.4	1.1	6.0
Alyssum desertorum Stapf	—	0.03	—	0.05	0.2	0.05	1.5	0.9	0.7	0.7	0.2	—
Antennaria Gaertn. sp.	—	—	**4.6**	—	—	—	—	—	—	—	—	—
Artemisia frigida Willd.	—	**2.1**	—	—	—	—	—	—	—	—	—	—
Balsamorhiza sagittata (Pursh) Nutt.	—	—	—	—	—	—	**8.3**	3.5	**19.0**	—	—	—
Cerastium arvense L.	—	—	—	—	—	—	2.1	3.4	6.3	—	—	—
Lycopodium L. sp.	—	—	—	—	—	—	7.5	**12.3**	11.0	—	—	—
Lupinus sericeus Pursh	—	—	—	—	—	—	2.4	6.1	11.2	—	—	—
Medicago sativa L.	—	—	—	**37.3**	0.2	—	—	—	—	—	—	—
Melilotus officinalis (L.)	**17.1**	0.1	0.7	—	—	—	—	—	—	**17.6**	—	**5.3**
Microsteris gracilis (Hook.)	—	—	—	0.4	0.03	—	0.7	0.8	0.3	0.1	**0.4**	0.03
Vicia americana Muhl.	1.3	—	0.2	—	**4.1**	**0.5**	—	—	—	—	—	—

TABLE 2. Taxa of leafhoppers collected at Gallatin Valley sites. Taxon number refers to that used in Figures 1 and 4.

Taxon number	Taxon	Taxon number	Taxon
1	*Amblysellus grex* (Oman)	30	*Forcipata loca* (DeLong and Caldwell)
2	*Attenuipyga platyrhynchus minor* (Osborn)	31	*Frigartus frigidus* (Ball)
3	*Athysanella* spp.[1]	32	*Hardya dentata* (Osborn and Ball)
4	*Athysanus argentarius* Metcalf	33	*Hebecephalus rostratus* Beamer and Tuthill
5	*Auridius auratus* (Gillette and Baker)	34	*Hecalus* spp. Stål[5]
6	*Auridius helvus* (DeLong)	35	*Idiodonus aurantiacus* (Provancher)
7	*Auridius ordinatus* (Ball)	36	*Laevicephalus* sp. DeLong
8	*Balclutha neglectus* (DeLong and Davidson)	37	*Latalus missellus* (Ball)
9	*Balclutha punctata* (Thunberg)	38	*Lonatura* sp. Osborn and Ball
10	*Ballana veruta* Van Duzee	39	*Macrosteles quadrilineatus* (Forbes)
11	*Ceratagallia* spp.[2]	40	*Mesamia coloradensis* (Gillette and Baker)
12	*Chlorotettix unicolor* (Fitch)	41	*Mocuellus caprillus* Ross and Hamilton
13	*Cloanthanus* spp.[3]	42	*Neocoelidia tumidifrons* Gillette and Baker
14	*Colladonus geminatus* (Van Duzee)	43	*Norvellina seminuda* (Say)
15	*Colladonus montanus* (Van Duzee)	44	*Orocastus labeculus* DeLong
16	*Commellus sexvittatus* (Van Duzee)	45	*Orocastus perpusillus* (Ball and DeLong)
17	*Cuerna striata* (Walker)	46	*Paraphlepsius occidentalis* (Baker)
18	*Deltocephalus valens* Beamer and Tuthill	47	*Pinumius areatus* (Stål)
19	*Dikraneura* spp. Hardy[4]	48	*Prairiana cinerea* (Uhler)
20	*Dikrella* sp.	49	*Prairiana subta* Ball
21	*Diplocolenus configuratus* (Uhler)	50	*Psammotettix lividellus* (Zettinger)
22	*Doratura stylata* (Boheman)	51	*Rosenus cruciatus* (Osborn and Ball)
23	*Elymana circius* Hamilton	52	*Scleroracus* spp.[6]
24	*Elymana* spp.	53	*Sorhoanus* spp.[7]
25	*Empoasca* sp.	54	*Stenometopielus cookei* (Gillette)
26	*Endria inimica* (Say)	55	*Streptanus confinis* (Reuter)
27	*Endria rotunda* (Beamer)	56	*Texananus* spp.[8]
28	*Flexamia abbreviata* (Crumb)	57	*Xerophloea viridis* (Fabricius)
29	*Flexamia flexulosa* (Ball)		

[1]Includes *Athysanella acuticauda* Baker, *A. attenuata* Baker, *A. occidentalis* Baker, *A. robusta* (Osborn), *A. sinuata* (Osborn), *A. terebrans* (Gillette and Baker), *A. utahna* (Osborn).
[2]Includes *Ceratagallia* (*Aceratagallia*) *uhleri* (van Duzee).
[3]None identified to species.
[4]*Dikraneura shoshone* DeLong and Caldwell.
[5]Includes *Hecalus major* (Osborn), *H. viridis* (Uhler).
[6]None identified to species.
[7]Includes *Sorhoanus debilis* (Uhler), *S. flavovirens* (Gillette and Baker), *S. orientalis* (DeLong and Davidson).
[8]None identified to species.

them with males in samples. Some samples, in fact, contained only female specimens of particular taxa.

Statistical Analyses

We conducted chi-square goodness-of-fit tests to compare, among sites within the same vegetation assemblage, the total number of individuals collected in most common taxa; expected values were based on the null hypothesis of equal numbers of individuals per site. We used detrended correspondence analysis (DCA) to examine patterns of similarity in leafhopper communities among sites (CANOCO version 3.12). DCA is an ordination technique that summarizes counts from a site × taxon matrix (ter Braak 1988). In a site-based DCA, decreasing distance between sites on the ordination plot reflects increased similarity of assemblages from those sites. In a species-based DCA, decreasing distance between taxa indicates that they tend to occur at the same sites. To restrict analysis to a single taxonomic level, the DCA did not include the unresolved genera, whose abundances were examined using Kruskal-Wallis analyses. Using Spearmann's rank correlations, we examined the relationships of leafhopper taxon richness (number of species plus number of unresolved genera) to plant species richness, and leafhopper taxon diversity to plant species diversity. Using counts for each leafhopper taxon and total cover values for plant species, we calculated diversities for each site using Hill's #2 diversity index (Hill 1973), which has low sensitivity to small sample sizes (Magurran 1988).

TABLE 3. Total number of leafhoppers collected at each site in 1988 and 1991 and total richness and diversity values for leafhoppers and plants.

Sites	Plant species richness	Plant diversity (Hill's #2 index)	Number of leafhoppers collected		Number leafhopper taxa collected	Leafhopper diversity (Hill's #2 index)
			1988	1991		
SB1	21	3.58	1277	1652	29	4.66
SB2	16	2.21	2365	1267	27	2.40
SB3	19	4.20	705	1458	22	3.28
AM1	7	2.09	1674	1139	25	1.47
AM3	15	1.36	271	654	20	4.77
AM4	6	1.15	506	273	19	2.83
FA1	32	14.78	713	1213	28	5.56
FA2	27	7.89	479	953	27	4.27
FA3	30	7.05	602	710	34	4.46
BM1	8	2.43	2119	1045	19	2.00
BM2	11	1.44	1055	5282	26	2.97
BM3	11	2.91	5332	11,684	30	4.66

The index ranges upward from 0, a value of 0 occurring in assemblages consisting of 1 species (Ludwig and Reynolds 1988). We also used Spearmann's correlations to test the hypothesis that variation in abundance of particular taxa correlates with percent cover of known or suspected host plants. Although the literature contains numerous host records for leafhoppers, we analyzed only species for which at least 100 individuals were collected and which were found on >50% of the 12 sites.

RESULTS

Plant Assemblages

Among the 58 species of plants collected, 3 occurred at more than half of the sites, *Stipa comata, Alyssum desertorum,* and *Microsteris gracilis,* although neither of the latter 2 had high cover values on any site (Table 1). Among the 36 species found on 3 or fewer sites, 28 occurred in only 1 type of vegetation assemblage: 6 from SB, 16 from FA, and 3 each from AM and BM. Overall, the 4 vegetation assemblages differed in bare ground cover (Kruskal-Wallis test, $P = 0.03$), AM and BM sites having 5 of the 6 highest values, and in forb cover ($P = 0.06$), FA sites having the 3 highest values. The assemblages also differed in plant species richness ($P = 0.02$) and in plant species diversity ($P = 0.03$; Table 3), the highest values in both comparisons being from FA sites. Total grass cover did not differ among assemblages ($P = 0.41$).

Overall Leafhopper Fauna

Seven leafhopper taxa constituted 83% of the 44,428 adult leafhoppers collected (Table 2): *Doratura stylata* (26%), *Ceratagallia* spp. (18%), *Endria inimica* (17%), *Orocastus perpusillus* (7%), *Sorhoanus* spp. (6%), *Athysanella* spp. (5%), and *Psammotettix lividellus* (4%). Nineteen taxa were represented by fewer than 10 specimens each. We found no differences among vegetation assemblages in the number of leafhoppers collected in 1988 (Kruskal-Wallis test, $P = 0.15$) or 1991 ($P = 0.08$; Table 3).

Leafhoppers in *Stipa comata/ Bouteloua gracilis* Assemblages

The 8724 leafhoppers collected on SB sites included 28 species plus 6 of the unresolved genera (Fig. 1). Six taxa made up >90% of the leafhoppers collected: *Orocastus perpusillus* (33%), *Athysanella* (16%), *Ceratagallia* (22%), *Orocastus labeculus* (9%), *Mocuellus caprillus* (6%), and *Sorhoanus* spp. (5%). Relative abundance of all these taxa varied among SB sites (Fig. 2). Seven, mostly uncommon, species were collected only on SB sites: *Colladonus montanus* (8 individuals), *Endria rotunda* (3), *Flexamia abbreviata* (5), *F. flexulosa* (100), *Pinumius areatus* (2), *Prairiana subta* (2), and *Streptanus confinis* (1).
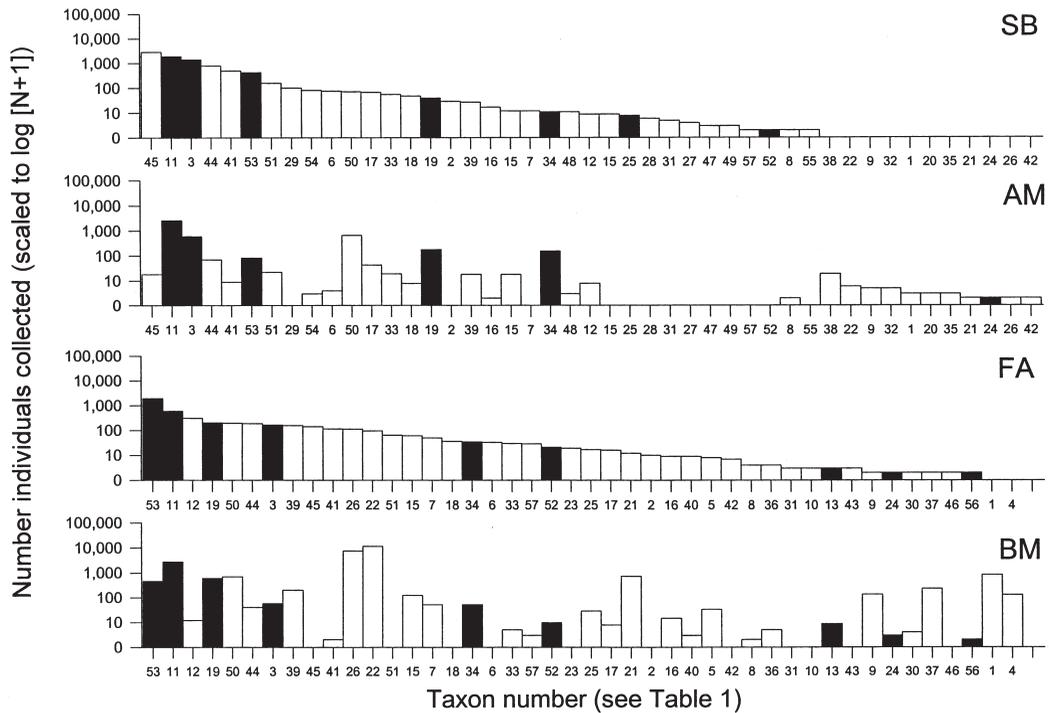
Fig. 1. Abundances of each species of leafhopper (both years combined). Numbers on x-axis refer to numbers given each species in Table 2. Taxa on SB sites were ranked from most to least abundant, and this order was used for AM assemblages; taxa on FA sites were ranked from most to least abundant, and this order was used for BM assemblages. Open bars are taxa consisting of 1 species; black bars indicate the unresolved genera.

Leafhoppers in *Agropyron cristatum / Medicago sativa* Assemblages

The 4517 leafhoppers collected on AM sites included 26 species plus 6 of the unresolved genera (Fig. 1). Three taxa made up 74% of the leafhoppers: *Ceratagallia* spp. (57%), *P. lividellus* (15%), and *Athysanella* spp. (13%). Variability among sites was striking for all 3 taxa (Fig. 2). No other taxon comprised more that 4% of the leafhoppers collected on AM sites. *Ballana veruta* and *Norvellina seminuda* (2 specimens each) were collected only on AM sites.

Comparing AM leafhoppers with those on SB sites (which contain the native vegetation formerly on AM sites), 13 taxa found on SB sites were absent from AM sites, whereas AM sites contained 11 taxa absent from SB sites. Other notable differences included the relative rarity on AM sites of *O. perpusillus* (17 vs. 2862 individuals on SB), *O. labecullus* (71 vs. 789 individuals), and *M. caprillus* (8 vs. 491 individuals). The only taxon common on AM but not SB sites was *P. lividellus* (661 vs. 71 individuals).

Leafhoppers in *Festuca idahoensis / Agropyron spicatum* Assemblages

The 4670 leafhoppers collected on FA sites included 33 species plus all 9 unresolved genera (Fig. 1). Members of 3 taxa made up 54% of the leafhoppers collected (Fig 1): *Sorhoanus* (41%), *Ceratagallia* (13%), and *Chlorotettix unicolor* (7%). All 3 varied in abundance among FA sites (Fig. 2). The next most common taxa were *Dikraneura* spp. (4%), *P. lividellus* (4%), and *O. labeculus* (4%). Four species were found only on FA sites: *Dikrella* sp. (2 specimens), *Hardya dentata* (4), *Idiodonus aurantiacus* (2), and *Lonatura* sp. (18).

Comparison of the abundance rankings of the species collected in SB and FA (the 2 native assemblages) indicates that 9 species present on SB sites were absent on FA sites, most notably *F. flexulosa* and *Stenometopielus cookei*. Conversely, we collected 15 species on FA sites
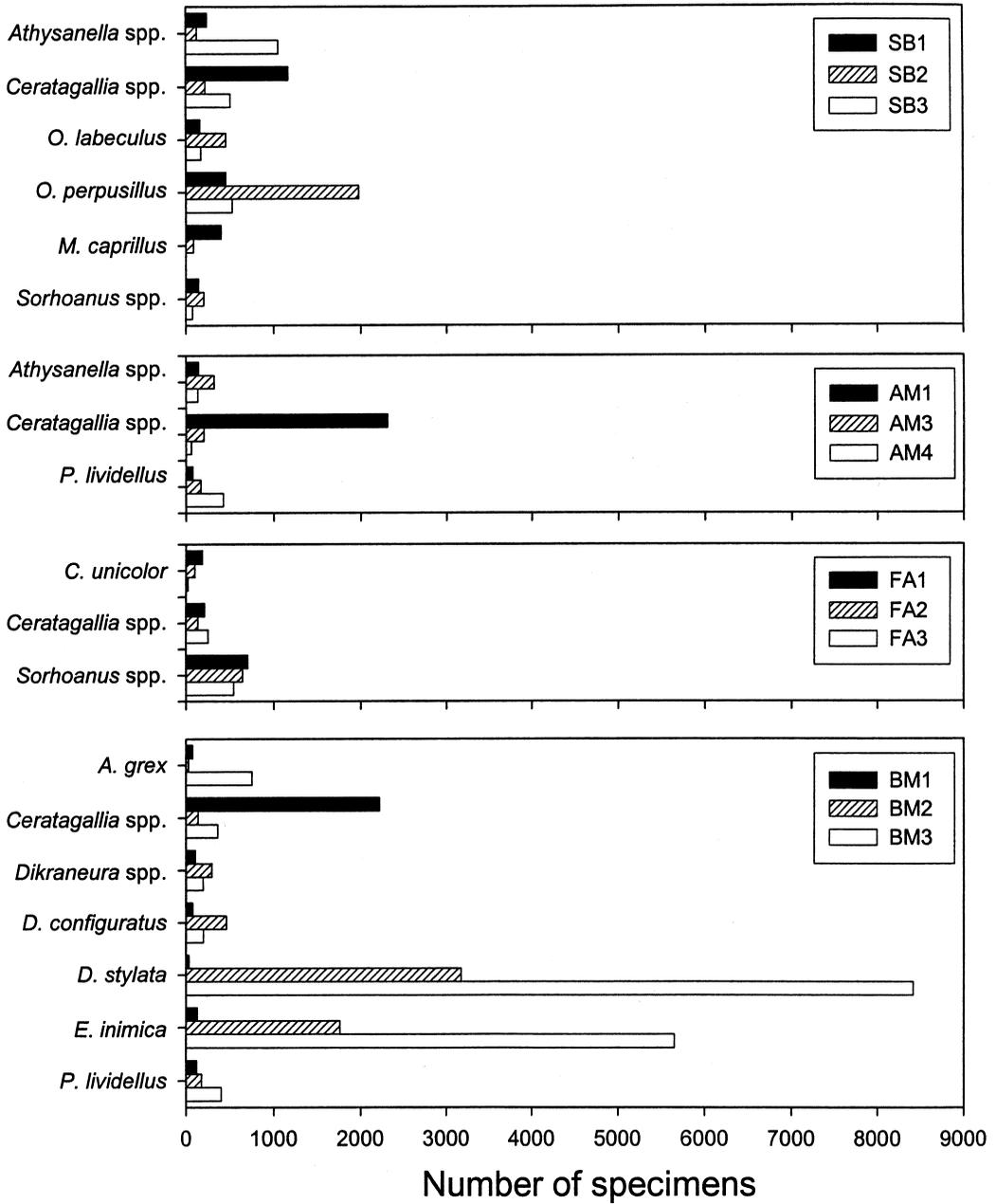
Fig. 2. Total number of individuals of most common taxa collected at each site. For each species/vegetation assemblage, we conducted a chi-square value goodness-of-fit test, the expected values being based on the null hypothesis of equal numbers of individuals per site. All chi-square values were significant at $P < 0.001$.

not found on SB sites, the most abundant being *E. inimica* and *D. stylata. Orocastus perpusillus,* the most common leafhopper identified to species on SB sites (2862 specimens), was the 8th most abundant species on FA sites (139). FA sites had among the highest values for leafhopper taxon richness and diversity (Table 3).

Leafhoppers in *Bromus inermis / Medicago sativa* Assemblages

The 26,517 leafhoppers collected on BM sites included 24 species and all 9 unresolved genera (Fig. 1). Two species comprised 72% of the leafhoppers on BM (Fig. 1): *D. stylata* (44%) and *E. inimica* (28%). Some of the relatively less abundant taxa occurred in numbers comparable to common taxa on other vegetation assemblages: *Ceratagallia* spp., *Amblysellus grex, Diplocolenus configuratus, P. lividellus,* and *Dikraneura* spp., which together made up another 21% of the leafhoppers on BM sites. All 7 taxa varied in abundance among sites (Fig. 2). *Athysanus argentarius* (135 specimens) was collected only on BM sites.

Comparing BM leafhoppers with those on FA sites (which contain the native vegetation formerly on BM sites), 10 species were present on FA but absent from BM (e.g., *Attenuipyga platyrhynchus*), whereas BM sites contained only 2 species absent from FA (*A. grex* and *A. argentarius;* Fig. 1). The most striking differences were in abundance of *D. stylata* and *E. inimica* on contiguous sites. We collected 10,371 individuals of these species on BM3 but only 83 on FA3; a similar comparison for BM2 and FA2 was 4934 vs. 33 specimens.

It is also clear that the SB and BM sites differed considerably. The 3 most common taxa identified to species on SB sites (*O. perpusillus, O. labeculus,* and *M. caprillus*), as well as *Athysanella* spp., were rare to absent on BM sites. BM sites, on the other hand, were dominated by 2 species not present on SB sites (*D. stylata* and *E. inimica*).

Ordination Analyses

In the 1988 site-based DCA (Fig. 3), SB and FA native habitats formed fairly discrete clusters separated from the reseeded forms of each native assemblage. AM3 and AM4 also form a pair, as do BM2 and BM3. However, AM1 and BM1 are closer to each other on the plot than to other sites in their respective veg-

etation assemblages, indicating that they shared relatively similar leafhopper assemblages. Unlike other BM sites, BM1 had few *D. stylata* and *E. inimica.* BM1 also shared high numbers of *Ceratagallia* spp. with AM1 (which were not abundant on AM3 or AM4), although that genus was not included in the DCA. In the DCA for 1988, axis 1 accounted for 27.7% of variance in the data, whereas axis 2 accounted for 12.6%. In the 1991 site-based DCA, sites with similar vegetation were less closely associated than in 1988, although some separation by vegetation type was still evident, particularly along axis 1. Axis 1 accounted for 39.5% of variance in the data, whereas axis 2 accounted for 7.2%. In contrast to 1988, there were several instances in 1991 in which native sites clustered fairly closely with their contiguous reseeded sites: SB3 was more closely associated with AM3 than with other SB sites, and BM1 was more closely associated with FA1 than with other BM sites. In both years the separation among SB sites appeared to be due to higher abundance of the certain taxa on 1 site, but not the other 2: *M. caprillus* on SB1, *Orocastus* spp. on SB2, and *F. flexulosa* and *Athysanella* spp. on SB3. Similarly, compared to FA1 and FA2, FA3 had the lowest numbers of *C. unicolor* and *Macrosteles quadrilineatus* in both years and of *Elymana circius* in 1991.

We observed similar patterns when we compared the species-based DCA for the 2 years (Fig. 4). For 1988, two clusters of species occur on opposite ends of axis 1. On the left side is a cluster of 11 species. For 10 of these, >50% of the specimens were collected on SB sites; the exception was *Hebecephalus rostratus* (species 33 on the plot), 49% of which were found on SB sites. *Cuerna striata* (species 17), below and to the right of this cluster, was found primarily on SB sites (54% of specimens), but it was nearly as common on AM1 (37%). On the right side of the plot is a tight cluster of 8 species for which 96%–100% of the specimens were collected on BM sites. Among the 5 species between these 2 clusters were *C. unicolor* (species 12, 96% FA) and *Balclutha punctata* (species 9, 99% BM). The remaining 3 species were present in sizable proportions in more than 1 vegetation assemblage: *Colladonus geminatus* (species 14, 35% BM but present in all 4 assemblages), *M. quadrilineatus* (species 39, 66% BM, 34% FA), and *P. lividellus* (species
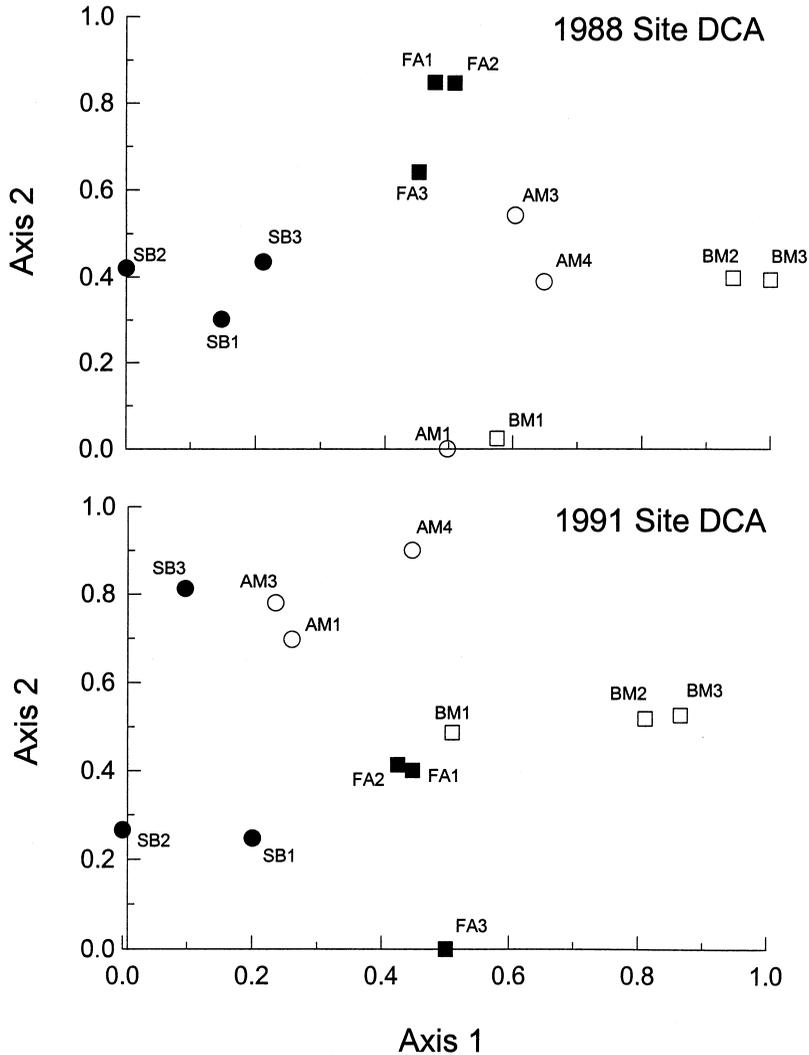
Fig. 3. Site-based detrended correspondence analysis. SB = ●; FA = ■; AM = ○; BM = □.

50, 51% AM, 36% BM, 12% FA). On the 1991 species plot, discrete clusters of species were much less apparent, although species showing an affinity for SB sites were again on the left side of the plot, whereas those most common on BM sites were on the right side. In most cases these were the same species in those locations in the 1988 ordination. The more widespread species *C. geminatus, M. quadrilineatus,* and *P. lividellus* were again in the middle of the plot.

Distribution of the Unresolved Genera

In both years numbers of *Athysanella* spp. and *Sorhoanus* spp. differed among sites, *Athysanella* being most abundant on SB sites and *Sorhoanus* spp. on FA sites (Fig. 5). Neither *Ceratagallia* spp. nor *Dikraneura* spp. exhibited differences in 1988, but *Dikraneura* spp. were more abundant on BM sites in 1991.
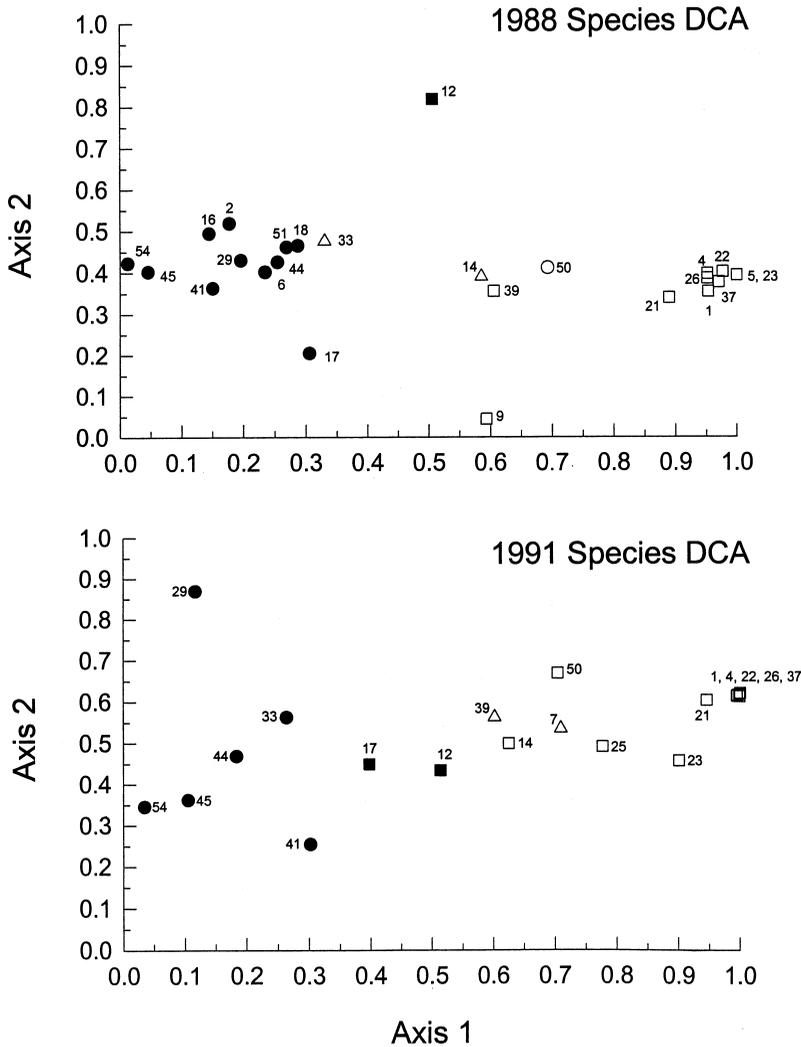
Fig. 4. Species-based detrended correspondence analysis. Analyses included all species of grasshoppers (46 in 1988 and 37 in 1991, but not the unresolved genera), but only those for which at least 20 individuals were collected are included on the plot. Symbols assigned based on which vegetation assemblage yielded >50% of the specimens collected for a given species: SB = ●; FA = ■; AM = ○; BM = □; no vegetation assemblage had more than 50% of the specimens = △.

Plant-Leafhopper Correlations

Leafhopper taxon richness was significantly correlated with plant species richness (Spearmann correlation, $r = 0.65$, $P = 0.02$, Table 3), but leafhopper diversity was not correlated with plant diversity ($r = 0.44$, $P = 0.14$). For all 8 of the relatively widespread and abundant leafhopper taxa that we examined, we found significant correlations between abundance and percent cover of reported hosts (Table 4).

DISCUSSION

Our results are consistent with the hypothesis that the distribution of leafhopper species and the composition of local assemblages are related to the composition of local plant assemblages (DeLong 1965, Whitcomb 1987, Whitcomb et al. 1987a, 1987b, 1994; but see Brown
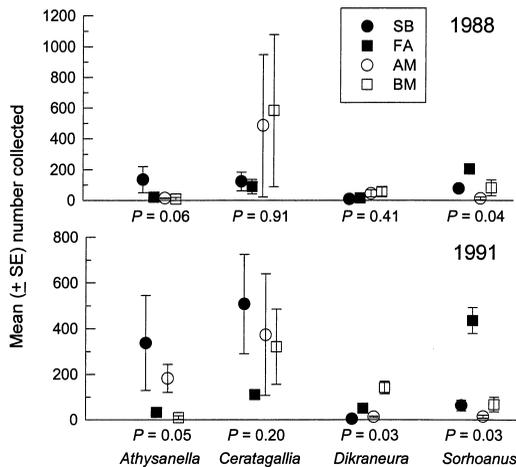
Fig. 5. Number of individuals of the 4 major unresolved genera collected in each of the vegetation assemblages in 1988 and 1991 ($N = 4$). P-values refer to results of Kruskal-Wallis tests.

et al. 1992). The greatest differences occurred between the relatively xeric SB sites in the western part of the valley and the more mesic, higher-elevation BM sites in the east near the Bridger Mountains. Leafhopper assemblages at a site tended to be more similar to those on noncontiguous sites with the same overall vegetation than to those on contiguous sites with different vegetation. However, there were also differences in leafhopper assemblages when we compared sites within the same vegetation assemblage. This is not surprising because each site had its own unique frequency distribution of plant cover values despite similarities in dominant grass species.

Among 29 leafhopper taxa for which we found >50 specimens, 16 occurred primarily within 1 type of vegetation assemblage (defined here as having more than two-thirds of the individuals collected in 1 type of assemblage). Six occurred mainly on SB sites: *F. flexulosa* (100% of all specimens), *S. cookei* (98%), *O. perpusillus* (95%), *M. caprillus* (80%), *O. labecullus* (73%), and *Auridius helvus* (68%). Another 8 were found mainly on BM sites: *A. argentarius* (100%), *A. grex* (99.8%), *L. missellus* (99.6%), *D. stylata* (99%), *E. inimica* (99%), *D. configuratus* (98%), *B. punctata* (97%), and *E. circius* (87%). Together, these 14 species constituted >88% of the leafhoppers identified to species, so contrasts between these 2 groups likely influenced the positioning of SB and BM sites in

the ordinations. Two taxa, *C. unicolor* (92%) and *Sorhoanus* spp. (67%), were found mainly on FA sites, but none were located predominantly on AM sites. Of 14 taxa collected in only a single type of vegetation assemblage, only *F. flexulosa* (100 specimens) and *A. argentarius* (135) were represented by >18 individuals.

There are perhaps several reasons why we did not observe better separation among sites with different vegetation assemblages in the site-based DCA. First, only a few leafhoppers showed their greatest abundance on FA sites, and none did on AM sites. Second, there was considerable variation within vegetation assemblages in the abundance of some of the common species. Third, the abundant unresolved genera *Athysanella, Ceratagallia,* and *Sorhoanus* were not included in the analysis. If they had been identified to species, differences among habitats may have been more apparent. For example, *Ceratagallia* feeds on legumes (Hamilton 1998) and was abundant in SB (1894 specimens), AM (2578), and BM (2716) assemblages. The distribution of legumes varied among assemblages. *Melilotus officinalis* was found only on the 3 SB sites and 1 AM site, whereas *Vicia americana* was the most common forb on the 2 other AM sites, and *Lupinus sericeus* was found only on the 3 BM sites. *Medicago sativa* was absent from SB and FA sites, and *Astragalus* spp. were not found on BM sites. Thus, depending on host preferences, the species of *Ceratagallia* in the Gallatin Valley may have consistently sorted themselves among vegetation assemblages. However, this remains to be examined. A similar situation may occur for *Athysanella,* whose host preferences may extend to particular species within grass genera (Whitcomb et al. 1986, 1994).

Although leafhopper species frequencies differed between SB and AM sites, reseeding the native SB sites to create *A. cristatum*–dominated pastures apparently did not result in habitats with a unique array of dominant leafhopper species. All species present on SB sites but not AM sites (and vice versa) consisted of <20 individuals in our samples. Only *P. lividellus* appeared to benefit from reseeding to *A. cristatum,* although the *Stipa*-feeding *Orocastus* apparently declined following the change. However, the creation of *Bromus inermis* pastures that also contained greater cover of *Poa pratensis* was associated with a major shift in the dominant leafhopper species. This

TABLE 4. Spearmann's correlation (r) between leafhopper taxon abundance and cover of known or suspected host plants; significance levels: $P > 0.05$, $*P < 0.05$, $**P < 0.001$. Data on leafhopper abundance were combined for 1988 and 1991.

Leafhopper	Plant taxon	r	Number of individuals	Number of sites on which taxon found	Source of host records
Athysanella spp.	*Bouteloua gracilis*	0.76**	2,231	12	Whitcomb et al. 1994[a]
Ceratagallia spp.	Fabaceae	0.66*	7,781	12	DeLong 1948, Hamilton 1998
Diplocolenus configuratus	*Poa* spp.	0.89**	746	7	DeLong 1948
Doratura stylata	*Poa* spp.	0.92**	11,720	7	DeLong 1948
Endria inimica	*Poa* spp.	0.96**	7,655	7	Bess personal observation
Mocuellus caprillus	*Agropyron smithii*	0.59*	613	9	K. Hamilton and R. Whitcomb personal communication
Orocastus labeculus	*Stipa comata*	0.94**	1,089	9	K. Hamilton personal communication
O. perpusillus	*Stipa comata*	0.95**	3,018	11	K. Hamilton personal communication

[a]Includes records for many *Athysanella* on *Bouteloua* spp., although none on the list were collected at our sites.

was particularly evident in numbers of *D. stylata* and *E. inimica* which, overall, were nearly 100 times higher on BM than on FA sites. Although there were also considerably greater numbers of *A. grex, A. argentarius, D. configuratus,* and *L. missellus* on BM sites, only *C. unicolor* and *Sorhoanus* spp. showed an appreciable decline relative to FA sites. Across the Gallatin Valley leafhopper diversity may actually be higher at the present due to the existence of both native and reseeded grasslands.

The relationship of leafhopper distribution to plant distribution is also evident when we examined species with known host plant preferences. Abundances of *D. configuratus, D. stylata,* and *E. inimica* were positively correlated with percent cover of *Poa.* All 3 exhibited their greatest abundance on BM sites, where *Poa pratensis* was the 1st or 2nd most abundant grass. The abundance of *Mocuellus caprillus,* which feeds on *Agropyron smithii,* correlated with percent cover of that species, which was most common on SB sites. Several other genera most common on SB sites were likely feeding on the 2 grasses that defined that vegetation assemblage. Both species of *Orocastus* were most abundant here and are reportedly *Stipa* feeders. Whitcomb et al. (1986, 1994) indicate that many *Athysanella* feed on *Bouteloua,* though their leafhopper species list does not overlap with ours. They also indicate that some *Athysanella* feed on grasses of the genera *Aristida, Buchloe, Hilaria,* and *Sporobolus,* but these 4 genera did not occur on our sites. Restricting our analysis to *Bouteloua gracilis,* we found that percent cover of this

grass was significantly correlated with *Athysanella* spp. abundance. *Flexamia flexulosa* occurred only on the 3 SB sites where *B. gracilis* was common. The abundance of *Ceratagallia* spp. increased with percent cover of Fabaceae. *Ceratagallia* were most abundant on SB1, SB3, and AM1, all of which had high *Melilotus officinalis* (yellow sweetclover) cover, and BM1 with its abundant *Medicago sativa* (alfalfa).

As noted by Brown et al. (1992) in their study of British grasslands, much variability in leafhopper community composition is left unexplained by host plant availability. This could perhaps be related to the predominance of cool-season grasses on British grasslands, and it also applies to northern U.S. grasslands (Whitcomb et al. 1986). In addition, abiotic conditions differed among our sites, the FA and BM sites (1450–1700 m elevation) being cooler and receiving about 30% more precipitation than the SB and AM sites (1300–1400 m; Kemp et al. 1990a). Although climate cannot account for differences in leafhopper assemblages between contiguous SB/AM or FA/BM sites, there may have been microclimatic differences driven by variation in vegetation height, density, and patchiness. In fact, Brown et al. (1992) found that leafhopper assemblages were affected by grazing-induced changes in plant architecture.

Urbanization, cultivation, grazing, reseeding, and invasion of exotic weeds have fragmented and diversified the grasslands within the Gallatin Valley. Habitat fragmentation also isolates small areas from patches of similar

vegetation that form potential sources of migrants. Thus, the distribution of leafhoppers in the valley may be influenced by distances between patches of suitable habitat, combined with limitations on the dispersal of leafhoppers (Whitcomb et al. 1987a, Brown et al. 1992, Stiling 1994). However, recency of introduction was clearly not always a limiting factor. *Athysanus argentarius* and *D. stylata* were common on BM sites and uncommon or absent in other vegetation assemblages. Both *A. argentarius* (Beirne 1956) and *D. stylata* (Hamilton 1983) have spread rapidly westward following their introduction to eastern North America in the last century. This large-scale range expansion suggests that their limited distribution in the valley is not due to poor dispersal capabilities.

One concern in studies of this type is that a strong effect of habitat area on insect species richness may confound correlations between plant variables and insect richness. However, in an analysis of leafhopper diversity on tallgrass prairie remnants in the midwestern U.S., Panzer and Schwartz (1998) found that, when the effect of habitat area was removed, plant species richness and generic richness remained as significant predictors of leafhopper species richness. Kruess and Tscharntke (2000) noted that fragmentation of agricultural landscapes caused greater reductions in parasitoid than herbivore diversity.

We have now examined the distribution of both leafhoppers and grasshoppers (Kemp et al. 1990a, 1990b, 2002, Wachter et al. 1998) across different vegetation assemblages in the Gallatin Valley. A comparison of the distribution patterns of the 2 groups is of interest because these 2 families include many of the important insect herbivores on grasslands. Variation in plant cover apparently goes further in explaining leafhopper distribution than it does grasshopper distribution. The cover of known host plants explained much of the variation in abundance of the 8 taxa we examined, taxa that made up the vast majority of leafhoppers collected. In contrast, when examined in fields containing both SB and AM patches, variation in the abundance of major grass species explained just 5%–28% of the variation in grasshopper numbers among plots (Kemp et al. 2002). This could be due partly to the different spatial scales at which the families were studied. However, it is also likely due to the fact that many Cicadellidae are host specialists (Whitcomb et al. 1994), while most grassland Acrididae are generalists that, at most, restrict their feeding to grasses vs. forbs (Mulkern et al. 1969).

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