



Endophytic insect communities of two prairie perennials (Asteraceae: *Silphium* spp.)

JOHN F. TOOKER and LAWRENCE M. HANKS*

*Department of Entomology, University of Illinois at Urbana-Champaign, 320 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA; * Author for correspondence (e-mail: hanks@life.uiuc.edu)*

Received 6 November 2002; accepted in revised form 1 September 2003

Key words: *Antistrophus*, Community structure, Cynipidae, *Eurytoma*, Eurytomidae, Fire, Mordellidae, *Mordellistena*, Multitrophic interactions

Abstract. Little is known of the biology of most insects that are endemic to prairie ecosystems of North America, with the exception of large and conspicuous species. In particular, species that are sequestered within plant tissues are commonly overlooked. In this paper, we assess the biodiversity of endophytic insects that inhabit stems of *Silphium laciniatum* L. and *S. terebinthinaceum* Jacquin (Asteraceae), endemic plants of tallgrass prairies. Endophytic herbivores, gall wasps *Antistrophus rufus* Gillette and *A. minor* Gillette (Hymenoptera: Cynipidae) and stem-boring larvae of the beetle *Mordellistena aethiops* Smith (Coleoptera: Mordellidae) were attacked by 10 species of natural enemies. We report new host plant associations for herbivores, and new host insect associations for parasitoids. The two plant species differed significantly in their densities of gall wasps and the vertical dispersion of galls within stems. Interactions within and between trophic levels attest to the biodiversity of endophytic insect communities, and the specialized nature of these insects suggests they are highly vulnerable to habitat conservation practices that involve destruction of dead vegetation.

Introduction

Prairies are the most imperiled of North American ecosystems (Samson and Knopf 1994; Steinauer and Collins 1996). Of the original 9 million hectares of Illinois prairie, only ~0.01% remains (ILENR 1994; Samson and Knopf 1994). Small patches of prairie are subjected to a variety of management practices that are intended to exclude invasive weeds and preserve endemicity of prairie plant communities, including grazing, haying, but especially prescribed burning (Steinauer and Collins 1996). However, these practices can have a detrimental impact on prairie fauna. For example, livestock grazing and prescribed burns alter habitat structure, resulting in reduced densities and/or abundances of birds, reptiles, and land snails (Corn and Peterson 1996; Byre 1997; Walk and Warner 2000; Nekola 2002).

Insect communities of prairies are highly diverse (Arenz and Joern 1996; Taron 1997; Williams 1999), but are poorly known (e.g., Favret et al. 2004). Thus, their vulnerability to prairie management practices is difficult to assess. Only a few prairie insect guilds have been surveyed (e.g., Whitfield and Lewis 2001), and as many as one half of North American prairie insect species

have yet to be described (Kosztarab and Schaefer 1990; Arenz and Joern 1996). Of the species known to science, there is little information on biology other than for large-bodied and conspicuous species (Arenz and Joern 1996). In particular, endophytic species have rarely been studied (Williams 1999) but appear especially vulnerable to management practices that destroy vegetation, such as burning.

The goals of the research described here were to: (1) identify members of endophytic insect communities of two plant species that occur in prairies of east central Illinois; (2) determine where insects feed within plants to assess their vulnerability to prescribed burning; (3) characterize the phenology of insect species; (4) describe the behavior of the dominant insect species; and (5) assess trophic relationships among species. This research will be of value in assessing the impact of management tactics on insect communities and in evaluating the efficacy of methods of restoring prairie ecosystems. In a companion paper, we assess the impact of prescribed burning on this endophytic insect community (Tooker and Hanks 2004a).

We studied endophytic insect communities of two sibling plant species, *Silphium laciniatum* L. and *S. terebinthinaceum* Jacquin (Asteraceae), common herbaceous perennials in tallgrass prairies of the mid-western United States (Gleason and Cronquist 1991; Clevinger and Panero 2000). Stems of *Silphium* species harbor a diverse, yet poorly characterized insect community (see Rathke 1976). These plants produce as many as 12 flowering stems that can be 2–4.5 m tall (Weaver 1954). In central Illinois, *S. laciniatum* bolts in mid- to late May and *S. terebinthinaceum* in mid- to late June. *S. laciniatum* usually has many alternate leaves (>20-cm long) with large, thick clasping stipules along the basal third of the stem, while *S. terebinthinaceum* has only a few small (<7-cm long) alternate leaves with smaller and thinner clasping stipules along the basal two-thirds. Flowering stems senesce in fall, detaching from the taproot and falling to the ground during winter.

Materials and methods

Study sites

Our studies were conducted in six tallgrass prairie remnants and two restorations in five counties of central Illinois (Table 1, Figure 1). To ensure that insect communities were well represented, we chose sites that were either unmanaged or subjected to annual spring or fall burning over only half their area (grazing and haying are not typically used for managing small prairies in central Illinois). All of our prairie study sites were mesic black soil prairies dominated by *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michaux) Nash, and *Sorghastrum nutans* (L.) Nash and had at least 20 mature plants of *S. laciniatum* and/or *S. terebinthinaceum*.

Table 1. Prairie sites where we collected *Silphium* stems and observed insect behavior. 'Remnants' are prairie sites that have never been plowed, while 'restorations' are sites that have been replanted with prairie vegetation.

County	Prairie site (acronym)	Site description	Area (ha)	GPS coordinates
Champaign	Red bison prairie corridor (RBP)	Managed railroad right-of-way, restoration	1.7	N40°04.81 W88°14.83
	Trelease prairie (TP)	Managed restoration	7.3	N40°07.76 W88°08.59
Iroquois	Rt. 45 prairie (R45P)	Unmanaged railroad right-of-way, remnant	0.5	N40°31.26 W88°04.26
	Loda cemetery prairie nature preserve (LCP) ^a	Managed remnant	1.4	N40°31.61 W88°04.57
Ford	Prospect cemetery prairie nature preserve (PCP) ^a	Managed remnant	2	N40°26.71 W88°05.87
McLean	Weston cemetery prairie nature preserve (WCP) ^a	Managed remnant	2	N40°44.79 W88°36.80
Will	Grant creek prairie nature preserve (GCP) ^a	Managed remnant	31	N41°22.10 W88°11.55
	Midewin national tallgrass prairie (MNTP)	Mixed managed and unmanaged habitats, including restored and remnant prairie	~7700	N41°20.59 W88°07.96

^aIllinois nature preserves system (McFall and Karnes 1995).

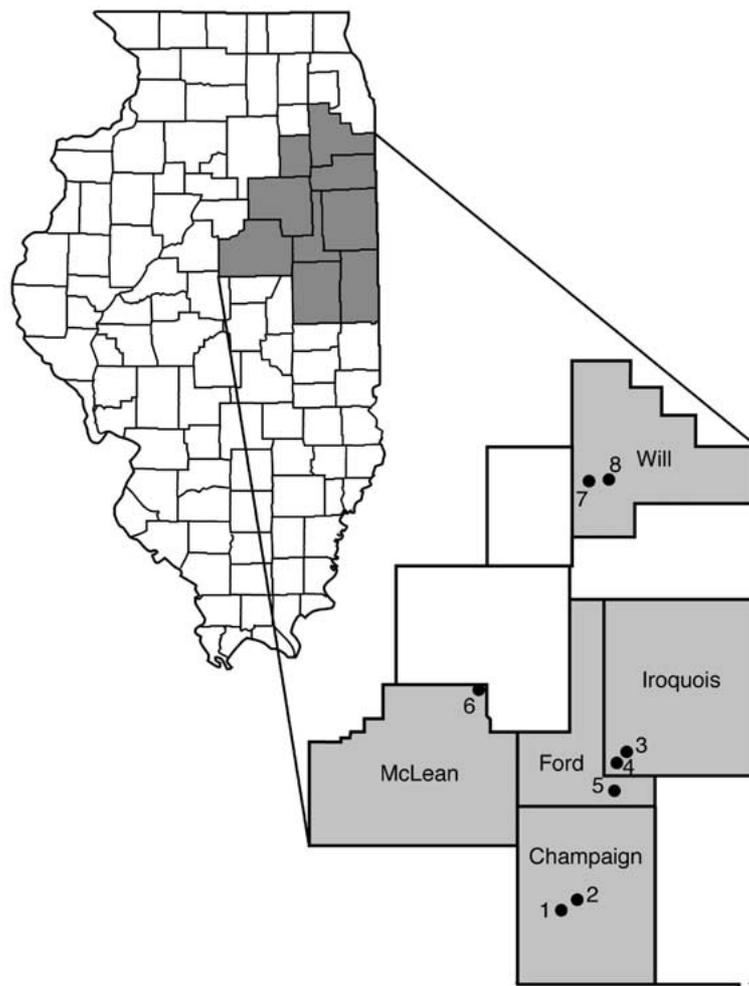


Figure 1. Location of study sites in east central Illinois: (1) Red bison prairie corridor, (2) Trelease prairie, (3) Rt. 45 Prairie, (4) Loda cemetery prairie nature preserve, (5) Prospect cemetery prairie nature preserve, (6) Weston cemetery prairie nature preserve, (7) Grant creek prairie nature preserve, (8) Midewin national tallgrass prairie.

Insect community and dispersion within stems

The pith and cambium of *Silphium* stems were inhabited by larvae of gall wasps in the genus *Antistrophus* that fed within one-chambered ellipsoid galls (Gillette 1891; Beutenmüller 1910; Weld 1959; Felt 1965). Densities could exceed 600 galls per plant stem (unpublished data). Galls did not alter the stem surface, however, and so were not discernible externally (Figure 2; Tooker et al. 2002).

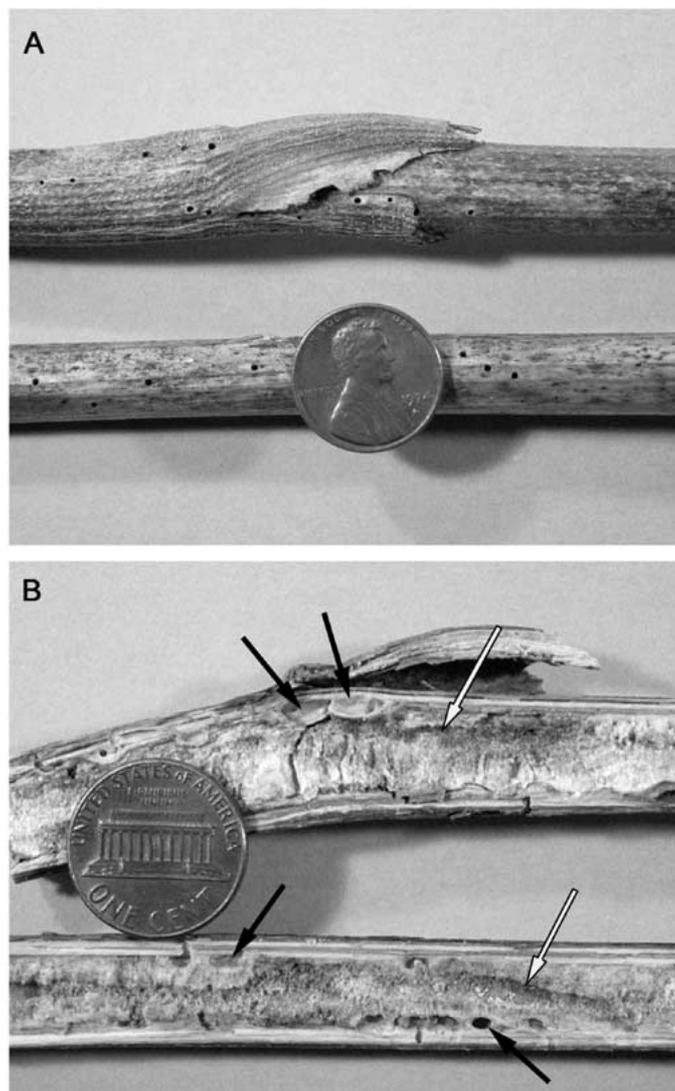


Figure 2. Dead flowering stems of *Silphium* species. (A) Emergence holes of gall wasp adults in proximity to stipules of *S. laciniatum* (top, with petiole removed) and in internode region of *S. terebinthinaceum* (bottom). (B) Stems of *S. laciniatum* (top) and *S. terebinthinaceum* (bottom) cut open longitudinally to reveal *Antistrophus* galls (black arrows) and galleries of *M. aethiops* (white arrows).

To identify gall wasps and other species overwintering in flowering stems, we collected dead stems of both *S. laciniatum* and *S. terebinthinaceum* in November 1999 and March 2000 from three prairie sites (LCP, PCP, WCP;

Table 1, Figure 1) and stems of *S. terebinthinaceum* from five additional sites (RBP, TP, Rt45P, GCP, MNTP). We arbitrarily collected 8–20 stems per site from different plants, limiting our samples to minimize impacts on *Silphium* insect communities. Stems of *S. laciniatum* ($N = 44$) averaged 190 ± 31 cm (mean \pm SD) tall and 0.98 ± 0.09 cm diameter at the base tapering to 0.40 ± 0.14 cm at the apex. Stems of *S. terebinthinaceum* ($N = 82$) were 176 ± 36 cm tall and 0.61 ± 0.07 cm at the base tapering to 0.32 ± 0.08 cm. We removed dried flower heads and leaves and cut stems into 20-cm sections. Average section diameters of *S. laciniatum* and *S. terebinthinaceum* were 0.73 ± 0.03 and 0.39 ± 0.02 cm, respectively ($t = 10.9$, d.f. = 672, $P < 0.0001$). The 1729 sections were placed in individual plastic storage bags that were stored in an unheated outbuilding in Urbana, Illinois, until all adult insects had emerged. We compared average numbers of insects emerging from *S. laciniatum* and *S. terebinthinaceum*, and rates of parasitism of gall wasps in the two plant species, using pooled t -tests (equal variances between groups) or Satterthwaite t -tests (unequal variances; PROC TTEST, SAS Institute 2001). We were not able to identify species of gall wasps that were hosts of parasitoids, and so could not evaluate parasitism rates of gall wasp species separately.

To examine the vertical dispersion of galls within stems, we averaged the number of insects by section number (= height) for each plant species within each study site, then generated a mean across study sites. We combined into one category data for sections from heights of 200 cm or greater, increasing sample size for insects inhabiting the apices of stems. Vertical dispersion of insects was tested for the two plant species by ANOVA with number of insects being the response variable, plant species and stem section number as fixed effects, and study site as the replicate (PROC MIXED, SAS Institute 2001). To determine whether the interaction of fixed effects was significantly different from zero, we used t -tests generated by PROC MIXED (SAS Institute 2001). We used linear regression (PROC REG, SAS Institute 2001) to visualize the relationship between stem height and gall density.

We also studied the dispersion of galls in relation to stipules of the two *Silphium* species, because we had observed that adult gall wasps appeared to prefer to oviposit near leaf axils in *S. laciniatum* but in internodes of *S. terebinthinaceum* (see Results). Emergence holes of adult gall wasps and their parasitoids indicated the position of galls in stem sections. Proximity to stipules was quantified by determining the proportion of emergence holes that were within 2 cm of stipule bases ($N = 10$ entire stems of *S. laciniatum* and *S. terebinthinaceum* from site LCP).

Insect behavior

We studied the behavior of adult insects on *Silphium* plants at all eight prairie sites between 0900 and 1600 h at least twice weekly from May – October 2000. We searched dead stems of the previous year's growth and adjacent vegetation

for emerging or active adult insects to observe behaviors associated with mate location, courtship, and mating, and we searched for females on stems of the current year's growth and surrounding vegetation to observe behaviors associated with host plant location and oviposition.

Phenology of emergence

To characterize emergence phenology of endophytic species, we reared insects from nine stems each of *S. laciniatum* and *S. terebinthinaceum* that were collected in December 2000 from two sites that had large populations of both plant species (LCP, PCP). In Spring 2001, we cut stems into ~50-cm long sections, placed three stems of each species into each of three tomato cages (107 cm tall, 29 cm diameter at top) covered with a sleeve of organdy gathered at top and bottom. We randomly positioned these cages ~1 m apart in a straight line in the unshaded, grassy yard of a residence in Urbana, Illinois. We checked these cages at least every other day, collecting insects with an aspirator, from 1 April until no more insects emerged. We tested for differences between the two plant species in emergence times of insect species by ANOVA, with plant species and insect species as fixed effects and cage a random effect (nested within plant species), comparing emergence date of insect species between plant species with *t*-tests of least squared means (PROC MIXED, SAS Institute 2001).

Adult insects were submitted to specialists for identification (see Acknowledgements). Voucher specimens of all species (Cat. No. 18206–18239) have been submitted to the Insect Collection of the Illinois Natural History Survey (Champaign, Illinois).

We present means \pm 1 SE throughout, except where stated otherwise.

Results

Insect community and dispersion within stems

We reared 8653 insects of 24 species from the 126 *Silphium* stems. Densities of insects averaged 79.8 ± 76 (SD) insects per stem in *S. laciniatum* and 62.5 ± 56 insects per stem in *S. terebinthinaceum* ($t = 1.31$, d.f. = 66, $P = 0.20$). More than 95% of reared insects were the gall wasps *Antistrophus rufus* Gillette and *A. minor* Gillette and their hymenopteran parasitoids (Table 2). More adult gall wasps (*Antistrophus* species combined) emerged from stems of *S. laciniatum* than from *S. terebinthinaceum* (51.2 ± 10.2 and 30.1 ± 3.4 adults per stem, respectively; $t = 2.41$, $P = 0.018$). Across the two plant species, *A. rufus* was more than three times as abundant as *A. minor* (28.9 ± 2.7 and 8.5 ± 1.7 adults per stem, respectively; $t = 6.34$, $P < 0.0001$).

Parasitism rates of gall wasps (species combined) exceeded 80% in some stems and were similar in *S. laciniatum* and *S. terebinthinaceum* ($41.4 \pm 0.03\%$

Table 2. Total number of individual gall wasps, mordellid beetles, and natural enemies reared from flowering stems of *S. laciniatum* and *S. terebinthinaceum*. See Discussion for information on trophic levels.

	Insect family	Insect species	Trophic level	<i>S. laciniatum</i> (n = 44 stems)	<i>S. terebinthinaceum</i> (n = 82 stems)
From galls of <i>Antistrophus</i> spp.	Cynipidae	<i>A. rufus</i> Gillette	Herbivore	1562	2151
		<i>A. minor</i> Gillette	Herbivore	756	319
	Eurytomidae	<i>E. lutea</i> Bugbee	1° parasitoid (omnivore?)	943	2042
		<i>Eurytoma</i> sp. 1	1° parasitoid (omnivore?)	25	136
	Ormyridae	<i>Ormyrus labotus</i> Walker	1° parasitoid	49	156
	Eupelmidae	<i>Eupelmus vesicularis</i> (Retzius)	1° or 2° parasitoid?	6	2
		<i>Brasema</i> sp. 1	1° or 2° parasitoid?	51	22
		<i>Brasema</i> sp. 2	1° or 2° parasitoid?	26	27
		<i>Homoporus</i> sp. 1	1° or 2° parasitoid?	10	53
		<i>Mordellistena aethiops</i> Smith	Omnivore	20	62
Not from galls					
	Mordellidae				
	Braconidae	<i>Schizopyrmnus</i> sp. 1	1° parasitoid	20	38
		<i>Heterospilus</i> sp. 1	1° parasitoid	2	3
	Eulophidae	<i>Tetrastichus</i> sp. 1	1° parasitoid	40	109

and $39.5 \pm 0.03\%$, respectively; $t = 0.43$, $P = 0.67$). Parasitoids emerging from *Antistrophus* galls included *Eurytoma lutea* Bugbee (accounting for 84.2% of all parasitoids; Table 2) and *Eurytoma* species 1 (4.5%), *O. labotus* Walker (5.8%), *E. vesicularis* (Retzius) (0.2%), *Brasema* species 1 and 2 (7%), and *Homoporus* species 1 (1.8%). Both species of *Antistrophus* and the two dominant parasitoid species, *E. lutea* and *O. labotus*, were present at all eight of our prairie sites, but the less abundant parasitoid species were absent in samples from some sites.

Other insects reared from *Silphium* stems, but not inhabiting galls, were the mordellid beetle *M. aethiops* Smith and hymenopterans emerging from its galleries and presumably its parasitoids. Larvae of *M. aethiops* burrowed through stems consuming primarily pith tissue, and as many as seven adults emerged from single stems. Parasitism rates of *M. aethiops* were similar in *S. laciniatum* and *S. terebinthinaceum* ($56.0 \pm 0.11\%$ and $41.6 \pm 0.07\%$, respectively; $t = 1.19$, $P = 0.24$). Parasitoids included two braconid species, *Schizopyrmnus* sp. 1 (accounting for 80.6% of parasitism) and *Heterospilus* sp. 1 (6.9%), and the gregarious eulophid *Tetrastichus* species 1 (12.5%; Table 2). *M. aethiops* emerged from stems collected at all prairie sites, but parasitoids of some species were absent in samples from some sites.

A few specimens of beetle species not clearly associated with *Silphium* stems appeared in our emergence bags, including six individuals of a lathridiid species, three individuals of a bruchid species, and single specimens of elaterid, phalacrid, carabid, and clerid species (the last possibly an endophytic predator). There also were single specimens of *Diabrotica virgifera* LeConte, *D. barberi* Smith and Lawrence, and *D. undecimpunctata* Mannerheim that may have overwintered under stipules of stems or were concealed in debris adhering to stems. We also reared seven individuals of a braconid in the genus *Chorebus* (Braconidae: Alysiinae), parasitoids of cyclorrhaphous dipterans (Wharton 1997) not present in our samples.

Linear relationships between density of *Antistrophus* galls and height of stem sections differed significantly between plant species (Figure 3; ANOVA plant species effect $F_{1,9} = 13.1$, $P = 0.006$). Densities declined significantly with height in *S. laciniatum* (Figure 3; slope significantly different from zero, $t = 6.3$, $P < 0.0001$), but not in *S. terebinthinaceum* ($t = 1.0$, $P = 0.32$). The proportion of galls in the bottom 60 cm of stems of both plant species was inversely correlated with total number of galls per stem (*S. laciniatum*: $r^2 = 0.49$, $P < 0.0001$; *S. terebinthinaceum*: $r^2 = 0.25$, $P = 0.004$), suggesting that vertical dispersion of galls increased with density. For *S. laciniatum*, $62 \pm 3\%$ of *Antistrophus* galls (species combined) were located within 2 cm of the bases of leaf stipules compared to only $10 \pm 2\%$ for *S. terebinthinaceum* ($t = 13.5$, $P < 0.0001$; see Figure 2).

Insect behavior

Antistrophus species overwintered in dead *Silphium* stems and pupated in the early spring. *A. rufus* adults began emerging from *S. laciniatum* in mid-May

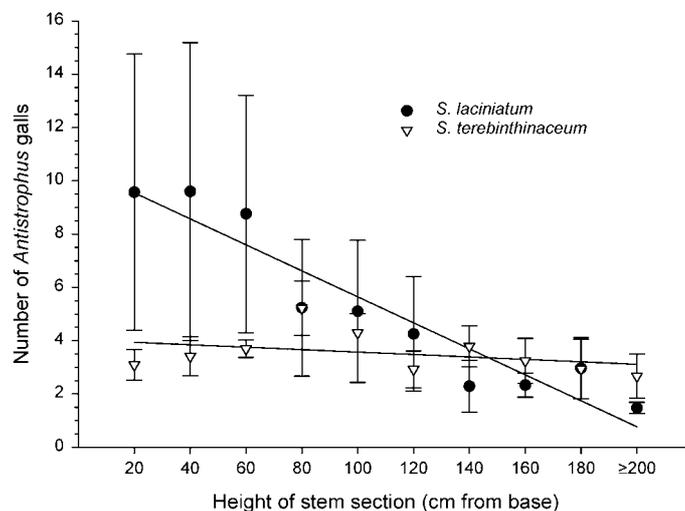


Figure 3. Relationship between number of galls (*Antistrophus* species combined) in 20-cm long sections of flowering stems of *S. laciniatum* and *S. terebinthinaceum* and stem height. Each point represents the mean (± 1 SE) number of *Antistrophus* galls in sections averaged within study sites ($N = 8$ –20 stems per site) and these means were averaged across three study sites for *S. laciniatum* ($N = 44$ plants) and five sites for *S. terebinthinaceum* ($N = 82$ plants). Best fit regression equations: *S. laciniatum*, $Y = -0.05X + 10.5$; *S. terebinthinaceum*, $Y = -0.005X + 4.03$ (see text for statistics).

and from *S. terebinthinaceum* in mid-June 2000. Although adults of both sexes have fully developed and functional wings, they did not fly readily but rather walked, with occasional hopping flights to nearby plants. On both plant species, males emerged first and were present only on dead stems of the previous year. There they guarded areas of stem where females later emerged, driving off other males by charging or butting with the head ($N > 10$ observations). Females mated immediately upon emerging and then moved to nearby developing *Silphium* stems ($N > 10$). As many as 20 females oviposited in one stem at the same time. Oviposition usually lasted less than 1 min ($N > 10$). Females oviposited in axils of *S. laciniatum* before bolting, but in *S. terebinthinaceum* they oviposited in the internodes after bolting, accounting for the greater proportion of emergence holes near stipules of *S. laciniatum* (see previous section).

Adults of *E. lutea* appeared on *Silphium* stems in mid-June. Females flew between stems of *S. laciniatum* and *S. terebinthinaceum* apparently in search of hosts ($N > 5$ observations). Oviposition by *E. lutea* females lasted less than 1 min ($N > 5$).

Larvae of *M. aethiops* overwintered in stems and pupated in spring with adults emerging in early June. Female *M. aethiops* deposited their eggs singly on the surface of stems, dragging their ovipositor over the oviposition site after laying the egg ($N = 4$ observations), presumably applying a material that may protect the egg or discourage oviposition by conspecifics.

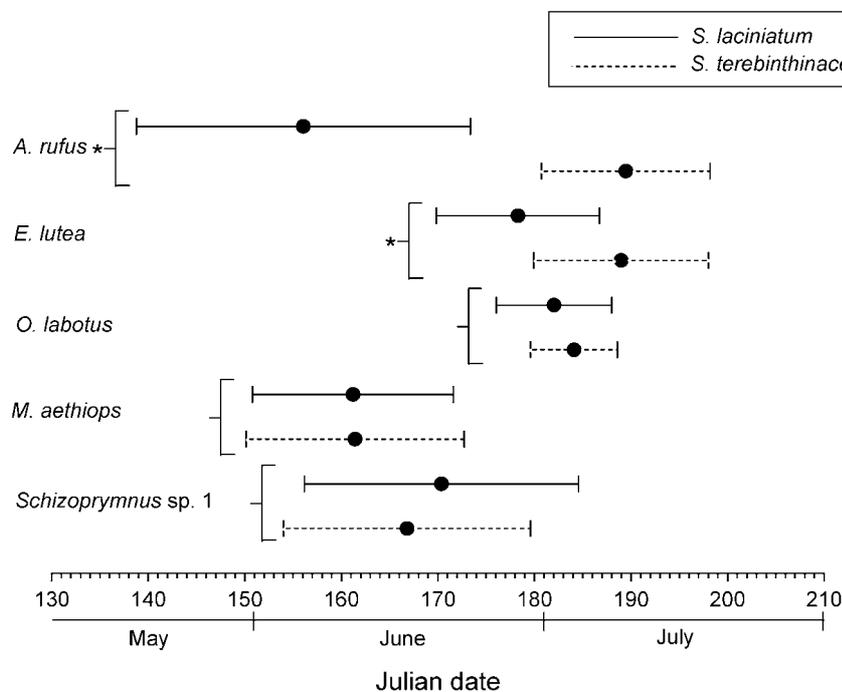


Figure 4. Emergence times (mean \pm 1 SD) of adult *A. rufus*, *M. aethiops*, and their parasitoids from *S. laciniatum* and *S. terebinthinaceum*. Asterisks indicate statistically significant differences between plant species for individual insect species (t -test $P < 0.05$; see text).

Phenology of emergence

We did not rear enough *A. minor* in cages to allow a reliable estimate of emergence time. Adult *A. rufus* emerged in cages from *S. laciniatum* about 1 month earlier than from *S. terebinthinaceum* (Figure 4; ANOVA plant species effect $F_{1, 1227} = 10.2$, $P < 0.002$; mean Julian dates correspond to 5 June \pm 0.53 day and 8 July \pm 0.30 day, respectively; $t = 21.9$, $P < 0.0001$). Emergence phenology of the parasitoid *E. lutea* showed a similar plant species effect, but with a smaller time difference (Figure 4; means 27 June \pm 0.53 and 7 July \pm 0.30 day; $t = 6.58$, $P < 0.0001$). Emergence times of the gall wasp parasitoid *O. labotus*, *M. aethiops*, and its parasitoid *Schizoprymnus* sp. 1 did not differ between plant species (Figure 4; t -tests of least squared means, $P > 0.05$).

Discussion

Our research findings certainly are consistent with the notion that insect communities of prairies are poorly known (Kosztarab and Schaefer 1990;

Arenz and Joern 1996), and attest to the biodiversity of insects and intricacies of trophic relationships in these endemic ecosystems. We present new information on the biology of insect species that inhabit stems of *Silphium* plants, and on host associations of phytophagous species and their natural enemies.

The insect community that inhabits stems of *S. laciniatum* and *S. terebinthinaceum* was dominated by the gall wasps *A. rufus* and *A. minor* and their hymenopteran parasitoids. The two cynipid species are associated with flowering stems of *S. laciniatum* and *S. terebinthinaceum* and possibly other *Silphium* species (Gillette 1891; Beutenmüller 1910; Weld 1959). Five species of *Antistrophus* (including *A. rufus* and *A. minor*) form galls in either the stems or flower heads of *Silphium* species (Burks 1979c). Prior to our research, little was known of these species other than *A. silphii* Gillette which forms apical galls in stems of *Silphium perfoliatum* L. and *S. integrifolium* Michaux (Weld 1959; Burks 1979c; Fay and Hartnett 1991).

Although the inconspicuous quality of *A. rufus* and *A. minor* galls may have evolved to eliminate visual cues for natural enemies (Ronquist and Liljeblad 2001), we discovered that the larvae suffer high rates of mortality by specialized natural enemies. *A. rufus* and *A. minor* appear to be new host records for all of the parasitoid species we reared. The sole published record for *E. lutea* is from Michigan for a plant species native to Europe, *Inula helenium* L. (Asteraceae; Burks 1979a), that is not a recorded host of *Antistrophus* species (Gillette 1891; Beutenmüller 1910; Weld 1959). Other *Eurytoma* consume plant tissues as well as insect host species (Bugbee 1967). We have confirmed that *E. lutea* is a parasitoid of *A. rufus* and *A. minor*, but have not reared this species from any other gall formers at our prairie sites, including other *Antistrophus* species in different *Silphium* species, other cynipids in *Rosa* species (Rosaceae), or cecidomyiids in *Helianthus* species (Asteraceae). We conclude, therefore, that *E. lutea* is specialized on gall wasps that inhabit stems of *S. laciniatum* and *S. terebinthinaceum*, at least at our study sites.

There also are no records of *O. labotus* parasitizing *A. rufus* and *A. minor*. This parasitoid is highly polyphagous, feeding on a few species of gall midges (Diptera: Cecidomyiidae) and at least 65 gall wasp species, including *Antistrophus laciniatus* Gillette in flower heads of *S. laciniatum* (personal observation) and cynipid species of different genera that inhabit oak galls (Hanson 1992; Eliason and Potter 2000). Similarly, *E. vesicularis* previously has not been associated with our gall wasp species, but this apparently European species is among the most polyphagous of chalcidoids, a primary or secondary parasitoid of orthopterans, hemipterans, coleopterans, lepidopterans, dipterans, and hymenopterans (Burks 1979b; Gibson 1990). We conclude that *Antistrophus* is a new host record for the *Brasema* and *Homoporus* species because we know of no reports of their being reared from stems of *Silphium*. *Brasema* and *Homoporus* individuals could not be identified to species because of the poor state of their taxonomy, and their trophic position is uncertain because these genera include both primary and secondary parasitoids (Boucek and Heydon 1997; Gibson 1997).

M. aethiops is rarely collected, and although it appears to be endemic to North America (Liljeblad 1945), the sole host record is for a Eurasian weed, *Cirsium vulgare* (Savi) Tenore (Asteraceae; Ford and Jackman 1996). Densities of the beetle that we report, up to seven larvae per stem, are exceptional since congeners rarely exceed one larva per stem (Ford and Jackman 1996). Although most mordellid species are phytophagous, and reports of predation have been considered artifactual or inconsequential (Ford and Jackman 1996), we found unequivocal evidence that *M. aethiops* larvae are facultative, but active predators of gall inhabitants (Tooker and Hanks 2004b). Galleries of *M. aethiops* extend into stem apices, however, ~90% of larvae feed within the basal 1.5 m of *Silphium* stems where they are vulnerable to fire (Tooker and Hanks 2004a). Taxonomic uncertainties prevented our identifying the species of *Schizopyrmnus*, *Heterospilus*, and *Tetrastichus* that parasitized *M. aethiops* larvae. Because ours apparently are the first reports of these genera emerging from stems of *Silphium*, however, these probably represent new host records.

Densities of galls were significantly greater in *S. laciniatum* than in *S. terebinthinaceum*, perhaps due to its thicker stems. Galls were concentrated in the basal portions of *S. laciniatum* stems (Figure 3), but at high densities there was a greater proportion of galls in stem tops. Most galls in *S. laciniatum* were in proximity to stipules, which is consistent with oviposition behavior of *A. rufus* females. Thick clasping stipules may offer ovipositing females protection from predators and refuge for larvae from parasitoids, but offer no protection from fire (Tooker and Hanks 2004a). Galls in *S. terebinthinaceum* were more evenly distributed along stems (Figure 3), suggesting that the thinner stipules of this species provide no refuge from natural enemies.

Earlier phenology of bolting in *S. laciniatum* compared to *S. terebinthinaceum* (unpublished data) apparently causes a similar phenological difference in emergence and oviposition in *A. rufus* and its parasitoid *E. lutea* (Figure 4). Wasps emerging from *S. laciniatum* therefore are unlikely to encounter individuals emerging from *S. terebinthinaceum*, inhibiting gene flow across plant species. In fact, allozyme studies indicate species level differences between *A. rufus* emerging from *S. laciniatum* and *S. terebinthinaceum* (Tooker et al. 2002a, 2004). Natural enemies such as *E. lutea* may be less likely to undergo genetic differentiation due to variation in plant phenology because females search for hosts across plant species (Abrahamson and Weis 1997; Gratton and Welter 1999; but see Eubanks et al. 2003).

Acknowledgements

We thank M.R. Berenbaum, S.H. Berlocher, J.B. Whitfield, R.N. Wiedenmann, and one anonymous reviewer for helpful comments on the manuscript, and E.J. Kron, A.L. Crumrin, and M.W. Tooker for assistance in the field and lab. We thank the following taxonomists for identifying specimens: E.E. Grissell (Smithsonian Institution), P.E. Hanson (Universidad de Costa Rica), J.A.

Jackman (Texas A&M University), Z. Liu (Field Museum, Chicago), J.W. Kim (University of California, Riverside), S.L. Heydon (Bohart Museum, University of California, Davis), and A.R. Deans (University of Illinois at Urbana-Champaign [UIUC]). Thanks also to S. Aref and the Illinois Statistics Office, UIUC, for advice on statistical analyses. We also thank the Illinois Nature Preserves Commission, Red Bison (a University of Illinois Registered Student Organization), and Steve Buck and the Committee of Natural Areas of the School of Integrative Biology, UIUC, for research access to sites. This work was in partial fulfillment of a Ph.D. degree for J.F.T. from UIUC. Funding was provided by a Sigma Xi Grant-in-Aid of Research and a Summer Research Grant from the Program in Ecology and Evolutionary Biology in the School of Integrative Biology, UIUC.

References

- Abrahamson W.G. and Weis A.E. 1997. *Evolutionary Ecology Across Three Trophic Levels*. Princeton University Press, Princeton, New Jersey.
- Arenz C.L. and Joern A. 1996. Prairie legacies – invertebrates. In: Samson F.B. and Knopf F.L. (eds) *Prairie Conservation: Preserving North America's Most Endangered Ecosystem*. Island Press, Washington, DC, pp. 91–110.
- Beutenmüller W. 1910. The North American species of *Aylax* and their galls. *Bulletin of the American Museum of Natural History* 28: 137–144.
- Boucek Z. and Heydon S.L. 1997. Pteromalidae. In: Gibson G.A.P., Huber J.T. and Woolley J.B. (eds) *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)*. NRC Research Press, Ottawa, Ontario, Canada, pp. 541–692.
- Bugbee R.E. 1967. Revision of chalcid wasps of genus *Eurytoma* in America north of Mexico. *Proceeding of the United States National Museum* 118: 433–552.
- Burks B.D. 1979a. Family Eurytomidae. In: Krombein K.V., Hurd Jr. P.D., Smith D.R. and Burks B.D. (eds) *Catalog of Hymenoptera in America North of Mexico*. Vol. 1. Smithsonian Press, Washington, DC, pp. 835–860.
- Burks B.D. 1979b. Family Eupelmidae. In: Krombein K.V., Hurd Jr. P.D., Smith D.R. and Burks B.D. (eds) *Catalog of Hymenoptera in America North of Mexico*. Vol. 1. Smithsonian Press, Washington, DC, pp. 878–889.
- Burks B.D. 1979c. Superfamily Cynipoidea. In: Krombein K.V., Hurd Jr. P.D., Smith D.R. and Burks B.D. (eds) *Catalog of Hymenoptera in America North of Mexico*. Vol. 1. Smithsonian Press, Washington, DC, pp. 1045–1107.
- Byre V.J. 1997. Birds. In: Packard S. and Mutel C.F. (eds) *The Tallgrass Restoration Handbook for Prairies, Savannas, and Woodlands*. Island Press, Washington, DC, pp. 327–337.
- Clevinger J.A. and Panero J.L. 2000. Phylogenetic analysis of *Silphium* and subtribe Engelmanniinae (Asteraceae: Heliantheae) based on ITS and ETS sequence data. *American Journal of Botany* 87: 565–572.
- Corn P.S. and Peterson C.R. 1996. Prairie legacies – amphibians and reptiles. In: Samson F.B. and Knopf F.L. (eds) *Prairie Conservation: Preserving North America's Most Endangered Ecosystem*. Island Press, Washington, DC, pp. 125–134.
- Eliason E.A. and Potter D.A. 2000. Biology of *Callirhytis cornigera* (Hymenoptera: Cynipidae) and the arthropod community inhabiting its galls. *Environmental Entomology* 29: 551–559.
- Eubanks M.D., Blair C.P. and Abrahamson W.G. 2003. One host shift leads to another? Evidence of host race formation in a predaceous gall-boring beetle. *Evolution* 57: 168–172.
- Favret C., Tooker J.F. and Hanks L.M. 2004. *Iowana frisoni* Hottes (Homoptera: Aphididae) re-described with notes on its biology. *Proceedings of the Entomological Society of Washington* 106: 26–34.

- Fay P.A. and Hartnett D.C. 1991. Constraints on growth and allocation patterns of *Silphium integrifolium* (Asteraceae) caused by a cynipid gall wasp. *Oecologia* 88: 243–250.
- Fay P.A. and Samenus R.J. Jr. 1993. Gall wasp (Hymenoptera: Cynipidae) mortality in a spring tallgrass prairie fire. *Environmental Entomology* 22: 1333–1337.
- Felt E.P. 1965. *Plant Galls and Gall Makers*. Hafner Publishing Company, New York.
- Ford E.J. and Jackman J.A. 1996. New larval host plant associations of tumbling flower beetles (Coleoptera: Mordellidae) in North America. *Coleopterists Bulletin* 50: 361–368.
- Gibson G.A.P. 1990. Revision of the genus *Macroneura* Walker in American north of Mexico (Hymenoptera: Eupelmidae). *Canadian Entomologist* 122: 837–873.
- Gibson G.A.P. 1997. Eupelmidae. In: Gibson G.A.P., Huber J.T. and Woolley J.B. (eds) *Annotated Keys to the Genera of Nearctic Chalcidoidea* (Hymenoptera). NRC Research Press, Ottawa, Ontario, Canada, pp. 430–476.
- Gillette C.P. 1891. Descriptions of new Cynipidae in the collection of the Illinois State Laboratory of Natural History. *Bulletin of the Illinois State Laboratory of Natural History* 3: 191–197.
- Gleason H.A. and Cronquist A. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. 2nd edn. The New York Botanical Garden, The Bronx, New York.
- Gratton C. and Welter S.C. 1999. Does 'enemy-free space' exist? Experimental host shifts of an herbivorous fly. *Ecology* 80: 773–785.
- Hanson P. 1992. The Nearctic species of *Ormyrus* Westwood (Hymenoptera: Chalcidoidea: Ormyridae). *Journal of Natural History* 26: 1333–1365.
- ILENR 1994. *The Changing Illinois Environment: Critical Trends, Summary Report of the Critical Trends Assessment Project, Vol. 3: Ecological Resources*, ILENR/RE-EA- 94/05. Illinois Department of Energy and Natural Resources, Springfield, Illinois.
- Kosztarab M. and Schaefer C.W. 1990. Conclusions. In: Kosztarab M. and Schaefer C.W. (eds) *Systematics of the North American Insects and Arachnids: Status and Needs*. Virginia Agricultural Experiment Station Information Series 90–1, Blacksburg, Virginia, pp. 241–247.
- Liljeblad E. 1945. *Monograph of the family Mordellidae (Coleoptera) of North America, north of Mexico*. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan* 62: 1–229.
- McFall D. and Karnes J. (eds) 1995. *A Directory of Illinois Nature Preserves, Vols. 1 and 2*. Illinois Department of Natural Resources, Springfield, Illinois.
- Nekola J.C. 2002. Effects of fire management on the richness and abundance of central North American grassland land snail faunas. *Animal Biodiversity and Conservation* 25: 53–66.
- Rathke B.J. 1976. Competition and coexistence within a guild of herbivorous insects. *Ecology* 57: 76–87.
- Rice L.A. 1932. The effect of fire on the prairie animal communities. *Ecology* 13: 392–401.
- Ronquist F. and Liljeblad J. 2001. Evolution of the gall wasp–host plant association. *Evolution* 55: 2503–2522.
- Samson F.B. and Knopf F.L. 1994. *Prairie conservation in North America*. *BioScience* 44: 418–421.
- SAS Institute 2001. *SAS/STAT User's Guide for Personal Computers, release 8.01*. SAS Institute, Cary, North Carolina.
- Steinauer E.M. and Collins S.L. 1996. *Prairie ecology – the tallgrass prairie*. In: Samson F.B. and Knopf F.L. (eds) *Prairie Conservation: Preserving North America's Most Endangered Ecosystem*. Island Press, Washington, DC, pp. 39–52.
- Taron D.J. 1997. Insects. In: Packard S. and Mutel C.F. (eds) *The Tallgrass Restoration Handbook for Prairies, Savannas, and Woodlands*. Island Press, Washington, DC, pp. 305–318.
- Tooker J.F. and Hanks L.M. 2004a. Impact of prescribed burning on endophytic insect communities of prairie perennials (Asteraceae: *Silphium* spp.). *Biodiversity and Conservation* 13: 1875–1888.
- Tooker J.F. and Hanks L.M. 2004b. Trophic position of the endophytic beetle, *Mordellistena aethiops* Smith (Coleoptera: Mordellidae). *Environmental Entomology* 33: 291–296.
- Tooker J.F., Koenig W.A. and Hanks L.M. 2002. Altered host plant volatiles are proxies for sex pheromones in the gall wasp *Antistrophus rufus*. *Proceedings of the National Academy of Sciences USA* 99: 15486–15491.

- Tooker J.F., Deans A.R. and Hanks L.M. 2004. Description of the *Antistrophus rufus* (Hymenoptera: Cynipidae) species complex, including two new species. *Journal of Hymenopteran Research* 13: 125–133.
- Walk J.W. and Warner R.E. 2000. Grassland management for the conservation of songbirds in the midwestern USA. *Biological Conservation* 94: 165–172.
- Weaver J.E. 1954. *North American Prairie*. Johnsen Publishing Co., Lincoln, Nebraska.
- Weld L.H. 1959. *Cynipid Galls of the Eastern United States*. Privately published, Ann Arbor, Michigan.
- Wharton R.A. 1997. Alysiniinae. In: Wharton R.A., Marsh P.M. and Sharkey M.J. (eds) *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*. Special Publication No. 1, The International Society of Hymenopterists, Washington, DC, pp. 85–116.
- Whitfield J.B. and Lewis C.N. 2001. Analytical survey of the braconid wasp fauna (Hymenoptera: Braconidae) on six Midwestern US tallgrass prairies. *Annals of the Entomological Society of America* 94: 230–238.
- Williams A.H. 1999. Fauna overwintering in or on stems of Wisconsin prairie forbs. In: Springer J.T. (ed) *Proceedings of the Sixteenth North American Prairie Conference*. University of Nebraska, Kearney, Nebraska, pp. 157–161.