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Description, Life History, and Parasitism of a New Species of Delphacid Planthopper (Hemiptera: Fulgoroidea)

JAMES T. CRONIN[1] AND STEPHEN W. WILSON[2]

ABSTRACT *Delphacodes scolochloa* Cronin & Wilson (Hemiptera: Fulgoroidea) is a newly discovered delphacid planthopper that feeds and oviposits exclusively on the stems of sprangletop, *Scolochloa festucacea* (Willd.) Link (Poaceae: Pooidae), in the prairie pothole region of northeastern North Dakota. *D. scolochloa* is bivoltine. It is also wing dimorphic, but populations are composed predominantly of flightless brachypters. Macropters incur a substantial cost in terms of reduced longevity and fecundity relative to brachypters. The parasitoid complex attacking *D. scolochloa* consists of two egg parasitoids, *Anagrus nigriventris* Girault and *Anagrus columbi* Perkins (Hymenoptera: Mymaridae), and one undescribed dryinid. The proportion of eggs parasitized averages 21%, and egg parasitization is density independent.

KEY WORDS *Anagrus nigriventris*, egg parasitoid, planthopper, prairie potholes, *Scolochloa festucacea*

Grass-feeding delphacids have been the subject of extensive ecological research, primarily because several species are vectors of pathogens of economically important grasses (Wilson 2005). In North American grasslands and salt marshes, researchers have focused on faunal surveys (e.g., Hendrickson, 1930, Wilson et al. 1993, Hamilton 2002), systematics and morphology (e.g., Wilson 1982, Miller and Wilson 1999), life histories (e.g., Holder and Wilson 1992), and mating behavior (e.g., Heady and Denno 1991, Heady and Wilson 1990). Delphacids also have been used to address a broad range of ecological questions regarding plant–herbivore interactions (e.g., Tallamy and Denno 1979, Denno 1983, Denno et al. 1986, Wilson et al. 1994), life history theory (e.g., Denno and Dingle 1981, Denno and McCloud 1985, Huberty and Denno 2006), population dynamics (e.g., Denno 1983, Strong 1989, Reeve et al. 1994), interspecific competition (Denno and Roderick 1992, Denno et al. 2000, Ferrenberg and Denno 2003), predator–prey interactions (Döbel and Denno 1994, Cronin et al. 2004, Fagan and Denno 2004), host–parasitoid interactions (e.g., Stiling and Strong 1982; Cronin and Strong 1990, 1993, 1999; Cronin 2003b), food web structure (e.g., Denno et al. 2002, Finke and Denno 2003, Gratton and Denno 2003), dispersal and metapopulation dynamics (Cronin 2003a, Haynes and Cronin 2006), and landscape ecology (Haynes and Cronin 2003, 2006; Cronin and Haynes 2004).

Some grass-feeding delphacids are ecologically similar to pests such as the brown planthopper, *Nilaparvata lugens* (Stål.), a serious pest of rice, *Oryza sativa* L. (Kiritani 1979, Wilson and Claridge 1985). These delphacids also serve as hosts to mymarid, strepsipteran, and dryinid parasitoids, an assemblage of parasitoids very comparable to that found for many planthopper pest species (e.g., Ôtake 1970, Bentur et al. 1982, Fowler et al. 1991). The study of host–parasitoid interactions in species of grassland delphacids may provide insight or potential biocontrol agents for the suppression of related pest species.

Here, we describe a new species of delphacid planthopper and provide data on its biology, host range, rate of macroptery, and population dynamics. We also identify the parasitoid species that attack the planthopper, quantify rates of parasitism, and test whether the proportion parasitized among host plant patches depends on host density.

Materials and Methods

Study Location and Host Plant. Collection of specimens and census of planthopper and parasitoid populations occurred in the prairie pothole region of northeastern North Dakota (Petersburg, Nelson County; 48.02097° N, 98.12230° W). This formerly glaciated area is characterized by numerous seasonal and permanent ponds (van der Valk 1989), and it is an important breeding habitat for waterfowl (Batt et al. 1989). Among the wetland plants bordering these ponds is the native sprangletop or common river grass, *Scolochloa festucacea* (Willd.) Link (Poaceae: Pooidae). Sprangletop is circumpolar in distribution and in North America ranges from northern Iowa and Nebraska to southcentral Canada and west to Oregon (Gould 1968, Clayton and Renvoize 1986). Ecologically, it is an emergent hydrophyte, and it is found where water levels fluctuate from 0 to 150 cm above

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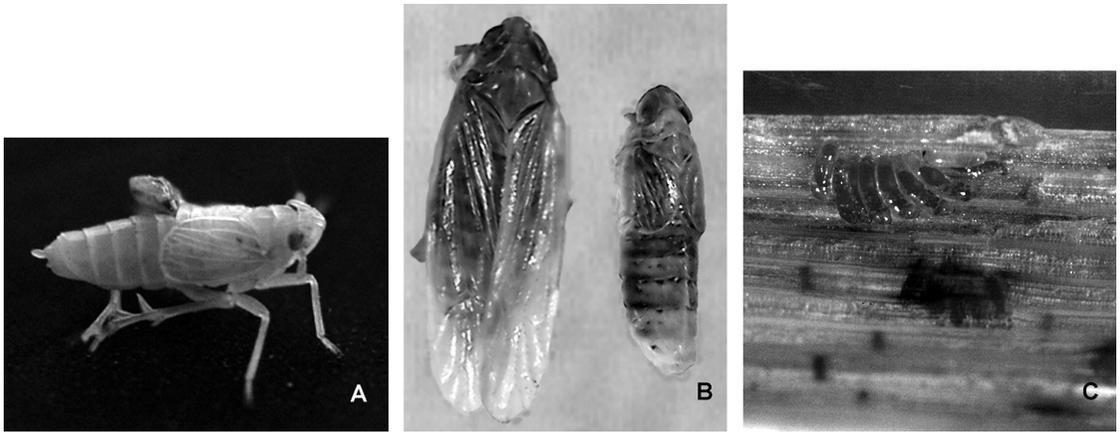
Fig. 1. *D. scolochloa*. (A) Adult brachypterous female with dryinid parasitoid sac. (B) Macropterous and brachypterous females. (C) Egg clusters on *S. festucacea* stems that have by parasitized by *Anagrus* spp. (plant epidermis has been removed to expose eggs in the upper egg cluster).

the soil surface (Sculthorpe 1967). Sprangletop often forms pure stands several meters deep along the pond margins and as small clonal patches further in open shallow water (Smith 1973; J.T.C., unpublished data).

Population Census. Three semipermanent ponds, broadly bordered by sprangletop, were used in this study (Ponds 100, 109, and N29-1). The ponds were 1–3 ha in size and were separated from each other by 1.8–5.6 km. Shortly after spring thaw, mid-May 1998, the sprangletop bordering each pond was sampled with a sweepnet. Three sets of 10 sweeps each were conducted per pond. Sweep samples were transported on ice to the laboratory, and planthoppers were inspected to determine stage (nymph or adult), sex, wing morph (brachypters versus macropters; Fig. 1, A and B), and presence of parasitoids protruding from between the abdominal segments (dryinid larval sac or strepsipteran cephalothorax) (Fig. 1A). Surveys were conducted at 2-wk intervals until the end of the summer when sprangletop had completely senesced (early September). The survey was continued each season for 3 yr.

For each planthopper generation, after adults had become scarce, we conducted a census of planthopper eggs. Twenty-five sprangletop stems with planthopper eggs were haphazardly collected from each pond. Stems were left to incubate for 3 d at room temperature (stem bases were submerged in water) to ensure that recently parasitized hosts could be identified. Stems were subsequently dissected under a stereoscopic dissecting microscope (10×) to expose planthopper eggs inserted just beneath the stem epidermis (Fig. 1C). Planthopper eggs were identified as either healthy (developing white embryos or as cast chorions, indicating successful emergence), parasitized (red immatures, or host chorions with circular exit holes, indicating successful emergence), or dead (deflated or brown eggs). A subset of planthopper nymphs and adults and egg parasitoids were preserved in 70% ethanol for later identification of species.

Planthopper Taxonomy. The specimens collected from *S. festucacea* represent a new species, and they are described below. Descriptions are based on nine males and 34 females. Using an ocular micrometer, body length was measured from the apex of the vertex to posterior aspect of the abdomen. Thoracic length was measured along the midline from the anterior aspect of the pronotum to the posterior aspect of the mesonotal scutellum as the metanotum is obscured by the forewings. To describe and illustrate the male and female genitalia, the abdomen was removed and placed in a 10% KOH solution overnight, then washed in distilled water; genitalia were stored in genitalia capsules filled with glycerol (Wilson 2005). The terminology used in describing the female genitalia follows Heady and Wilson (1990).

Host Range of *D. scolochloa*. To ascertain the host range of the planthopper, we caged planthopper adults onto potted stems of the 11 dominant plant species at our field sites. These plant species were the grasses sprangletop, switch grass (*Panicum virgatum* L.), prairie cordgrass (*Spartina pectinata* Link) and smooth brome (*Bromus inermis* Leyss.); common reed [*Phragmites australis* (Cav.) Trin]; sedges (*Carex* sp.); rushes (*Scirpus* sp.); cattails (*Typha* spp.); Canada goldenrod (*Solidago canadensis* L.); smart weed (*Polygonum* sp.); and thistle (*Circium* sp.). Two common grass crops, corn (*Zea mays* L.) and wheat (*Triticum aestivum* L.), also were included in this study. Young, nonflowering shoots of the noncrop plants were excavated from the field in early June 1999 and potted in Pro-mix BX soil (20-cm-diameter pots). Corn was grown from seed (Burpee Seed Co., Warminster, PA, Early Choice Hybrid SE variety), and wheat was obtained as seedlings from a local farmer. Both crop plants were grown in 20-cm pots by using Pro-Mix BX. Clear Mylar sheeting, formed into tubes, were inserted over the plants. The tops of the cages were constructed of mosquito netting hot-glued to the Mylar. Twenty-five recently eclosed adult planthoppers were added to each cage, and there were three caged plants per plant spe-

cies. Cages were inspected daily for live planthoppers and evidence of feeding (excretion of honeydew). After all planthoppers had died, the plants were carefully inspected for planthopper eggs.

Longevity and Fecundity of Wing-Dimorphic Females. Several hundred late instars of *D. scolochloa*, collected from the field in late May 1998, were placed on potted sprangletop plants that were enclosed with a Mylar cage (see above). Each day, newly eclosed adults were removed and sorted by sex and wing type. Adults were quickly transferred to stem cages in groups of either six brachypterous or six macropterous females. In addition, two macropterous males were added to each cage (>99% of males are macropterous in this species). The stem cage was constructed of a 10-cm-long by 2.5-cm-diameter acetate tube. High-density foam sealed the ends of the tube around the stem and kept the stem positioned in the center of the tube. The experiment consisted of 10 replicate cages per wing type.

Every day until all planthoppers had died, the cages were inspected, and the number of live females was counted. Planthoppers were gently aspirated and transferred to new stem cages at 2-day intervals. This procedure ensured that planthoppers had high-quality host material for feeding and oviposition. Also, males were maintained at two individuals per cage throughout the experiment to ensure that females were not sperm limited.

Differences in survival curves between female brachypters and macropters were analyzed with a Wilcoxon's rank test (Pyke and Thompson 1986). We also tested for differences in median and maximum life spans (days to 50 and 100% mortality per replicate, respectively) and fecundity by using two-sample *t*-tests. We used two fecundity metrics, mean daily fecundity (=total eggs laid/summation of females alive to start each day) and mean lifetime fecundity (=total eggs laid/initial number of females) per replicate cage. All tests were performed in SYSTAT 11 (Systat Software, Inc., Point Richmond, CA).

Parasitism and Host Density. Based on stem collections made during the census, we examined the relationship between host density and proportion parasitized among stems. Spatial density dependence was examined using separate least-squares regression models for each site ($n = 3$) and planthopper generation ($n = 6$) for a total of 18 tests. Eggs per stem was ln transformed, and proportion parasitized was arcsine square root transformed to achieve normality and homogeneity of variances (Sokal and Rohlf 1995). We report the fraction of tests that had a positive or negative slope and how many were statistically significant ($P < 0.05$).

Results

Delphacodes scolochloa Cronin & Wilson, New Species

Salient Features. Total length: male 1.92 ± 0.095 mm, female 3.04 ± 0.227 mm; thoracic length: male
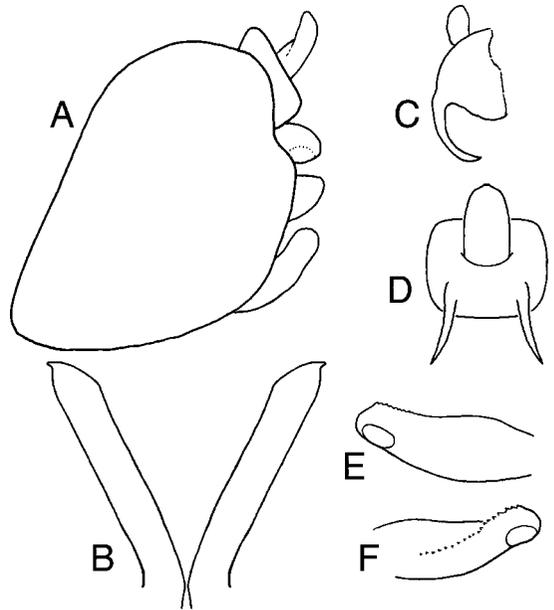

Fig. 2. *D. scolochloa* male external genitalia. (A) Pygofer, anal tube, aedeagus, and style, left lateral view. (B) Styles, caudal view. (C) Anal tube, right lateral view. (D) Anal tube, caudal view. (E) Aedeagus, right lateral view. (F) Aedeagus, left lateral view.

0.60 ± 0.022 mm, female 0.70 ± 0.057 mm; $n = 7$ males, 32 females.

Body pale, yellow/light brown to dark brown with fuscous markings. Vertex subquadrate with prominent darker lateral carina, concolorous V-shaped posteriorly directed carina near middle; in lateral view, vertex curving onto frons. Frons narrow, approximately twice as long as wide, bordered by darker subparallel lateral carinae, with concolorous weak median longitudinal carina. Clypeus with prominent partial median longitudinal carina. Antennal scape subcylindrical, pedicel length ≈2.5× that of scape.

Pronotum with lateral carinae curving posterolaterally, paralleling curvature of compound eyes; with prominent median longitudinal carina. Mesonotum length about twice that of pronotum; with straight, posterolaterally directed lateral carinae and a median longitudinal carina. Forewings translucent pale brown, veins concolorous bearing short setae; macropters with forewing narrow, broadly rounded apically and extending well beyond apex of abdomen; brachypters with forewing subquadrate extending to abdominal tergite 6. Legs with apices of tarsi fuscous; metatibial spur subequal in length to that of basal metatarsomere, with row of very small black tipped teeth on posterolateral aspect; basal metatarosmere ≈3× length of middle metatarsomere, which is subequal in length to that of terminal metatarsomere.

Abdominal tergite 3 fuscous.

Male genitalia (Fig. 2). Pygofer pale brown with black marking on ventrocaudal aspect; in lateral view, subquadrate, with caudal margin in dorsal one third gently concave; diaphragm armature shining black,
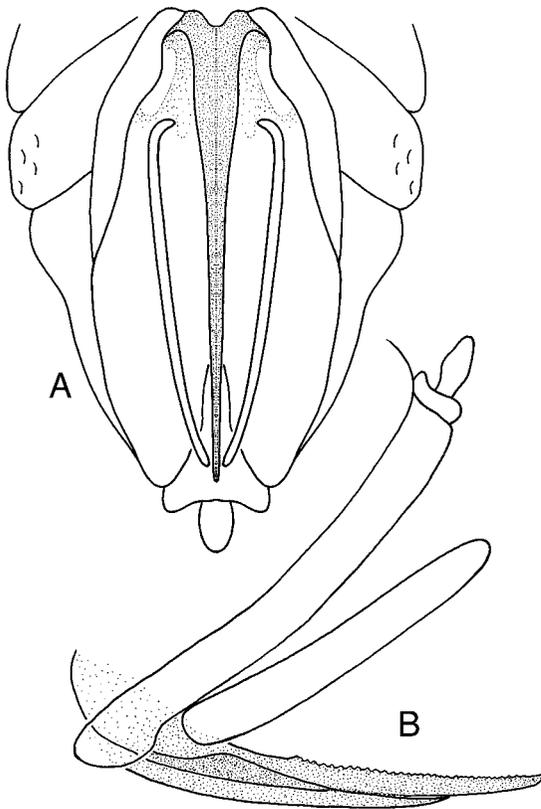
Fig. 3. *D. scolochloa* female external genitalia. (A) Apical portion of abdomen, ventral view. (B) Apical portion of abdomen, left lateral view.

Fig. 4. Mean ± SE number of adult *D. scolochloa* (sum of three sets of sweeps) among three prairie potholes based on biweekly samples for 3 yr (1998–2000).

extending posteriorly as a bulbous process. Anal tube, in lateral view, with a pair of broadly separated, curved, ventroanteriorly directed spinose processes originating on the ventrocaudal aspect of the tube. Styles, fuscous; in caudal view, curved dorsolaterally at base then elongate, subparallel narrowing abruptly to a small pointed apex. Aedeagus subcylindrical, apex broadly rounded, gonopore on ventral aspect near apex; with curving row of ≈20 teeth extending from dorsal aspect anterolaterally on left side to near middle.

Female genitalia (Fig. 3). Tergite 9, in ventral view, elongate, each side broad with length ≈3× width, apex rounded. Anal tube subcylindrical. Valvifers of segment 8 each covering tergite 9 anterolaterally; elongate, slender, broadly convex on lateral aspect, sinuate on median aspect. Lateral gonapophyses of segment 9 elongate, spatulate posteriorly. In lateral view, median gonapophyses of segment 9 saber-shaped, with ≈30 prominent small teeth on dorsal margin in distal one half. Gonapophyses of segment 8 adhering tightly to median gonopophyses of segment 9; slender, acute apically.

Types. HOLOTYPE: male, North Dakota, Nelson Co., Petersburg, 48.00206° N, 97.97222° W, 4 June 1998, *ex. Scolochloa festucacea*, coll. J. Cronin.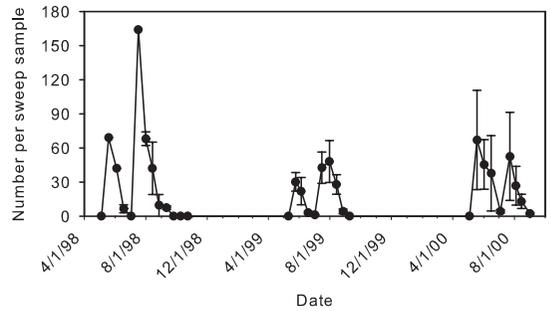 ALLOTYPE: female, same data (primary types deposited in the Snow Museum, University of Kansas). PARATYPES: 8 males, 33 females, same data (2 males, 4 females deposited in the Snow Museum, the remainder deposited in SWW Collection).

Distribution. This species is known from *S. festucacea* from eastern North Dakota, but it is likely to be more widely distributed in North America because its host plant is found along the margins of lakes and prairie potholes from central Canada south to Iowa and west to Oregon.

Etymology. *D. scolochloa* is named for the genus of its host plant.

Life History. *D. scolochloa* overwinters as mid-instar nymphs concealed beneath the senescent leaf sheaths that are loosely attached to the sprangletop stems. In early May, corresponding with the emergence of new sprangletop shoots, the nymphs emerge from their winter refuge and begin to feed. Planthoppers extract phloem from the stems, typically feeding above the water line but below the lowest unfurled leaf. However, on occasion, some feeding does take place at the base and abaxial surface of leaves. Toward the end of May, adults achieve maximal density (Fig. 4). Females lay eggs in clusters just beneath the stem epidermis (Fig. 1C) and in complete overlap with their feeding sites. Emergence of nymphs follows egg laying by ≈2 wk. Planthoppers have two nonoverlapping generations per summer; peak adult densities for the second generation occur in the middle of July (Fig. 4). By the latter half of August, no adults are present in the population.

Feeding and oviposition on the stems of sprangletop caused necrotic lesions to form and be visible within 2 wk. The damage was especially evident after the outbreak of planthoppers in July 1998 (Fig. 4). However, heavy stem damage at this time did not translate into a reduction in plant height or flowering frequency at the end of the growing season. Based on a sample of 100 heavily scarred and 100 unscarred stems at site 100, heights differed by only 3% (scarred, 1.22 ± 0.04 m and unscarred, 1.26 ± 0.05 m; t_{198} = 0.62, P = 0.27). Flowering rates were actually slightly higher for the damaged plants (scarred, 38%; unscarred, 33%).

Based on census data, the percentage of males over all 3 yr was 34 ± 5% (mean ± SE; n = 3 sites). One hundred percent of the collected males were mac-
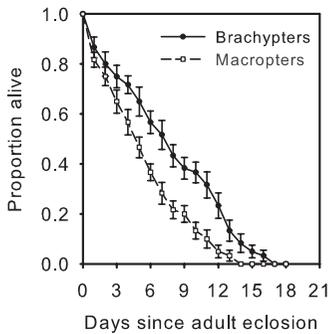
Fig. 5. Survivorship curves for brachypterous and macropterous female *D. scolochloa*. Mean ± SE proportion alive per cage per day ($n = 10$).

ropterous (forewings extending beyond the abdomen). In contrast, only $9.1 \pm 5.1\%$ of the females were macropterous. Brachypterous *D. scolochloa* have wings that are too small to allow sustained flight. Individuals were observed to weakly "flutter" their forewings between stems.

D. scolochloa seems to be monophagous in the prairie pothole region of northeastern North Dakota. Of the 13 species of plants on which this planthopper was caged, feeding, as indicated by the presence of honeydew, was only evident on sprangletop. Caged planthoppers on sprangletop had a median adult life span of 6.6 ± 1.8 d, whereas planthoppers on the remaining 12 species had a median life span of <1 d. Finally, all three caged sprangletop plants were heavily infested with planthopper eggs, but none of the other plant species had eggs.

Brachypterous and macropterous females differed significantly in survivorship curves (Wilcoxon test: $Z = 3.52$, $P < 0.001$) (Fig. 5). Median (number of days to 50% mortality) and maximum (days to 100% mortality) adult life span was 23 and 21% higher, respectively, for brachypters than macropters (Fig. 6A). The difference between wing morphs was highly significant for maximum life span ($t_{18} = 3.37$, $P = 0.003$), but only marginally significant for median life span ($t_{18} = 1.91$, $P = 0.072$). Daily oviposition rates (eggs laid per alive female per day per replicate) were 21% higher for brachypters than macropters (Fig. 6B), but this difference was not significant ($t_{18} = 1.57$, $P = 0.13$). In contrast, brachypters had a substantial advantage (46%) over macropters in terms of lifetime fecundity (total eggs laid per female per replicate) ($t_{18} = 4.31$, $P = 0.004$).

Parasitoids. Over the course of six planthopper generations, an average of $21.2 \pm 4.6\%$ of the planthopper eggs was parasitized. Two species of parasitoids were reared from these collections, *Anagrus nigriventris* Girault and *Anagrus columbi* Perkins (Hymenoptera: Mymaridae; Chiappini et al. 1996, Triapitsyn 1997). Voucher specimens can be found at the Department of Entomology, University of California, Riverside. Based on a subsample of parasitoids spanning all sites and years ($n = 64$), 92% of the individuals were identified as *A. nigriventris*.
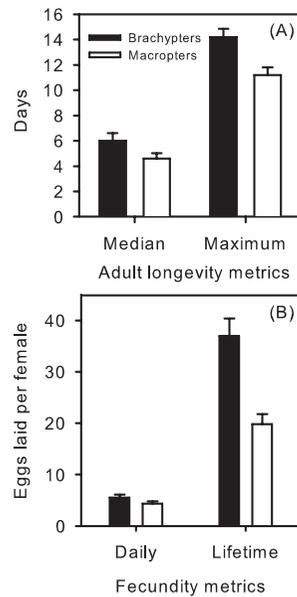

Fig. 6. Longevity and fecundity of newly eclosed *D. scolochloa* females. (A) Mean ± SE days to 50% (median longevity) and 100% (maximum longevity) survivorship of planthoppers. (B) Mean ± SE eggs laid per female per day given that it survived the day (daily fecundity) and eggs produced over the life span of the females (lifetime fecundity).

At the spatial scale of individual sprangletop stems, we detected no evidence that parasitism was density dependent. None of the 18 regression analyses was statistically significant. Moreover, there was no trend with regard to the slopes of the density–parasitism relationship: exactly one half of the tests had a positive or negative slope.

Based on the 3-yr census, 2.7% of the late instars and 1.5% of adults exhibited a sac protruding from the abdominal segments. Parasitized specimens were collected and placed in small stem cages on sprangletop. For some individuals, a larva emerged from the sac and spun a cocoon at the bottom of the cage. Wingless female dryinids emerged from these cocoons.

Discussion

Diagnostic morphological characters that serve to separate *D. scolochloa* from similar delphacids include the narrow, parallel-sided frons, the curved pronotal lateral carinae, and the distinctive male genitalia. This species shares some features with members of the genus *Nothodelphax* such as its small but relatively robust body form, small pygofer, elongate paired anal tube spines, and flattened simple genital styles. It differs from *Nothodelphax* in its lighter coloration (most *Nothodelphax* are black), slightly larger body size, broader pygofer in caudal aspect, and larger diaphragm opening, longer styles, and lack of a distinctive flange along the length of the aedeagus. Due to the difficulty in placing this species, we assigned it to the

genus *Delphacodes* (sensu lato), recognizing that its generic placement will be reassigned upon revision of the North American *Delphacodes.*

This is the first species of delphacid planthopper known to feed on *S. festucacea*, which is very patchy in its distribution, limited to the margins of ponds, drainages, and wet depressions. In the prairie pothole region of North Dakota, farmland is the primary intervening habitat. In the habitat in which this study was conducted, prairie cordgrass, the host for a similar delphacid, *Prokelisia crocea* (Van Duzee), can be found growing adjacent to sprangletop along pond margins. *D. scolochloa* has a very similar biology, life history, and parasitoid fauna to that of the well-studied members of the genus *Prokelisia* (*P. marginata, P. dolus,* and *P. crocea*). All four species are found in wetlands, and they are monophagous on their host plants (Denno and Grissell 1979, Denno et al. 1987, Holder and Wilson 1992, Cronin 2003a). Nymphs are the overwintering stage, with individuals seeking refuge in the leaf litter or rolled dead leaves or sheaths of standing vegetation (Denno 1977, Cronin 2003a). Eggs are laid in the subepidermis, but *D. scolochloa* is unique in that its eggs are laid predominantly in the stems of its host. For all species, feeding and oviposition sites completely overlap.

As with many species of delphacids, *D. scolochloa* is wing-dimorphic (Denno et al. 1991). Females are predominantly brachypterous, whereas males are almost entirely macropterous. *P. dolus* females are also predominantly brachypterous, but the opposite pattern is observed for *P. marginata* and *P. crocea* females. Mark–recapture experiments with macropterous and brachypterous *D. scolochloa* confirm the importance of long wings to both within- and among-patch movements (J.T.C., unpublished data). Not only was the rate of spread within a sprangletop patch significantly higher for macropterous females, but colonization of isolated patches located >5 m away was predominantly by macropterous females.

For *D. scolochloa,* there is a significant trade-off between dispersal ability and fitness. Adult maximum life span and lifetime fecundity of macropters were reduced by 21 and 46%, respectively, in comparison with brachypterous individuals. Such trade-offs are also evident in *P. marginata* and *P. dolus* (Denno et al. 1989) and with numerous other wing-dimorphic species (e.g., Roff 1984, 1986; Zera 1984). Because of the fitness costs associated with macroptery, evolutionary theory suggests that insects should exhibit reduced dispersal in persistent as compared with temporary habitats (Roff 1990, Denno et al. 1991). Moreover, Denno et al. (1996) found a significant negative relationship between dispersal capacity (macroptery rates) and habitat persistence for *P. dolus* and *P. marginata* (for reviews of other insects, see Roff 1990 and Denno et al. 1996). A priori, we therefore might expect that *P. crocea* and *D. scolochloa* exist in relatively ephemeral and permanent habitats, respectively, in the Great Plains. This prediction remains to be tested.

Despite the dominance of *D. scolochloa* as an herbivore of sprangletop, we found no evidence that it

had an effect on plant performance (e.g., stem height and flowering frequency), even in high-density situations. However, it would be premature to conclude that sprangletop does not suffer damage from *D. scolochloa.* Long-term or cumulative effects of herbivory and impact on seedlings have not been addressed. Studies with *P. dolus* and *P. marginata* have revealed significant impacts on host plant fitness, especially in areas where the host–herbivore interaction is relatively recent (e.g., < 100 yr; Olmstead et al. 1997; Daehler and Strong 1995, 1997; Garcia-Rossi et al. 2003). Of course, ecologically similar species of planthoppers, such as the pests *Delphacodes kuscheli* Fennah and *N. lugens,* have a tremendous impact on their hosts (Kiritani 1979, Brentassi and Maldonado 2002, March et al. 2002).

As is typical for delphacid planthoppers, *D. scolochloa* is host to egg parasitoids in the genus *Anagrus*. *A. nigriventris,* the dominant egg parasitoid (accounting for an estimated 92% of the parasitized hosts), is a common and widespread North American species (Chiappini et al. 1996). *A. columbi,* was known from only a few specimens and localities (Chiappini et al. 1996), but recently it has been discovered in *P. crocea* eggs in northeastern North Dakota (Cronin 2003b). *P. crocea* and *D. scolochloa* share both *Anagrus* parasitoids at our field sites in Petersburg, Co., ND, and there is evidence that apparent competition occurs between these two planthopper species (Cronin 2007). Apparent competition is a type of indirect interaction in which one species has a negative effect on another species mediated through a shared natural enemy (Holt 1977; Holt and Lawton 1993, 1994). Interestingly, 50 km to the east, where *S. festucacea* is uncommon, *P. crocea* is only parasitized by *A. columbi* (Cronin 2003b). Members of the genus *Anagrus* are important natural enemies of pests in a variety of agricultural crops, including rice (Ôtake 1970), corn (Liljestrom and Virla 2004), sugarcane (*Saccharum officinarum* L) (Metcalfe 1972) (Poaceae), grapes (*Vitis* spp.; Vitaceae) (Settle and Wilson 1990, English-Loeb et al. 2003), sugar beets (*Beta vulgaris* L.; Chenopodiaceae) (Meyerdirk and Moratorio 1987), and apples (*Malus domestica* Borkh.; Rosaceae) (Teulon and Penman 1986).

Parasitism of *D. scolochloa* eggs was modest, averaging only 21%, and there was no evidence of spatial density-dependent parasitism at the scale of individual stems. The absence of density-dependent parasitism contrasts with the findings for *D. kuscheli* (Liljestrom and Virla 2004), but it is typical of the pattern for many planthoppers and leafhoppers (Cronin and Strong 1990, 1994; Cronin 2003a).

Nymphal–adult parasitism by dryinids is rare, averaging only ≈2%. Stiling and Strong (1982), Stiling et al. (1991), and Cronin (2003b) found similarly low levels of parasitism for *Prokelisia* spp. With regard to parasitoid assemblages, the two prairie planthoppers (*D. scolochloa* and *P. crocea*) have less diversity than the coastal *Prokelisia* in that they lack strepsipteran parasitoids. Along the gulf coast of Florida, up to 20% of the

nymphs are parasitized by *Elenchus koebelei* Pierce (Strepsiptera: Elenchidae) (Stiling et al. 1991).

In summary, we have identified a new species of delphacid planthopper in North America whose biology, life history, and natural enemy complex are similar to other well-studied nonpest grass-feeding delphacids. It exists in a highly fragmented wetland environment, feeds on a novel host plant, and is predominantly brachypterous. This species also serves as a reservoir for two *Anagrus* parasitoids that could potentially be useful in biological control programs. Owing to an extraordinary base of ecological research on grass-feeding delphacids, we have the opportunity to examine how differences in key life history parameters or habitat structure influence various ecological processes. For example, we plan to conduct a comparative analysis of the metapopulation dynamics of *P. crocea* and *D. scolochloa* that occupy the same habitat (prairie potholes) but that differ fundamentally in dispersal ability (J.T.C., unpublished data). We also can explore differences in population dynamics between species that live in highly fragmented (*P. crocea* and *D. scolochloa*) versus relatively large continuous habitats (*P. dolus* and *P. marginata*) and the consequences of shared parasitoids between sympatrically occurring planthopper species.

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