POPULATION BIOLOGY OF PLANTHOPPERS

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INTRODUCTION

Planthoppers are herbivorous, sap-feeding homopterans that include several world-class agricultural pests. Twenty families of planthoppers are recognized and collectively form the superfamily Fulgoroidea (175). Despite the tremendous diversity of the group (>9000 described species), ecological information is available for only a handful of species, most of which are in the Delphacidae. This bias in knowledge exists because many delphacids are grass feeders and devastating pests on major agricultural crops (rice, corn, cereals, sorghum, sugar cane) around the world (20, 82, 149, 174, 199, 266). Planthoppers damage plants directly by feeding, which causes a characteristic yellowing of tissues known as "hopperburn," or indirectly as vectors of a variety of plant pathogens (16, 37, 169, 230, 231). Because of the paucity of biological information on planthoppers other than delphacids, we limit the scope of our review to this family.

The Delphacidae is the most diverse family of Fulgoroidea (>1800 species); although cosmopolitan in distribution, over one third of the species occur in the Oriental Region (175). Most species are small (<5 mm), and many exhibit wing dimorphism (53, 66, 126, 175), a feature that affords great flexibility in life history features and allows effective tracking and exploitation of changing host plants (56, 80, 126, 211). Prior discussions of planthoppers have considered feeding physiology (230), responses to vegetation texture (69), life history styles (66), communication systems (28), natural enemies (27, 184, 257), economic importance and vector potential (3, 11, 107, 123, 170), and interactions with resistant crop varieties (107). However, for agronomic reasons, many compilations have focused on a single species (e.g. the rice brown planthopper, *Nilaparvata lugens;* 3, 107, 86). Few discussions have attempted to synthesize the widely scattered information on

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planthoppers from both agricultural and natural systems, and fewer yet have done so with an ecological focus (but see 257). It is our intent to draw together some of these data and, in particular, to unite the longstanding and elegant work conducted in Asia and Europe with the relatively recent research developing in North America. In this review we emphasize plant-insect interactions, population dynamics, and natural enemies, and we accent how delphacid planthoppers can be used as models for exploring contemporary issues in population biology.

HOST PLANT INTERACTIONS

Host Plant Taxa

It is commonly believed that most delphacid planthoppers feed, oviposit, and develop primarily on monocots (53, 175, 257, 276). Of the monocots, grasses (Poaceae) are by far the most frequently recorded host plants, but sedges (Cyperaceae), rushes (Juncaceae), and other families (Araceae, Arecaceae, Nymphaeaceae, Pontederiaceae, Typhaceae) also serve as hosts (53, 139, 179, 197, 257, 259, 264, 266). However, a minority of species feed on dicots (particularly Asteraceae) in North America (53, 146, 205) and ferns in Hawaii and the Orient (270, 276). Furthermore, none of the 135+ endemic Hawaiian species is a monocot feeder and most are associated with dicotyledonous trees and shrubs (87, 276). Thus, our perception that planthoppers feed primarily on monocots may change if the pattern in Hawaii is representative of the tropics in general and is not an isolated example of insular radiation.

Host Plant Specialization and Host Shifting

Patterns of host plant association are often confounded by reports of planthopper occurrence on nonhosts. For example, *Nilaparvata lugens* has been reported on 4 families of plants and on over 20 genera of grasses; in fact, it is monophagous on *Oryza* and *Leersia* (formerly *Oryza*) (158, 230). Moreover, recent evidence suggests that the populations on *Oryza* and *Leersia* are reproductively isolated, sibling species (33, 35). Monophagy (feeding and development on one or several closely related plant species) is widespread in the Delphacidae and occurs in species of *Delphacodes, Megamelus, Muellerianella, Nilaparvata, Prokelisia, Ribautodelphax, Stenocranus,* and *Stobaera,* to name a few (7, 45, 53, 72, 79, 145, 259, 266). The trend toward dietary specialization in planthoppers contrasts with the feeding patterns of grassland leafhoppers (Cicadellidae) in which examples of oligophagy are more common (261). Factors implicated in the dietary specialization of sap-feeding insects include physiological efficiency, tolerance of fluctuating

levels of host nitrogen, and enhanced success of dispersal or defense (160, 194–197), but in planthoppers evidence exists only for tolerance of fluctuating levels of host nitrogen. For example, monophagy has been favored in species (e.g. *Dicranotropis hamata)* that synchronize their life histories with peaks of nitrogen availability and yet tolerate periods of low nitrogen (194, 195, 197).

Oligophagous (*Peregrinus maidis* and *Saccharosydne saccharivora*) and polyphagous feeding styles (*Javesella pellucida* and *Laodelphax striatellus*) also occur, but with less frequency than monophagy (73, 89, 149, 197, 199). Some cases of oligophagy result from host range expansions in which planthoppers have included introduced hosts in their feeding repertoire (149). Others may result from selective pressures associated with a common habitat. For example, two intertidal grasses, *Spartina patens* and *Distichilis spicata,* are structurally similar but taxonomically distant; they share four species of planthoppers (52, 245). Also, polyphagy may be promoted in species (e.g. *Javesella pellucida*) that switch hosts seasonally to satisfy specific nutrient requirements (194, 197).

Available evidence suggests, however, that planthoppers do not easily adapt to novel host species. In several species of *Ribautodelphax,* females preferred to feed and oviposit on hosts where nymphal performance was highest (45). A strong genetic correlation between preference and performance (implicated only for *Ribautodelphax*) could make host shifting more difficult (247); selection experiments in planthoppers confirm this notion (45).

Rapid adapatation to resistant plant varieties provides conflicting evidence for the potential to shift to novel host genotypes. Physiological or genetic strains adapted to a particular plant variety have been termed "biotypes" (188, 230, 232). In *Nilaparvata lugens,* adaptation to particular rice cultivars can occur rapidly, often within ten generations (31, 189, 230, 265). The genetic basis for both adaptation (virulence) by *N. lugens* and varietal resistance in rice is well understood. Even though varietal resistance in rice is based on major genes (4, 17, 114, 121, 140, 188), a gene-for-gene correspondence between resistance and virulence by *N. lugens* does not exist as previously thought. Instead, selection experiments (31, 189), hybridization studies (34, 50), high variation in virulence among individuals of the same biotype (30, 32, 86a), and large overlap between biotypes in their virulence across varieties (30, 86a), are all consistent with a polygenic determination of virulence and potentially rapid adaptation to novel plant genotypes. Moreover, these results suggest that the use of the term biotype is misleading (30, 31, 50, 86a). Thus, the potential exists for rapid adaptation to host varieties, but the step to include a novel plant species in the diet is apparently much more difficult.

Plant Defense

Phloem-feeding planthoppers (230, 257; but see 16, 97, 227) are thought to avoid many allelochemicals that are compartmentalized in nonvascular tissues (230). For example, silicic acid, a strong feeding inhibitor in *N. lugens,* is localized in the parenchymal cells of rice where planthoppers generally do not feed (230, 272). Also, complex secondary chemicals (e.g. alkaloids, flavanoids, terpenoids, phenolics) are either absent or occur in low concentrations in grasses (13, 42, 88, 197, 203, 257). For these reasons, host plant nutritional factors are often the focus of planthopper feeding ecology (57, 58, 63, 148, 196, 257).

Few data are available on the chemical factors involved in plant defense against planthoppers; most existing information emerges only from studies on varietal resistance in corn and rice (84, 229, 230). Phenolic acids in corn interfere with settling behavior and deter feeding in *Peregrinus maidis* (84, 269). Oxalic acid present in resistant rice varieties is a strong feeding inhibitor (230, 273, 274). Decarboxylated derivatives of aromatic amino acids inhibit feeding in *N. lugens* (reviewed in 230), and high concentrations of certain amino acids inhibit oviposition in *Laodelphax striatellus* (153). Resistance in rice appears to be chemical and not behavioral or physical. Colonizing planthoppers readily settle on resistant plants and effectively insert their stylets into the phloem; rejection occurs only after tasting the phloem sap (230, 232). However, physical characteristics (glandular and hooked trichomes) can be effective defenses against cicadellids (249) and should be considered in future studies of planthoppers. Also our perspective on the role of allelochemicals in planthopper/host interactions is likely to change as species other than grass-feeders are studied.

Host Plant Nutrition

Host plant nutrition (nitrogen in particular) has figured prominently in the understanding of planthopper/host plants relationships, life history patterns, population dynamics, and community structure (56, 57, 58, 63, 148, 196, 197, 257). In general, planthoppers survive better (85), molt into larger adults (63, 65, 252), and are more fecund (150, 228, 252) if they develop on nitrogen-rich host plants. These increases in fitness are associated with higher feeding rates on more nutritious hosts (230). Certain amino acids (e.g. asparagine) and sucrose are known feeding stimulants for *N. lugens* and may be responsible for accelerated feeding on susceptible rice varieties (14, 228).

When given a choice in the laboratory, planthoppers select nitrogen-rich plants on which to feed and oviposit (57, 227). Under field conditions, macropterous adults accumulate rapidly and are less likely to emigrate from nitrogen-rich (fertilized) host plants (56, 68, 213). Fertilization can result in elevated levels of plant nitrogen, more robust plants with increased

living space, and more favorable microhabitats (80, 171, 195, 251). The combined effects of increased colonization and improved performance on nitrogen-rich plants often result in rapid population growth and larger population size (1, 24, 56, 57, 80, 118, 195, 252, 257, 262). For several sap-feeding homopterans, including the planthopper *Dicranotropis hamata,* maximum nitrogen utilization efficiencies occur at different plant nitrogen levels, which suggests that each species may be associated with and seek out a particular concentration of host nitrogen (194). Thus, it is not surprising that different planthopper species respond uniquely to nitrogen fertilizer treatments (195).

The sensitivity of planthopper reproduction and development to levels of available nitrogen has resulted in a variety of adaptations that minimize contact with or buffer these insects against low host nitrogen (58, 148, 196). Adaptations in planthoppers that attest to the limiting nature of nitrogen are:

1. Increased feeding rate on nitrogen-deficient foliage. Nymphs of *Dicranotropis hamata* have high weight-specific ingestion rates and low nitrogen utilization efficiencies when leaf nitrogen is low; on high nitrogen plants they show the opposite physiology (97, 257).
2. Selection of more nutritious feeding sites on plants. *Prokelisia marginata* and *D. hamata* prefer to feed on the most nitrogen-rich plant parts such as developing seed heads, terminal blades, or senescing leaves (56, 68, 97).
3. Synchronization of life cycle with periods of increased plant nitrogen. The spring and fall occurrences of adult reproduction in *D. hamata* and *P. marginata* are synchronized with periods of peak nitrogen availability in their hosts (56, 61, 64, 68, 97, 194, 259).
4. Dispersal to more nutritious host plants. Macropterous adults are produced in several species of planthoppers when they are raised on poor quality hosts (63, 126, 224). The interhabitat movements of *P. marginata* among stands of the same host species and the distribution of *Javesella pellucida* across hosts are associated with changing levels of plant nitrogen (56, 57, 58, 68, 195–197). Thus, both monophagous and polyphagous species may disperse in response to changing levels of host plant nitrogen (56, 64, 265).
5. Modification of plant nutritional physiology by feeding. Heavy feeding by *N. lugens* on rice induces proteolysis and dramatic increases in several amino acids, which may result in increased fecundity (14, 58).
6. Nutrients from other sources. Yeast-like and rickettsia-like endosymbiotes are thought to provide planthoppers with essential nutrients that are otherwise rare or absent in host plants (reviewed in 15). The extent to which symbiotes allow planthoppers to exploit otherwise nutritionally inadequate hosts awaits further study.

Responses to Vegetation Texture

Several components of vegetation texture contribute to the distribution and abundance of sap-feeding insects (reviewed in 69): patch size, plant density, and vegetation diversity (frequency of nonhosts) (115). We briefly outline the specific responses of planthoppers to these features of vegetation texture.

Along a gradient of patch sizes of *Spartina patens* that ranged from $>100,000$ m^2 to <50 m^2, *Tumidagena minuta* was abundant in large patches and virtually absent in small ones. Two other planthopper species were similarly abundant along most of the patch size gradient but were slightly more abundant in the very largest patches. In general, small patches contained fewer species (67, 204). Those planthoppers able to persist on small patches of *Spartina* were more dispersive (more macropterous with higher potential for colonization) and/or overwintered as concealed eggs (low extinction rate) and not as nymphs (67, 69). These findings are consistent with the notion that immigration rates increase and extinction rates decline as patch area increases and that larger populations and more diverse communities are found on large patches (209).

The influence of plant density and vegetation diversity on planthoppers is not well understood. One study of *Nilaparvata lugens* showed that the number of nymphs/tiller was similar in sparse and dense plantings of rice (80). However, several studies show that aphid and cicadellid abundance (number per plant) declines with increased plant density (number per area) (69, 83). Primarily as a result of lower rates of colonization, leafhoppers and some aphids tend to be less abundant in mixed, compared to pure, stands of their hosts (101, 141). However, vegetation texture can influence the functional and numerical responses of planthopper predators and thus can mask the direct effects of vegetation on planthopper abundance (77).

LIFE HISTORY PATTERNS

Reproduction is the cornerstone of life history theory; nevertheless, migration and diapause, traits that synchronize reproduction with favorable resources, are also essential components of an insect's life history (60). The integration of traits (life history syndrome) varies among planthopper species and depends on genetic variance and covariance among traits, phenotypic trade-offs and costs, and selection (60, 66, 211). A key feature of planthopper life histories is remarkable flexibility in migration and diapause. Such flexibility allows planthoppers to successfully track changing resources and predisposes them to be agricultural pests (56, 60, 127, 211).

Wing Dimorphism and Flexible Life Histories: Trade-offs Between Dispersal and Reproduction

Many delphacids exhibit wing dimorphism (53, 66, 71, 257). Because flight-less and migratory forms are so easily recognized, planthoppers are ideal organisms for investigating the evolution of dispersal and for testing hypotheses concerning the costs of dispersal and reproduction (62, 66, 211). Brachypterous adults have reduced wings and cannot fly, while macropterous adults possess fully developed wings and can disperse long distances (64, 66, 68, 129, 137, 199, 211). Field populations of many delphacids contain both wing forms, but the proportion of each can vary tremendously among different species (51, 53, 67, 71, 72, 79, 257) or within the same species geographically (64, 109, 111, 202, 216), seasonally (40, 253), and between the sexes (59, 62, 66, 71, 126, 211).

Fitness costs associated with dispersal can be assessed by comparing other components of fitness of the two wing forms. Brachypterous females are generally more fecund than macropterous females and reproduce earlier in life (short preoviposition period) (66, 79, 126, 156, 211, 253). The reproductive delay and reduced fecundity observed in the macropterous form of dimorphic planthoppers supports the notion that flight capability is costly and that phenotypic trade-offs between dispersal and reproduction exist (66, 217). In *Prokelisia dolus, P. marginata,* and *Stenocranus minutus,* brachypters survive longer than macropters; but this is not a general pattern (66, 145, 211). Increased survival contributes to higher fecundity because longevity and fecundity are positively related in many species of planthoppers (66, 79, 126, 156, 257). The advantage of brachyptery in males is less clear. There is no evidence for a delay in gonadal development in macropterous males as there is in females (156). However, brachypterous males of *Nilaparvata lugens* outcompete macropterous males for mates under certain circumstances (104). In *P. marginata,* brachypterous males outlive macropterous ones (211). Thus, brachyptery is advantageous in both sexes as long as conditions remain favorable for development and mates are available (66, 71).

Models of the evolution of migration assume that dispersal traits have a genetic basis, at least in part (215). In planthoppers, wing form is heritable and under polygenic control, but it can be modified substantially by environmental factors (40, 112, 132, 143, 156, 211, 215, 216). Depending on the conditions it experiences as a nymph, an individual can molt into either a macropter or a brachypter. Various environmental cues such as crowding, host plant condition, temperature, and photoperiod act on a hormonal messenger that triggers a developmental switch to determine wing form (62, 79, 109, 110, 113, 156, 211, 224). Of the factors known to influence wing form, population density is clearly the most influential (40, 62, 85, 110, 113, 126,

244). Generally, the production of macropters is density-dependent and can be intensified on poor quality (aging, senescing, or wilting) hosts (40, 62, 63, 111, 126, 224, 275). Thus, macropters are able to escape deteriorating host plants by dispersing to new habitats (40, 64, 80, 199).

Levels of dispersal (percent macroptery) in field populations are influenced by a variety of factors including host plant architecture, habitat persistence, plant succession, and resource isolation. Species inhabiting architecturally complex trees, temporary habitats (agricultural crops and mowed lawns), and early successional vegetation are either mostly or entirely (monomorphic) macropterous. In contrast, species exploiting low-profile vegetation, persistent habitats (marshes, meadows, and pond edges), plants in the middle stages of plant succession, and isolated hosts are mostly brachypterous (12, 51, 53, 54, 56, 57, 64, 69, 87, 124, 147, 208, 239, 258). In dispersive species and populations, selection has favored a low density threshold whereby macropters are produced; in sedentary species the developmental switch is not nearly as sensitive to density, and macropters are produced only under very crowded conditions (51, 64, 71, 79).

Within a single species, geographic variation in wing form composition also occurs and results from genetically controlled differences among populations in their response to density (109, 112, 132, 168, 216). For example, Atlantic and Pacific Coast populations of *Prokelisia marginata* are largely macropterous, whereas Gulf Coast populations are predominantly brachypterous (56, 64, 72, 147, 211, 239). Differences in host plant persistence, nutritional heterogeneity, and isolation explain the discrepancy in wing form composition among North American populations (56, 64, 147, 239). In the case of *N. lugens* some tropical populations are predominantly brachypterous; wing form responds weakly to changes in nymphal density and is more influenced by host plant physiology (109, 224). By contrast, wing form in temperate populations tends to be much more sensitive to density (109).

Sexual differences in wing form also occur both among species and populations. Macroptery is density-dependent in both sexes of sedentary species (e.g. *Prokelisia dolus*); however, in highly dispersive species like *Nilaparvata lugens, Prokelisia marginata* (Atlantic populations), and *Laodelphax striatellus,* macroptery is density-dependent in females, but most males emerge macropterous even when raised under low-density conditions (58, 71, 109, 126, 211). Macroptery may be favored in males of colonizing species because males must actively search for females under very low-density conditions (58, 71, 137). Thus, selective pressures associated with mate finding, host plants, and habitats appear to influence the wing form and dispersal of planthoppers.

Overwintering Styles, Voltinism, and Diapause

Most planthoppers overwinter as nymphs, but some overwinter as eggs, and a few as adults (7, 67, 72, 128, 257). Winter mortality can be very high (50%), and if the litter in which nymphs overwinter is removed, survival is reduced further (199, 245). Overwintering as eggs embedded within plant tissue provides some degree of protection from cold temperatures. For example, in a guild of salt marsh-inhabiting species, those that overwinter as nymphs (e.g. *Delphacodes detecta*) show a strong negative relationship between winter survival and winter severity; for species that overwinter as eggs (e.g. *Megamelus lobatus*) winter severity does not adversely affect survival (67). In this same guild, those species that overwinter as nymphs are rare at northern latitudes (67). Given these data, one may ask why so many planthoppers overwinter as nymphs. By overwintering as an active nymph, feeding can begin as soon as temperatures permit in the spring when host plant quality is highest (67, 197).

Geographically, the number of generations obtained each year is highly variable and largely dependent on the length of the growing season (a latitudinal phenomenon). In widespread species, reduction in the number of generations per year at higher latitudes is common (72, 80, 89, 137, 199). For example, *Laodelphax striatellus* is bivoltine in Sweden (60°N) but produces eight generations annually in Israel (32°N) (89, 181). At high latitudes in Europe and North America most species are either univoltine or bivoltine while in the tropics many species reproduce continuously and obtain as many as 12 generations per year (67, 80, 149, 151, 201, 257). In addition to growing season, patterns of nitrogen availability in hosts may constrain the number of generations per year (195, 197).

Patterns of diapause provide further evidence for the flexible life histories of planthoppers. Northern populations of *Laodelphax striatellus* overwinter as diapausing nymphs while southern populations never diapause and reproduce continuously (89). Cues inducing diapause in the nymphs of *L. striatellus* and *Javesella pellucida* and in the eggs of *Muellerianella* are a short photoperiod and cold temperatures (79, 89, 125, 199, 267). There is little evidence for diapause capability in tropical species (e.g. *N. lugens*), which probably accounts for their inability to persist in regions with cold winters (130, 137, 159).

Oviposition Patterns

Female planthoppers make a slit in plant tissue with their ovipositors, insert their eggs in rows, and cover them with a secretion that later solidifies (155, 234, 263). Most species deposit their eggs in small groups (2–20 are common), but a few species *(Dicranotropis muiri)* place eggs singly (89, 159,

257, 263). By depositing eggs in small groups, planthoppers may "spread their risks" in space and may increase survival (194).

Most species prefer their developmental host(s) for oviposition, but *Muellerianella fairmairei* oviposits, during the second generation, in nonhost vegetation where eggs overwinter (7, 79, 89, 257). Oviposition sites vary tremendously among species; some prefer to oviposit in leaf blades (*Prokelisia marginata, Nilaparvata lugens, Peregrinus maidis,* and *Perkinsiella saccharicida;* 72, 155, 234, 263) while others select leaf sheaths or stems (*Dicranotropis hamata, Javesella pellucida,* and *Laodelphax striatellus;* 89, 199, 248). Several hypotheses seek to explain the restriction of oviposition to certain plant parts or plant species. These hypotheses include the physical characteristics of host plants (79, 89), the specialized behavior of egg parasitoids (36, 199), and competition for oviposition sites (257).

Density-Related Effects on Components of Fitness

At high population densities, intraspecific competition can be intense and adversely affects many components of fitness. When species live under crowded conditions rates of survival are reduced (70, 85, 96, 126), individuals develop more slowly (63, 70, 79, 126), and fecundity is lower because of competition for oviposition sites (96, 118). Thus high density populations result in decreased reproductive rate (R_0) and population growth (137, 138). However, certain species *(Sogatella furcifera)* are more negatively affected by density than others *(Nilaparvata lugens)* (137, 138). Even congeners can differ dramatically in their sensitivity to density. For example, at the same high densities, most components of fitness are adversely affected in *Prokelisia marginata,* but not in *P. dolus* (70). To a large extent, the negative effects of density on fitness are intensified on poor quality host plants (63, 85). Reductions in fitness may not only be associated with crowded conditions, but may occur at very low densities as well. For example, if individuals are very rare and scattered, mates may be limiting. Under these conditions for *N. lugens,* single matings compared to multiple matings result in reduced fecundity (176). Thus, fitness is not linearly related to density, and maximal fitness may be realized at some intermediate level.

Environmental Effects on Components of Fitness

At hot (30°C) compared to cool (10°C) temperatures, eggs and nymphs develop more rapidly, but rates of survival are reduced (126, 241, 250). In *Nilaparvata lugens,* the preoviposition period of macropters is extended at cool temperatures yet remains the same for brachypters across a wide range of temperatures (154). Therefore, differences in age to first reproduction between wing forms are maximized at cool temperatures. For three species, *Muellerianella fairmairei, Nilaparvata lugens,* and *Peregrinus maidis,*

individuals develop fastest between 25 and 28°C, and variations in tempera-
ture in either direction result in delayed development (79, 241, 250). In
Prokelisia marginata, the body size of eclosing adults (a correlate of fecund-
ity) is inversely related to developmental temperature (65; R. F. Denno
unpublished data). Under conditions of low humidity (60%), *M. fairmairei*
developed slower and survived less well than when humidity was high (100%)
(79). Although the data are limited, these findings may explain why so many
species of planthoppers occur in moist habitats (7, 53, 80, 181).

Evidence for a Life History Syndrome

Life history theory predicts that particular combinations of traits (life history
syndrome) will evolve under specific selective regimes. For example, in
temporary habitats, high dispersibility and high fecundity should be favored
to allow for colonization and subsequent success. However, the trade-offs
(typical of planthoppers) between dispersal (wing form) and reproduction
appear to constrain the extent to which selection might maximize both traits
(66, 217). Additionally, changes in other life history characters (e.g. egg size)
may influence the evolution of phenotypic trade-offs. For example, the small
eggs and resulting high fecundity of *Dicranotropis hamata* may have con-
strained the evolution of dispersal in this species (see 97, 257).

Whether selection on one trait (dispersal) will influence another (reproduc-
tion) depends on the genetic correlation between them. In *Prokelisia margina-
ta* no significant genetic correlations were found between dispersal and life
history traits associated with development and reproduction, which suggests
that selection for dispersal will not influence traits of reproduction (211, 214).
In *Nilaparvata lugens* macroptery was found to be genetically correlated with
dark body coloration (162), thus possibly providing a thermodynamic advan-
tage to long-winged forms. Nevertheless, at population and species levels,
patterns of dispersal and body size suggest a genetic link between these two
traits. For example, adults from migratory (highly macropterous) populations
of *P. marginata* and *P. dolus* were significantly larger in size than those from
more sedentary populations (216), as is predicted on bioenergetic grounds
(218).

Planthopper and leafhopper life histories have been discussed in the context
of an *r-K* continuum; *r*-strategists are predicted to be both highly mobile and
fecund (123, 257). However, in a comparison of migratory and nonmigratory
planthopper species, fecundity was variable and not consistently higher for
dispersive species (59). Dispersibility may also be an adaptation for spreading
the risk of reproductive failure (257). Whether planthopper life histories
uphold predictions from bet-hedging theory will depend on a better un-
derstanding of juvenile and adult mortality schedules than presently exists.
Nevertheless, certain life history traits can be predicted by habitat characteris-

tics. For example, dispersive species prevail in temporary habitats (53, 71). However, strong evidence is lacking for a cohesive life history syndrome expressed as a coadapted set of traits within an individual. Instead, selection has resulted in a partitioning of dispersive and reproductive functions between morphs, the ultimate in life history evolution. Macropterous individuals serve to locate new habitats while brachypters assure that the lineage contributes maximally to future generations (76). Within a morph, selection may fine tune the way traits are integrated. A survey of three genera containing both migratory and sedentary species supports this point. Within each genus, macropterous adults of migratory species were larger than macropters of their sedentary congeners (59).

MATING SYSTEMS, COMMUNICATION, AND REPRODUCTIVE ISOLATION

Sexual and Asexual Reproduction

Most planthoppers reproduce sexually; in many species sex is determined by an XO system with $2n = 30$ in females and 29 in males (48, 122). However, in populations of some *Ribautodelphax* and *Muellerianella* species, pseudogamous triploid females occur (8, 47–49, 79). Pseudogamy is a form of parthenogenetic reproduction in which females do not produce offspring unless they are inseminated; however, sperm does not contribute any genetic material to the all-female offspring (49). Thus, pseudogamous females must coexist with a sexual species and compete for males (49). Because pseudogamous females have a twofold reproductive advantage over sexual females (49, 79), populations should become increasingly biased towards pseudogamous females, which have to mate with a diminishing number of males (49). Mixed populations will become extinct when the remaining males inseminate only pseudogamous females (49). However, in field populations the ratios of pseudogamous to sexual females remain rather constant from year to year (10). This stability results from a balance between the reproductive advantage of pseudogamous females and active frequency-dependent mate discrimination by diploid males against triploid females (49). Most data suggest an autopolyploid origin for pseudogamous triploids rather than a hybrid origin (7, 46–49; but see 9).

Acoustic Communication and its Functions

Formerly it was thought that cicadas were the only homopterous insects able to produce sound and communicate acoustically. However, delphacids, cicadellids, and membracids also produce low intensity calls (180). Unlike the airborne signals of cicadas, the communications of planthoppers are transmitted through substrate vibrations (8, 28, 29, 44, 46, 74, 75, 91, 102,

103, 105, 106, 240). Both males and females produce sounds by vibrating their abdomens dorsoventrally, but the substrate is not contacted directly; vibrations are transferred to the host plant through the legs and perhaps through inserted feeding stylets (29, 152). Planthoppers sitting on the same host plant or on adjacent plants that are in physical contact with one another are able to sense the vibrations, communicate, and respond. If two adjacent plants are separated so that the foliage is no longer touching, communication ceases even though planthoppers continue to signal (105).

Acoustic signals in planthoppers serve a variety of behavioral functions that include (*a*) male aggression, (*b*) mate recognition, location, and attraction, and (*c*) courtship and mate choice (28, 29, 91, 104). Aggression calls are observed during male-male interactions, are more frequent at high densities, are associated with attack behavior, and play a role in male dominance (8, 104).

Attraction signals (common calls) are produced by both sexes and operate in species recognition and mate location (28, 29, 105). Male calls are more complex than female calls as predicted by sexual selection theory; greater divergence between male signals is expected if females discriminate between males and males are less selective (8). Sexually mature males and virgin females call spontaneously on their food plants. After sensing each other, they begin to alternate calls as in a duet (29, 105, 106). During this duet, a male moves toward a stationary female from as far away as 1 m; after locating her, courtship begins (105). Of all the acoustic signals studied, common calls show the greatest species specificity; they differ dramatically among species and are thought to act in part as premating isolating mechanisms (8, 28, 29, 44, 46, 74, 75, 91, 106). Courtship signals function in mate acceptance, the timing of insemination, and pair maintenance; they are also species-specific (8, 29).

Acoustic communication is essential for mate finding, particularly under low density conditions (71, 103). Because sexual maturation and mating generally occur after dispersal, planthoppers are forced to find mates upon arrival in new habitats (23, 127, 129, 133, 137, 173, 177, 253). For colonizing species such as *Nilaparvata lugens,* densities are extremely low and males fly among hills of rice searching for calling females (103).

Geographic variation in acoustic signals is known for several species (8, 34, 35, 44). Genetic differentiation in acoustic characters occurs among allopatric populations of *Nilaparvata lugens* on a single host plant species and is associated with reduced hybridization success (34). Call divergence also occurs between closely related, sympatric species of *Nilaparvata* that use different host plants (33). In such cases, it is tempting to conclude that host plants have played a role in speciation, which may have occurred sympatrically (29, 265). However, published studies on sympatric biotypes of *N.*

lugens on rice have failed to identify any acoustic differences that might represent intermediate stages in a process of sympatric speciation (29, 33). Also, there is little evidence for greater divergence in acoustical characters in areas of sympatry among closely related species (8). The available information concerning acoustic differentiation is most consistent with an allopatric speciation model (29).

POPULATION DYNAMICS

Planthopper populations fluctuate dramatically within and among seasons in the same patch as well as spatially among patches (56, 64, 67, 68, 79, 80, 136, 137, 199, 211, 238, 257). Population growth can be exponential during the growing season (67, 123, 126, 130, 137) and particularly rapid in local patches where aggregations of brachypterous adults occur (126). Numerous factors, including host plant nutrition, predators, parasites, pathogens, dispersal, competition, and physical stresses, influence population growth and determine spatial and temporal variation in population size.

Predators, Parasites, and Pathogens

The eggs of planthoppers are attacked by a variety of predators and parasitoids. Important egg predators include Hemiptera in the families Miridae (e.g. *Cyrtorhinus* and *Tytthus*) and Nabidae (27, 56, 98, 184, 235, 243, 257). Hymenoptera are frequent egg parasitoids (e.g. Mymaridae with *Anagrus* and *Gonatocerus* and Trichogrammatidae with *Paracentrobia* and *Oligosita*) (27, 151, 182–184, 199, 237, 257, 263, 271).

Common parasitoids of nymphs and adults are Dryinidae (Hymenoptera), Elenchidae (Strepsiptera), and Pipinculidae (Diptera) (27, 79, 89, 90, 135, 184, 185, 199, 243, 254, 255, 257, 260, 271). These endoparasitoids oviposit in and emerge from nymphs and/or adults, depending on the species (257). Parasitoids often kill their planthopper hosts but may sterilize adults by feeding on internal reproductive organs or by deforming the ovipositor or external genitalia (117, 135, 198).

The most abundant predators of nymphs and adults are spiders (e.g. Lycosidae, Linyphiidae, and Tetragnathidae), but Coleoptera (Coccinellidae, Carabidae), Hemiptera (Miridae and Veliidae), and Hymenoptera (Formicidae) are locally important (27, 56, 77, 108, 119, 123a, 144, 184, 220, 257). However, ants also tend some species of planthoppers (e.g. *Peregrinus maidis*), feed on their honeydew, and protect them from predators; as a result, ant and planthopper populations are positively related (85, 120).

Pathogens, fungi in the Entomophthorales, and a few viruses are known to infect planthoppers (27, 89, 151, 178, 226, 233). Fungal epizootics occur periodically under humid conditions, but infestation rates are often low

(<10%) as is planthopper mortality (27, 98, 233). However, cases of high egg mortality in planthoppers and leafhoppers have been attributed to fungus (257). Also, the plant virus MRDV that is vectored by *Laodelphax striatellus* can decrease the vector's reproductive capability, and local extinctions can occur as a result (89).

Relative Impact of Mortality Factors on Planthopper Populations

Egg mortality is thought to be the key factor in the population dynamics of planthoppers and leafhoppers (41, 257, 260). For example, high egg mortalities have been reported for *Dicranotropis hamata* (95%), *Nilaparvata lugens* (91%), *Saccharosydne saccharivora* (90%), *Javesella pellucida* (70%), and *Stenocranus minutus* (55%) (41, 119, 144, 151, 199, 260). However, the source of egg mortality differs from one planthopper species to the next. Populations of *Perkinsiella saccharicida* in sugar cane were completely "controlled" with the introduction of a mirid egg predator, and mirids inflict heavy mortality on other planthopper species as well (5, 27, 98, 243; but see 39). For *J. pellucida*, egg predators were also important; in *S. minutus* and *N. lugens* a combination of parasites, predators, and egg sterility contributed to high mortality; in *S. saccharivora* a host plant–related factor was responsible (119, 144, 151, 199). In one case in which total egg mortality was investigated by key factor analysis, it was not found to be density dependent (260).

Rates of parasitism by mymarids and trichogrammatids are generally low (<30%) (6, 27, 79, 119, 138, 151, 199, 212), although much higher rates (30–100%) can occur (27, 172, 184, 237, 243, 268). High rates of parasitism are associated frequently with low egg densities (151, 237) as is the case in the early stages of an agricultural crop (184). Instances of inverse density-dependent parasitism by hymenopterous egg parasitoids of planthoppers are common (2, 6, 19, 151, 199, 211, 212, 237). Inverse density dependence appears to be largely a result of the high potential for planthopper population increase (126, 137, 195, 257), combined with a lack of sufficient numerical response by parasitoids (237), Type II functional responses resulting in egg depletion (18, 161), mutual interference among parasitoids (18), and use of alternative hosts (27, 184, 257, 263). Given the high dispersal rates observed in many planthopper egg parasitoids (2, 199, 243), the relatively low fecundity of the parasitoid (161), rather than failure to locate patches of high host density, better explains patterns of inverse density dependence.

Although nymphal mortality can be very high, it has not been identified as a key mortality factor for planthoppers and leafhoppers (257, 260). Several factors contribute to nymphal mortality including predation (27, 77, 118, 220, 257), parasitism (144, 151, 260, 263), winter kill and summer drought (67,

199, 260), asynchrony with periods of peak host plant nitrogen (148, 194), and density-dependent interactions among individuals (118, 119).

Of these factors, predation is most often singled out as important, but its contribution to nymphal mortality may vary among systems (77, 118, 220, 257, 260). In both natural and agricultural habitats, spiders (27, 77, 119, 123a, 184, 221) and occasionally coccinellids and hemipterans (27, 39, 108, 119) are the most frequent predators of nymphs and adults. Confined with planthoppers in cages, spiders are able to inflict high mortality (77, 116). Spiders show strong preferences for certain prey species (77, 123a, 222). For example, 61% of the diet of *Pardosa* (Lycosidae) are *Prokelisia* planthoppers, which are highly preferred over larger and more active prey species (77). In the field the effectiveness of spiders as predators is also attributable to their aggregative behavior and strong numerical response to planthopper density (77, 118, 119, 211, 252, 257).

Nymphal and adult parasitism by Dryinidae, Elenchidae, and Pipinculidae is generally low (<20%) (27, 79, 119, 185, 190, 199, 236, 257). Although parasitism rates occasionally exceed 50% (144, 151, 166, 260, 271), nymphal parasitoids are not often implicated as important factors in population dynamics (27, 184; but see 151). Weak support for delayed density dependence between planthopper density and parasitism rate has been observed, but the relationship was irregular suggesting that other factors contributed to planthopper mortality (257). It has been proposed that nymphal parasitoids (Elenchidae) have a stabilizing effect on host populations (257) and that they play a role in synchronizing generations of planthoppers by sterilizing most adults and limiting oviposition to a narrow window (151). Because the females of these parasitoids are either apterous (Dryinidae) or remain within the planthopper adult (Elenchidae), they must rely on their dispersing hosts for the colonization of new habitats (200, 253, 257). However, because many nymphal parasitoids are polyphagous (254, 255, 257), exploiting alternate hosts in the same habitat may be an alternative to dispersal. That some parasitoids (Dryinidae) emerge mostly from sedentary nymphs (236, 260) and others from dispersing adults (199) is suggestive of alternative strategies.

After the action of egg and nymphal mortality factors, <4% of the population survives to become adults; this pattern is characteristic for species in natural *(Dicranotropis hamata, Stenocranus minutus)* and agricultural habitats *(Nilaparvata lugens, Javesella pellucida)* (119, 144, 199, 257, 260). Adults are subject to the same sources of mortality as are nymphs and may suffer further reductions in fitness under crowded conditions when oviposition sites become limiting (118, 119). Adults of species that exploit persistent habitats are mostly brachypterous, immobile, and subject to the vagaries of the local patch. Macropterous species that disperse among patches can incur tremendous mortality during migration (129, 131). However, during long distance migration, certain species *(N. lugens)* incur greater mortality than

others *(Sogatella furcifera)* (131). The greater mortality incurred by *N. lugens* may be attributable to higher wing loading and a lower proportion of individuals capable of extended flight (132, 133). Because they fly, macropters of *Prokelisia* are much more freqeuntly trapped in the webs of spiders *(Neoscona)* than are brachypters (78). However, brachypters are slightly more susceptible to predation from hunting spiders (77).

Dispersal

Dispersal allows planthoppers to exploit temporary habitats (53, 64, 80), track changes in host plant quality (56, 58, 64, 68, 196), escape crowded or otherwise fitness-reducing conditions (62, 63, 71, 126, 211), and locate mates (71, 103). A common "colonization syndrome" exists for several multivoltine planthoppers *(Nilaparvata lugens, Peregrinus maidis, Sogatella furcifera)* exploiting temporary habitats (crops), which illustrates the adaptive nature of polymorphic life histories. In a new crop, macropters colonize at very low densities, their offspring are mostly brachypterous, and rapid population growth ensues; in the following generation nymphs molt to macropterous adults, which can escape deteriorating conditions by dispersing to other habitats (38, 80, 85, 130, 137). This sequence of wing form change is mediated largely by increasing density and deteriorating plant quality (previously discussed). However, if macropters colonize temporary habitats in high densities (e.g. *Prokelisia marginata*), nymphs will be crowded and molt mostly into macropterous adults (56, 62, 64).

Although many delphacids develop and overwinter mainly in the same habitat, others undergo regular migrations between habitats, in which departure and return is by different individuals (253, 257). For example, interhabitat migrations of *Prokelisia marginata* and *Javesella pellucida* involve individuals of different generations moving to and from their development habitats and their overwintering habitats (62, 199). The literature strongly suggests that highly dispersive planthoppers have specific nutrient demands (62, 63, 68, 196). In seasonal environments, several species of planthoppers disperse in the spring and colonize their hosts when the nitrogen content is at its peak (2, 62, 63, 64, 253, 257). Other dispersal events occur in autumn and are associated with deteriorating hosts and/or movement to overwintering habitats (56, 62–64, 145, 199).

Nilaparvata lugens and *Sogatella furcifera* show bimodal periodicity in flight behavior and migrate during crepuscular hours with a larger flight at dusk than at dawn (23, 177, 186, 191, 193, 223). *Javesella pellucida* (199) and several species of *Prokelisia* and *Delphacodes* (R. F. Denno and G. K. Roderick, personal observations) migrate during the day. Most migrations take place on warm, often humid, days under low wind conditions (129, 131, 133, 191, 199, 201, 219, 257).

Although long-distance (600–1000 km) transoceanic migrations occur in

some species (e.g. *Nilaparvata lugens* and *Sogatella furcifera*) (127, 129, 131, 219), most planthoppers are weak fliers and migrate much shorter distances (1–3 km), (2, 64, 200, 225, 246). The transoceanic migrations of rice planthoppers that initiate in mainland China and are carried northeast by winds to Japan and Korea have been an enigma for two reasons. First, these planthoppers are tropical species and do not overwinter successfully in Japan; second, there is very little evidence for any return flight (25, 127, 129, 130, 131, 132, 133, 142, 219). Consequently, the adaptive nature of such migrations is unclear (133). Recent information suggests that *N. lugens* disperses mostly over short distances (192, 210). Thus, these wind-assisted migrations may be an artifact of a dispersal "strategy" that is favored on the mainland, where under certain climatic conditions dispersing macropters are swept off to sea. Nevertheless, these migrations pose a major threat to the rice industry in Japan and Korea (82).

Outbreaks

Planthopper outbreaks are a common phenomenon in both natural and agricultural systems, and records of outbreaks on rice crops date back to 18 AD (99, 119, 187, 231, 242). Data from several species provide evidence for an escape density, below which natural enemies (primarily predators) suppress planthopper populations and above which outbreaks occur. At low or endemic population densities, predators and parasites are more effective in limiting population growth (77, 151, 184). Outbreaks may occur if enemy-planthopper interactions are destabilized and result in a numerical advantage for the planthopper. Such an advantage may accrue from differential dispersal, survivorship, or fecundity.

Factors that improve host plant condition or synchronize populations with periods of improved plant quality can provide an advantage for the planthopper (196). For example, the use of high yielding crop varieties (80, 118, 151, 157, 188, 251), nitrogen fertilizers (24, 56, 80, 150, 252), and improved irrigation practices (80, 118, 157, 251) can lead to outbreaks. Even though the potential for rapid population growth is greater on nitrogen-rich hosts, enemies may offset this advantage, and the result may be little population change (77, 252). Also, climatic factors may affect plant condition directly or may synchronize planthopper populations with favorable plant conditions and result in escape from predation (97, 134, 148, 151, 257). Altering normal planthopper-host phenology by deploying early maturing rice varieties decreased the ratio of *N. lugens* to predators, thereby reducing the probability of population outbreaks (93).

When predators (spiders and hemipterans) are excluded experimentally or have not yet been introduced as biological control agents, outbreaks are frequent (118, 119, 243). Planthopper resurgence following insecticide

application provides further evidence for the suppressing role of natural enemies. Resurgence is most often attributed to predator kill or improved plant quality (21, 22, 81, 92, 94, 95, 119, 123, 206, 207), both of which favor planthopper population growth.

Differences in the population dynamics of *N. lugens* in temperate and tropical regions underscore the importance of synchrony between enemies and planthoppers as a factor in suppressing populations. In temperate Asia where agriculture is seasonal and *N. lugens* fails to overwinter, recolonization by settling migrants takes place annually (129, 137). Immigration occurs during a short period of time, and the density of colonists is highly correlated with the final population size that prevails in the paddy (99, 123, 130, 142). By destabilizing interactions with predators, the seasonality of the system enables planthopper populations to grow largely unchecked by natural enemies. By contrast, in tropical Asia continuous cropping practices allow greater synchrony in the colonization of rice paddies by *N. lugens* and its predators; the lack of a significant relationship between the density of immigrants and population growth implicates the involvement of predators, who exert a major influence on population size (39, 100, 119). If planthopper populations escape their natural enemies, populations can grow exponentially but are ultimately limited by intraspecific competition for food and oviposition sites (119). The observation that density-dependent reductions in fitness are severe at high densities is consistent with theories of population regulation based on ceilings or stochastic boundedness (26, 43, 167, 238). Below the ceiling, the effect of density on population growth is variable, and there is evidence for density independence (260), density vagueness (238), and density dependence (119).

COMMUNITY STRUCTURE

Competition, predation, and interactions with host plants are potentially important processes in the organization of planthopper-dominated communities. Even though planthopper and leafhopper species partition resources in time and space (55, 67, 256, 257) and show inverse density relationships (55, 67), there is very little evidence for interspecific competition (67, 98). In a laboratory study involving interspecific interactions between *Prokelisia marginata* and *P. dolus*, no component of fitness was directly affected in either species over the range of densities normally encountered in the field; however, interspecific crowding resulted in the production of migratory forms of both species (70). In the same study, intraspecific crowding had strong negative effects on survival and development, but only for *P. marginata*. Resource partitioning and the restriction of certain species to particular microhabitats on the plant are more likely the result of specific nutritional require-

ments, which are only found locally (148), and/or the action of natural enemies. For example, *Javesella pellucida* chooses to oviposit in the stems of oats and wheat rather than in leaves where rates of parasitism are much higher (199).

One very important factor influencing the richness of planthopper communities is the architecture (size and number of plant parts) of the host plant (69). Two lines of evidence suggest that structurally complex grasses, including those with thatch, provide greater microhabitat diversity and by so doing support a richer fauna of planthoppers and other sap-feeders. First, positive correlations exist between sap-feeder species richness and various components of architectural complexity such as foliage height (164, 195), foliage height diversity (245), and biomass (52, 195, 245). Second, when grass architecture is simplified by dethatching (52, 245), cutting, or grazing (163, 165, 257), sap-feeder richness is reduced. After dethatching *Spartina patens*, species inhabiting the upper strata *(Delphacodes detecta)* either showed population increases or were uninfluenced; planthoppers normally residing beneath the thatch layer *(Megamelus lobatus)* were adversely affected (52, 55, 245). Apparently, dethatching provided newly "uncovered" resources for upper strata residents but destroyed microhabitats normally exploited by lower strata inhabitants (69).

Thus, the architectural complexity of the host plant appears to set an upper limit on the number of coexisting species. Erosion of maximum richness results from a combination of factors including climatic harshness (67), small patch size (67, 204), short-lived host plants (69), and temporal changes in host plant condition (196, 197). Nonequilibrium conditions are common and interspecific competition does not appear to be important (67, 69).

PROSPECTUS

Because of their primary pest status, planthoppers have long been the focus of applied research, giving rise to an impressive data base that addresses nearly every aspect of population biology. This work has highlighted the value of planthoppers as model organisms for pursuing theoretical questions in natural systems. Yet, our ecological knowledge of the group is limited to a very few species that, without exception, feed on grasses. Consequently, as we learn more about other species, for example those that feed on tropical dicots, our views on planthopper population biology will probably change. Issues ripe for study are plant allelochemistry and its role in host plant utilization, dispersal and the genetic structure of populations, and the combined effects of predators and parasites in population dynamics and pest management. Despite the existing bias in knowledge, we believe that wing polymorphism and the flexibility it affords contribute significantly to the success of planthoppers in natural and agricultural habitats.

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