Caught Between the Devil and the Deep Blue Sea, Mobile Planthoppers Elude Natural Enemies and Deteriorating Host Plants

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Delphacid planthoppers (Hemiptera: Delphacidae) are mostly drab-colored, diminutive (<5mm) denizens of grassland habitats (Denno and Roderick 1990; Fig. 1). Their grass-feeding habit has predisposed a fair number of these phloem feeders for becoming severe agricultural pests of rice, corn, cereals, sorghum, and sugarcane throughout the world (Wilson and O'Brien 1987). Most of the remaining 2,000 delphacid species, however, occur in marshes, old fields, meadows, prairies, and pasture lands where they usually go unnoticed (Denno and Roderick 1990, Wilson et al. 1994). As with most taxa of phytophagous insects, delphacid species vary in how widely their populations fluctuate. Many planthopper species undergo dramatic fluctuations, reaching outbreak proportions at times and then crashing to barely detectible levels at others (Waloff 1980, Denno and Roderick 1990, Strong et al. 1990, Perfect and Cook 1994). In contrast, populations of other planthopper species exhibit a much more latent dynamic, fluctuating less and remaining at low levels much of the time (Waloff 1980, Denno et al. 1981).

Just why some species of phytophagous insects exhibit eruptive population dynamics whereas others consistently remain scarce has caught the attention of population ecologists for years (Price et al. 1990, Auerbach et al. 1995, Cappuccino et al. 1995, Hunter 1995). Because many agricultural and for-

Fig. 1. After their arrival in new habitats, colonists of the salt marsh-inhabiting planthopper *Prokelisia marginata* mate on their sole cordgrass host plant, *Spartina alterniflora* Lois. This mobile species migrates annually from overwintering sites on the high-marsh to better sites for development that occur in low-marsh habitats along the Atlantic coast of North America.

Fig. 2. Population outbreak of the brown planthopper, *Nilaparvata lugens,* on rice stems in Vietnam.
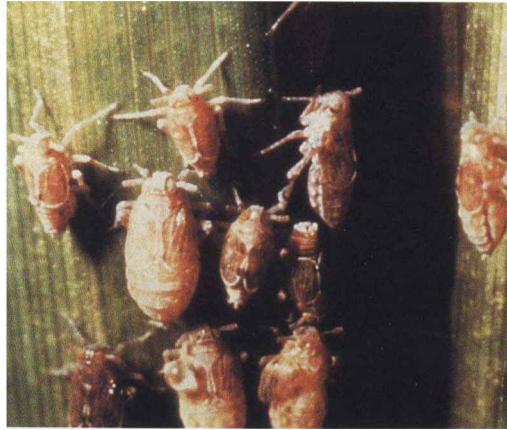
est insect pests, including planthoppers, exhibit outbreak dynamics (Barbosa and Schultz 1987, Ferro 1987, Perfect and Cook 1994, Reeve et al. 1995), understanding those factors that promote population explosions, and thereby improving our ability to predict them, is also the central concern of pest managers (Cheng et al. 1994; Fig. 2).

Historically, views on those factors underlying the suppression and outbreak of herbivorous insect populations have been polarized into two camps (Denno and McClure 1983). There are those who have championed natural enemies as the primary drivers of the population dynamics of phytophagous insects (e.g., Hairston et al. 1960), whereas others have espoused host plant-related factors such as plant nutrition, allelochemistry, or phenology as the causal forces largely responsible for population fluctuations (see Denno and McClure 1983). Fortunately, the long-standing debate over the absolute importance of so-called "top-down" (natural enemies) versus "bottom-up" forces (host plant resources) in the population and community ecology of phytophagous insects has given way to a more integrated expectation (Hunter and Price 1992, Rosenheim 1998). Early on, however, an insightful few embraced a more unified view and recognized that phytophagous insects were caught between the "devil" of natural enemies and the "deep blue sea" of phytochemistry (e.g., Lawton and McNeil 1979, Price et al. 1980). Recently, an increasing number of studies have shown the simultaneous effects of both plant resources and natural enemies on the population dynamics of herbivorous insects and mites (Karban 1989, Hanks and Denno 1993, Hartvigsen et al. 1995, Hunter et al. 1997, Hunter 1998, Rosenheim 1998). Nevertheless, there is extreme variation among different species and across populations of the same species in the relative contribution of top-down and bottom-up forces to population dynamics (Karban 1989).

For some species, host plant-related factors, more often than not, appear to underlie population change and outbreak. These factors are diverse and include plant nutrition (Dixon 1970), feeding-induced phytochemistry (Neuvonen and Haukioja 1991), plant phenology (Hunter 1992, Auerbach et al. 1995), drought stress (Raffa 1988),

and seed availability (Solbreck 1995). In contrast, natural enemies appear to contribute more than host-plant factors to the suppression and population dynamics of many other plant-feeding insects (McClure 1986, Karban 1989, Morris 1992, Hacker and Bertness 1995). Moreover, the effective suppression of agricultural pests with the introduction of specific biological control agents (DeBach and Rosen 1991, Benrey and Lamp 1994), and the resurgence of pest populations following the selective destruction of predators and parasitoids with insecticides (Heinrichs 1994), lend general support to the notion that natural enemies can be important in checking herbivorous insect populations.

Even though it generally is agreed that top-down and bottom-up forces typically act in concert on most phytophagous insects (Harrison and Cappuccino 1995, Hartvigsen et al. 1995, Hunter et al. 1997), one can ask what conditions dictate the relative impact of each force. Simply stated, can we explain some of the interspecific variation that exists concerning the relative importance of natural enemies and host plants to population dynamics? Although several factors undoubtedly bear on the relative strength of these forces (e.g., phylogeny and climate), one ingredient that emerges as potentially central is life history strategy, and, in particular, dispersal ability (Cappuccino et al. 1995, Denno and Peterson 1995, Hunter 1995). For example, one might hypothesize that dispersal facilitates both the location of more favorable host plants and the escape from natural enemies. If this were the case, then outbreaks should be commonplace, and bottom-up control likely would prevail for phytophagous insects with mobile life styles. In contrast, sedentary life histories may allow natural enemies to better track prey populations, promote less eruptive population dynamics in general, and shift the balance toward top-down regulation. In this article, we examine the extent to which dispersal capability influences the outbreak dynamics of delphacid planthoppers and, in particular, affects the primacy of host plant versus natural enemy control.

For several reasons, delphacid planthoppers provide an ideal opportunity to address these issues. First, dispersal capability can be easily quantified in delphacids because many of these sap-feeders are wing dimorphic, having flightless (Fig. 3) and flight-capable morphs (Fig. 4), thus elucidating the proportion of potential dispersing adults in populations (Denno et al. 1989). Also, there is extreme variation among delphacid species in their dispersal ability with both migratory and flightless species represented (Denno et al. 1991). Finally, responses to plant resources and natural enemy impacts are known for a sufficient number of delphacid species (see Cook and Denno 1994, Döbel and Denno 1994) that an interspecific comparison of the relative impacts of these forces can be made.

In the sections that follow, we review background information on delphacid planthoppers

regarding their wing dimorphism and ability to disperse, their reproductive capability and potential for population growth, the consequences of fluctuating host-plant quality on performance and population increase, and the effectiveness of important natural enemies in suppressing populations. Next, we couple data on dispersal capability with information on population dynamics, responses to changing host-plant quality, and natural enemy impacts to discover if dispersal enhances bottom-up regulation and fosters population outbreaks in this group of phytophagous insects. Finally, we will consider our findings in the context of pest management and provide some recommendations regarding the improved control of these mobile pests.

Wing Dimorphism, Dispersal, and Population Dynamics

Most delphacid planthoppers are wing dimorphic with both migratory adults (macropters) and flightless ones (brachypters) occurring in the same species (Denno 1994; Figs. 3 and 4). Macropterous adults possess fully developed wings and can disperse long distances, distances approaching 1,000 km in the case of the brown planthopper, *Nilaparvata lugens* Stål (Kisimoto and Rosenberg 1994). In contrast, brachypterous individuals have reduced wings and cannot fly (Denno et al. 1989, Perfect and Cook 1994). Populations of most delphacids are composed of both wing forms, although the proportion of each can vary tremendously among different species and geographically among populations of the same species (Iwanaga et al. 1987, Denno 1994, Denno et al. 1996). The fraction of macropterous adults in a population provides a convenient estimate of the dispersal potential for that population (Denno et al. 1991, Peterson and Denno 1997).

The mere existence of flight dimorphism in insects suggests there are penalties associated with dispersal ability (Roff 1984). To a large extent, the costs associated with flight capability in planthoppers, and in many other phytophagous insects as well, are imposed on reproduction (Roff 1986, Denno 1994). For female delphacids, flightless morphs are generally more fecund and reproduce earlier in adult life than macropterous individuals (Denno et al. 1989). Furthermore, the brachypterous males of some delphacids sire more offspring than macropterous males (Langellotto et al. 2000). Thus, for many delphacid planthoppers, flight capability is costly and phenotypic trade-offs between dispersal and reproduction are clearly evident (Denno et al. 1989, Zera and Denno 1997).

Although wing form is heritable in delphacid planthoppers, it can be modified substantially by environmental factors (Kisimoto 1981, Cook and Perfect 1985, Iwanaga et al. 1985, Denno 1994). 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 and host plant condition act on a hormonal messenger that triggers a devel-

Fig. 3. Flightless adults (brachypterous wing form) of planthoppers, the brown planthopper, *Nilaparvata lugens,* in this case, have reduced wings and can disperse only short distances by walking or jumping. Their reproductive potential is high, however, because of enhanced fecundity and an early age of first reproduction.

Fig. 4. Flight-capable morphs (macropterous wing form) of planthoppers (*Nilaparvata lugens* pictured here) have fully developed wings and can dispense long distances. Macropterous females are both less fecund and reproduce later in adult life than their flightless counterparts.

opmental switch to determine wing form (Iwanaga and Tojo 1986, Iwanaga et al. 1987). Of the factors known to influence wing form, population density is by far the most influential (Denno et al. 1994). Generally, the production of macropters is density-dependent and is intensified on deteriorating host plants (Kisimoto 1965, Cook and Perfect 1985, Denno et al. 1986). Consequently, macropters are able to escape declining host plants by dispersing to new habitats (Cook and Perfect 1985, Denno 1994). Brachypters, which lack the luxury of escape, are saddled with the constraints of the local habitat (Denno 1994). However, because brachypters have enhanced fecundity and early reproduction, they are the most favored morph as long as host-plant conditions remain suitable for development (Denno et al. 1989).

The potential for population increase is tremendous in certain planthopper species, although there is extreme interspecific variation (Denno 1994). High lifetime fecundities (>500 eggs per female in some species), coupled with early age of first reproduction and short generation times (4-6 weeks), all contribute to an explosive rate of increase for a number of delphacid species, including several major agricultural pest species (Napompeth 1973, Kisimoto 1981, Denno 1994; Fig. 5). Despite the high potential for increase, both plant-related factors and natural enemies can moderate dramatically the extent to which this prodigious reproductive potential is realized.

Fig. 5. The lifetime fecundity of some delphacids, such as the corn planthopper, *Peregrinus maidis,* is exceptionally high (>500 eggs per female), a trait that has the potential to promote explosive population growth.

Fig. 6. An adult of the coccinellid beetle *Micraspis hirashimai* Sasaji voraciously consuming nymphs of the brown planthopper, *Nilaparvata lugens*. In general, invertebrate predators are thought to exert more impact on planthopper populations than parasitoids.
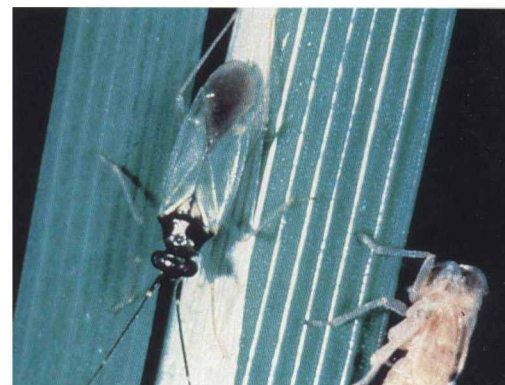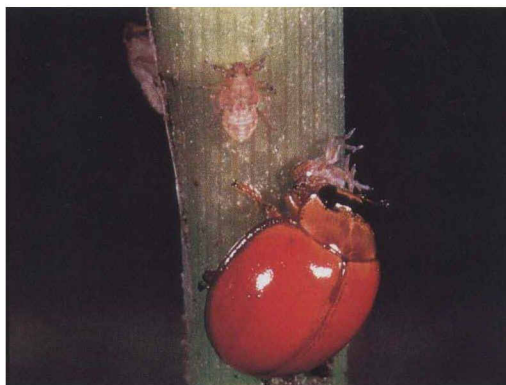

Fig. 8. Mirid bugs are voracious and quite specialized egg predators of planthoppers. Here, an adult *Cyrtorhinus lividipennis* Reuter scurries up and down rice stems probing in search of the embedded eggs of the brown planthopper, *Nilaparvata lugens*.

Fig. 7. Spiders, especially hunting spiders (e.g., Lycosidae), are one of the major predators on the active stages of planthoppers in a variety of natural and managed habitats. Here the wolf spider, *Pardosa littoralis* Banks, an abundant salt marsh-dwelling lycosid, has captured an adult male of *Prokelisia marginata*.

Fig. 9. With their pruning saw-like ovipositors, planthoppers insert their eggs into plant tissues. The eggs and oviposition scars of *Prokelisia marginata* occur abundantly throughout the growing season on the lower leaf blades of the cordgrass *Spartina alterniflora* growing in the intertidal marshes of North America.

Consequences of Variable Host-Plant Quality on Planthopper Survival and Performance

Historically, host plant quality (nutrition and allelochemistry) has figured prominently in explaining the population dynamics of phytophagous insects (McNeill and Southwood 1978, Denno and McClure 1983, White 1993). For sap-feeding insects like delphacid planthoppers, host plant nutrition is thought to influence population change more than allelochemistry because phloem-feeding allows them to avoid many secondary chemicals that are compartmentalized in nonvascular tissues (Waloff 1980, Sogawa 1982, Raven 1983). However, plant nitrogen is found in low concentration in most plant tissues, especially in the phloem, and is viewed as a limiting resource for many species of phytophagous insects including delphacid planthoppers (McNeill and Southwood 1978, White 1993, Cook and Denno 1994). As a consequence, it comes as no surprise to find that many delphacids survive better, develop faster, and are more fecund if they develop on nitrogen-rich host plants (Metcalfe 1970, Fisk et al. 1981, Cook and Denno 1994). Moreover, given a choice, delphacids often select nitrogen-rich plants over nitrogen-depleted hosts on which to feed and oviposit (Sogawa 1970, Denno 1985).

Natural-Enemy Impacts and Planthopper Population Suppression

Invertebrate predators are viewed as the most important natural enemies of delphacid planthoppers in both natural and managed habitats (Kenmore et al. 1984, Denno and Roderick 1990, Benrey and Lamp 1994, Settle et al. 1996; Fig. 6). Spiders, particularly hunting spiders such as wolf spiders (Lycosidae), voraciously attack the active nymphs and adults of delphacid planthoppers

(Fig. 7), whereas mirid bugs (e.g., *Cyrtorhinus* and *Tytthus*; Fig. 8) probe plant tissues and kill their embedded eggs (Kenmore et al. 1984, Döbel and Denno 1994; Fig. 9). Although a variety of parasitoids attack the eggs and nymphs of planthoppers (Waloff and Jervis 1987, Cronin and Strong 1994), they generally are less effective than invertebrate predators in suppressing planthopper populations (Kenmore et al. 1984, Döbel and Denno 1994, Perfect and Cook 1994, Settle et al. 1996). On occasion, however, parasitoids can be important sources of mortality for planthoppers, and the scarcity of parasitoids has been cited sporadically as the cause for outbreaks (Metcalfe 1972, Waloff 1980, Stiling 1994).

Evidence that invertebrate predators can inflict significant mortality on delphacid populations comes from a variety of sources. Delphacid populations frequently erupt when invertebrate predators, including mirids and spiders, are excluded experimentally (Matsumoto and Nishida 1966, Kenmore 1980, Döbel and Denno 1994). Also, when predators are killed with insecticides, delphacid populations often resurge shortly thereafter, a phenomenon that has occurred frequently in southeast Asian rice (Kenmore et al. 1984, Gallagher et al. 1994, Heinrichs 1994; Fig. 10). Contemporary pest management programs have resulted in drastic reductions in insecticide use, improved conservation of predator complexes, and diminished outbreaks of delphacid pests (Gallagher et al. 1994, Matteson et al. 1994, Settle et al. 1996). Key-factor analyses also corroborate the importance of egg predators in suppressing delphacid populations (Napompeth 1973, Waloff and Thompson 1980). Very convincing, however, is the near complete biological control of several pest delphacids by the introduction of mirid egg predators (Zimmerman 1948, Waterhouse and Norris 1987, Benrey and Lamp 1994). Together, these data suggest that top-down forces, particularly predation, can be significant factors in checking the population growth of some delphacid species.

Hypothesis Testing and the Data Set

Differences among delphacid species in the relative importance of top-down and bottom-up control (which factor explains more of the variation in population size), coupled with interspecific variation in mobility, allow us to assess how mobility influences which factor will limit population growth and to what degree. To test the hypotheses that a mobile life style (1) predisposes delphacid planthoppers for strong host-plant regulation, (2) provides partial escape from natural enemy control, and (3) promotes population outbreaks, we surveyed the literature on delphacid population dynamics. To test these predictions, we obtained information on four components of population ecology that could be evaluated collectively for the same delphacid species: (1) the dispersal capability of the delphacid species, (2) the strength of host-plant factors in driving population dynamics, (3) the strength of natural enemy impact in population suppression, and (4) the frequency of outbreaks (Table 1).

First, to assess mobility, we sought data on the frequency of macropterous adults in the population (% macroptery). We then arbitrarily placed species into one of two dispersal categories, either "mobile" (>50% macroptery in the population) or "sedentary" (<50% macroptery). No species fell near the 50% margin, making sorting decisions straightforward.

Second, we sought information on the strength of impact of host plant-related factors on population dynamics. The two most important factors we uncovered were plant quality (nutrition or condition) and plant genotype (variety or cultivar), and we scored their effects as "strong," "moderate," or "weak." Most authors made definitive statements about the role of bottom-up forces in their study system, thus simplifying the sorting. An example of a "strong" host plant effect is contained in a discussion by Waloff (1980), who concluded for the British grassland-inhabiting delphacid *Dicranotropus hamata* (Boheman) that "plant phenology and the state of the host plant greatly influence population levels." Similarly, a "strong" plant effect for the West Indian cane fly, *Saccharosydne saccharivora* (Westwood), was shown by Metcalfe (1971, 1972) who reported that "causes of outbreaks were associated with crop characteristics such as age and nutrition." By contrast, plant effects were scored as "weak" for the meadow-inhabiting delphacid *Conomelus anceps* (Germar) for which "there was no evidence to suggest that mortality was due to changes in the condition of the food-plant" (Rothschild 1966). Lateral effects such as competition and density-dependent dispersal usually were associated with deteriorating plant condition (Kuno and Hokyo 1970, Napompeth 1973, Prestidge and McNeill 1982, Denno 1983) and, thus, were subsumed in the evidence for bottom-up control (see Harrison and Cappuccino 1995).

Third, we assessed the role of natural enemies in the population suppression of each delphacid planthopper species. Again, and for simplicity, effects were scored as "strong," "moderate," or "weak." For instance, "strong" top-down effects were evident for *Perkinsiella saccharicida* Kirkaldy, whose populations on Hawaiian sugarcane were suppressed consistently by mirid egg predators (Waterhouse and Norris 1987). Enemy impact was scored as "moderate" for the salt marsh-inhabiting *Prokelisia marginata* Van Duzee, which experiences significant population suppression in some habitats but not in others (Denno 1983, Döbel and Denno 1994). "Weak" enemy effects were scored for *N. lugens* in Japanese rice fields based on Kuno and Hokyo's (1970) conclusion that "neither predators nor parasites can cause density-dependent stabilization" and that "regulation is achieved by intraspecific mechanisms" such as competition and dispersal.

Last, we scored the occurrence of population outbreaks as "frequent," "occasional," or "rare"

Table 1. Evidence for bottom-up (host plant) and top-down (natural enemies) effects on the population dynamics (suppression, outbreak) of delphacid planthoppers[a]

Planthopper species	Host plant (Growth form) [Habitat] {Origin}	Dispersal ability (% M)	Population outbreak (Frequent, occasional, rare)	Bottom-up effects (Strong, medium, weak)	Top-down effects (Strong, medium, weak)	Reference
			Mobile Taxa			
Javesella pellucida (F.)	*Avena, Festuca, Agrostis,* and others (Grassess and sedges) [Agricultural/cereal fields] {Native/Finland, UK}	Mobile (90% M)	Frequent	Strong (Large population increases on nitrogen-enriched host plants. Population size positively correlated with host plant nitogen).	Weak (Natural enemies unable to prevent rapid population growth even though egg and nymphal parasitoids inflict high mortality [50%]).	Raatikainen 1967, Prestidge 1982b, Prestidge and McNeill 1983
Nilaparvata lugens Stål	*Oriza sativa* L. (Grass) [Agricultural/field] {Introduced/Japan}	Mobile (69% M)	Frequent	Strong (Large population increases on nitrogen-enriched host plants. Outbreaks on susceptible varieties).	Weak (Predators and parasitoids are unable to consistently check population growth).	Kisimoto 1965, 1981; Kuno and Hokyo 1970; Cheng 1971; Hu et al. 1986; Heong 1988
Nilaparvata lugens	*Oriza sativa* L. (Grass) [Agricultural/field] {Introduced/Philippines}	Mobile (58% M)	Occasional (Pesticide induced)	Strong (Large population increases on nitrogen-enriched host plants).	Strong (Invertebrate predators frequently check population growth. Resurgence following predator kill with insecticides).	Kisimoto 1965, 1981; Cheng 1971; Kenmore et al. 1984; Cook and Perfect 1985; Hu et al. 1986; Heong 1988; Heong et al. 1992; Heinrichs 1994
Peregrinus maidis (Ashmead)	*Zea mays* L., *Sorghum bicolor* (L.) (Grasses) [Agricultural/field] {Introduced/Hawaii}	Mobile (67% M)	Frequent	Strong (Crop quality and quantity important in population regulation. Clear varietal effect on population growth).	Moderate (Density-dependent mortality from invertebrate predators, but predators often incapable of suppressing population due to poor synchrony with prey).	Napompeth 1973, Fisk et al. 1981
Perkinsiella saccharicida Kirkaldy	*Saccharum officinarum* L. (Grass) [Agricultural/field] {Native/Australia}	Mobile (>90% M)	Frequent	Strong (Outbreaks on susceptible varieties. Plant condition influences population size).	Moderate (Population suppression by invertebrate predators, but insufficient to prevent outbreaks on susceptible varieties).	Bull 1981
Perkinsiella saccharicida	*Saccharum officinarum* (Grass) [Agricultural/field] {Introduced/Hawaii}	Mobile (>90% M)	Rare (After introduction of invertebrate predator)	Moderate (Outbreaks on susceptible varieties. Plant condition influences population size).	Strong (Complete suppression with introduction of invertebrate predator).	Zimmerman 1948, Fennah 1969, Waterhouse and Norris 1987
Prokelisia marginata (Van Duzee)	*Spartina alterniflora* Lois. (Grass) [Natural/salt marsh] {Native/USA}	Mobile (98% M)	Frequent (Plant quality induced).	Strong (Large population increases on nitrogen-enriched host plants. Population eruption on naturally-occurring nutritious host).	Moderate (Invertebrate predators fail to suppress populations in low-marsh habitats; predator control in some high-marsh habitats).	Denno 1983, Denno et al. 1986, Denno and Roderick 1992, Döbel and Denno 1994; Denno, unpub. data

for each delphacid species. In most cases, we were able to extract information on the frequency of outbreaks from explicit statements made by the author. For example, *P. marginata* outbreaks annually in low-marsh habitats in the intertidal estuaries along the Atlantic coast of North America (Denno 1983). Metcalfe (1971) writes that *S. saccharivora* is "notorious for its intense and common outbreaks" on sugarcane throughout the Caribbean region. Kisimoto (1981) notes that for *N. lugens* on rice, "historical records show that serious outbreaks causing large-scale famines oc-

curred in Japan as far back as 1732." We categorized outbreaks as "frequent" for all of these cases because there was evidence for annual population explosions within the geographic area considered. With the reduction in insecticide use, outbreaks of *N. lugens* in southeast Asian rice occur only sporadically (Kenmore et al. 1984, Gallagher et al. 1994). Consequently, this case was placed in the "occasional" outbreak category. An example of a "rare" outbreaking species is *P. saccharicida* on Hawaiian sugarcane where consistent population suppression was achieved following the introduc-

Planthopper species	Host plant (Growth form) [Habitat] {Origin}	Dispersal ability (% M)	Population outbreak (Frequent, occasional, rare)	Bottom-up effects (Strong, medium, weak)	Top-down effects (Strong, medium, weak)	Reference
Saccharosydne saccharivora (Westwood)	*Saccharum officinarum Andropogon, Sorghum* (Grasses) [Agricultural/field] {Introduced/Jamaica}	Mobile (100% M)	Frequent	Strong (Outbreaks on fertilized cane, young cane, and susceptible varieties. Positive correlation between fecundity and plant nitrogen. Key factor is plant age-induced dispersal).	Moderate (Density-dependent mortality by nymphal parasitoid, but insufficient to deter most outbreaks. Resurgence following parasitoid kill with insecticide).	Metcalfe 1970, 1971, 1972
			Sedentary taxa			
Conomelus anceps (Germar)	*Juncus effusus* L. (Sedge) [Natural/meadow] {Native/United Kingdom}	Sedentary (10% M)	Rare	Weak (Host plant condition not important mortality source).	Strong (Invertebrate predators exercise main control over numbers of nymphs and adults).	Rothschild 1966
Dicranotropus hamata (Boheman)	*Holcus* (Grass) [Natural/meadow] {Native/United Kingdom}	Sedentary (2% M)	Occasional (Rain/plant quality induced).	Strong (Large populations on nitrogen-enriched host plants. Populations fluctuate relative to plant phenology and condition. Key factor is egg mortality with some mortality attributable to host plant).	Strong (Severe mortality inflicted by parasitoid. Delayed density-dependent parasitism of nymphs, likely legislated by plant condition).	Waloff 1980; Waloff and Thompson 1980; Prestidge 1982a,b; Prestidge and McNeill 1982
Prokelisia dolus Wilson	*Spartina alterniflora* (Grass) [Natural/salt marsh] {Native/USA}	Sedentary (33% M)	Occasional	Moderate (Delayed population increase on nitogen-enriched host plants).	Strong (Local population suppression by invertebrate predators. Predation mediated by vegetation structure}.	Denno and Roderick 1992, Döbel and Denno 1994; Denno, unpub. data
Stenocranus minutus (F.)	*Dactylus, Brachypodium* (Grasses) [Natural/field] {Native/United Kingdom}	Sedentary (34% M)	Rare	Weak (Population density not related to host plant nitrogen).	Strong (Invertebrate predation a significant source of mortality).	Waloff 1973; May 1975, 1978
Tarophagus colocasiae (Matsumura)	*Colocasia esculenta* Schott (Taro) [Agricultural/field] {Introduced/Hawaii}	Sedentary (<5% M)	Rare (After introduction of invertebrate predator)	Moderate (Population eruptions on irrigated but not dry taro).	Strong (Effective suppression following introduction of invertebrate predator. Population increase following experimental removal of predators).	Fullaway 1940, Matsumoto and Nishida 1966, Benrey and Lamp 1994

ᵃThe host plants, habitat, origin (native or introduced), and country where the study was conducted are shown for each delphacid species. Delphacid taxa are grouped into "mobile" (>50% macroptery) and "sedentary taxa" (<50% macroptery), and population-specific dispersal abilities (indexed as average percent macroptery [M] over the year in the study population) are presented. Also indicated for each planthopper species is its propensity for population outbreak (frequent, occasional, or rare), and whether bottom-up and top-down effects on population change are strong, moderate, or weak.

tion of a predaceous mirid (Waterhouse and Norris 1987). Abundance was not necessarily a criterion for outbreak. We scored population peaks as evidence for outbreaks only if there was an indication of feeding-induced plant damage (hopperburn or diminished plant growth or yield). Imposing this criterion made our decisions far less subjective in most cases. Thus, most assessments of outbreak frequency were made easily.

If information on all four of the components just outlined was not available, then a species was not included in our assessment. In all, 13 case stud-

ies involving 11 species in 10 genera were available for assessment (Table 1). Because the population dynamics of *N. lugens* differ so dramatically between temperate and tropical Asia (Kisimoto and Rosenberg 1994, Perfect and Cook 1994), we considered Japanese and Philippine populations as independent observations in our appraisal. Likewise, we treated Australian and Hawaiian studies of *P. saccharicida* on sugarcane separately.

In all, there were eight observations in the "mobile-species" category and five in the "sedentary-species" grouping to evaluate (Table 1). Macroptery
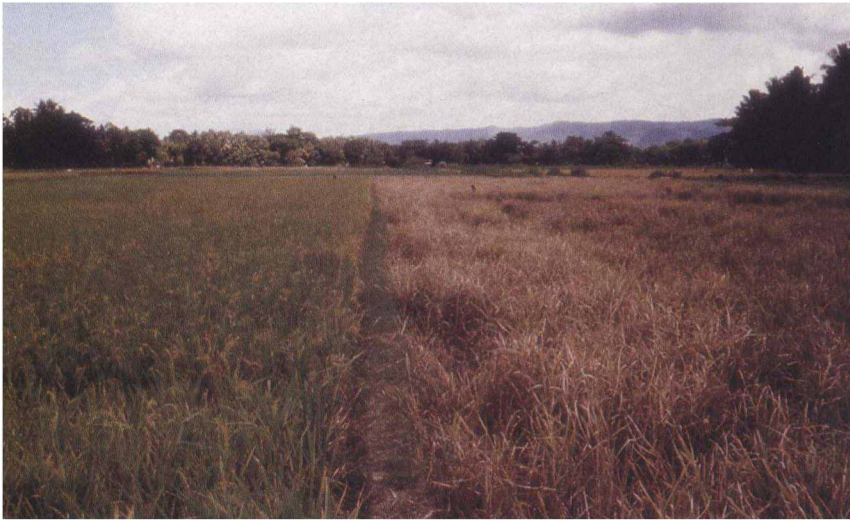
Fig. 10. The excessive use of insecticides in the Southeast Asian rice field on the right (not the left), killed natural enemies and promoted population resurgence in the brown planthopper, *Nilaparvata lugens.* Under such high-density conditions, plants become severely hopperburned from intense feeding, and crop loss can be extreme.

in mobile species ranged from 100% in *S. saccharivora* to 58% in Japanese populations of *N. lugens*, and in sedentary species from 34% in *Stenocranus minutus* (F.) to 2% *D. hamata*. To test the hypothesis that a mobile life style predisposes a delphacid species for strong bottom-up regulation, we compared the proportion of cases in which plant effects were "strong" versus not ("weak" or "moderate") between the mobile (>50% macroptery) and sedentary (<50% macroptery) species categories. Similarly, to assess the expectation that mobility provides partial escape from natural enemy control, we compared the proportion of species showing "strong" enemy impacts on population size (as opposed to "weak" or "moderate") between mobile and sedentary taxa. Finally, to test the prediction that mobility promotes population outbreaks, we determined the proportion of species exhibiting "frequent" outbreaks verses not ("occasional" or "rare") for both the mobile and sedentary categories. Proportions were compared statistically between mobile and sedentary species groups using chi-square tests on categorical counts (SAS Institute 1990). For these analyses, the small number of species precluded the use of phylogenetically independent contrasts (Denno et al. 1991). This would pose a problem particularly if all mobile species represented a single lineage within the Delphacidae. However, given that within a species (e.g., *P. marginata*) mobility can be a highly labile trait (Denno et al. 1996), we view this as an unlikely scenario.

Planthopper Mobility and the Strength of Bottom-Up Control

Indeed, we did find that host plant effects on population dynamics dominated for planthoppers with mobile life histories. "Strong" bottom-up effects were evident in seven of eight mobile taxa, whereas plant effects were "strong" in only one (*D. hamata*) of five sedentary species (Table 1), a difference which was significant ($\chi^2 = 5.92$, $P = 0.015$). Mobile species experiencing strong host-plant effects included both agricultural pests and inhabitants of natural grasslands. Severe outbreaks of pest planthoppers [*N. lugens* on rice, *Peregrinus*

maidis (Ashmead) on corn, and *P. saccharicida* and *S. saccharivora* on sugarcane] were associated with elevated plant nutrition, and in particular the use of high-yielding crop varieties that responded to nitrogen fertilizer with excessive vegetative growth (Metcalfe 1971, Napompeth 1973, Kenmore 1980, Bull 1981). Macropterous adults of the salt marsh-inhabiting planthopper *P. marginata* undergo mass annual migrations from high-marsh to low-marsh habitats where they selectively accumulate in enormous numbers on nitrogen-rich plants (Denno et al. 1980, Denno 1983). Following these mass colonization and oviposition events, populations erupt (>100,000 individuals per square meter) and plants are damaged frequently (Denno 1983, Denno et al. 1999). Similarly, *Javesella pellucida* (F.), a polyphagous species that exploits a variety of grasses, showed rapid population increases on nitrogen-enriched plants (Prestidge 1982a, b). Furthermore, across a variety of habitats in the field, the population density of most of these mobile planthopper species is related positively to the nitrogen content of their host plants (Metcalfe 1971, Denno et al. 1980, Prestidge and McNeill 1983, Hu et al. 1986).
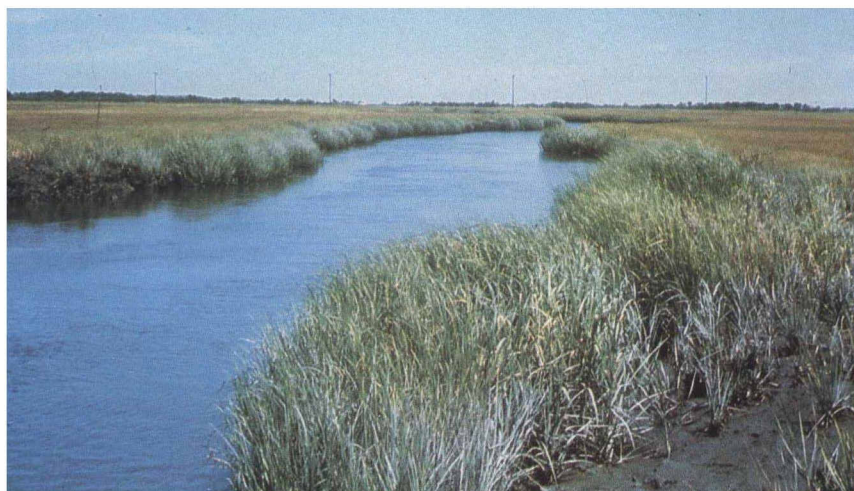
In contrast to mobile planthoppers, populations of sedentary species generally were impacted less by host-plant factors. For instance, the population size of the grassland-inhabiting *S. minutus* was not correlated with the nitrogen content of its host grass (Prestidge and McNeill 1983). Likewise, host plant condition imposed only a small fraction of the total mortality inflicted on populations of the moist meadow-dwelling *C. anceps* (Rothschild 1966). Two other mostly brachypterous species were affected only moderately by plant quality. Populations of *Prokelisia dolus* Wilson, a salt marsh inhabitant, show delayed population increases on nitrogen-enriched plants, a response that contrasts dramatically with the eruptive dynamics of its mobile congener *P. marginata* under the same field conditions (Denno 1983; R.F.D., unpublished data). Also, populations of the taro pest *Tarophagus colocasiae* (Matsumura) were influenced adversely in dry but not irrigated plantings (Matsumoto and Nishida 1966). One sedentary delphacid, *D. hamata*, was affected strongly by plant quality, with population eruptions on fertilized grasslands and positive population correlations with plant nitrogen (Prestidge 1982b, Prestidge and McNeill 1982).

Because the reproduction and development of many delphacid species are so sensitive to levels of host plant nitrogen, it is no wonder that life-history styles maximizing encounter with nitrogen-rich plants have evolved (McNeill and Southwood 1978, Prestidge and McNeill 1982, Denno and Roderick 1990). Dispersal, for instance, promotes the effective tracking of favorable host plants by allowing these sap-feeders to both selectively colonize nitrogen-rich plants and to escape stands of plants with declining levels of nitrogen (Denno and Roderick 1990). Together, selective colonization and enhanced performance can result in eruptive population growth on host plants high in nitrogen

(Prestidge 1982b, Heinrichs and Medrano 1985, Denno and Roderick 1990). Under such crowded conditions, delphacids ultimately deplete the amino-nitrogen content of their host plants through heavy feeding activities (Olmstead et al. 1997). Extensive feeding results in a characteristic yellowing of tissues known as "hopperburn" and often leads to reduced plant growth, diminished reproduction, and occasionally plant death (Sogawa 1982). Remaining in crowds on such nitrogen-poor plants has adverse effects on the survival and performance of most mobile planthopper species (*J. pellucida, N. lugens, P. maidis*, and *P. marginata*) (Denno et al. 1994). Other delphacids, sedentary species for the most part, are more tolerant of nitrogen-deficient plants and they simply persist until conditions improve (Prestidge and McNeill 1982, Denno et al. 1999). Adverse density effects are not nearly as prevalent in these species (*C. anceps, P. dolus*) (Rothschild 1966, Denno and Roderick 1992). Nymphs of nitrogen-sensitive species developing under crowded conditions often molt to macropterous adults that can disperse subsequently to more nutritious host plants elsewhere (Prestidge and McNeill 1982, Denno et al. 1994). Thus, mobility can promote the location of optimal resources and allow planthoppers to synchronize bouts of reproduction with favorable plant resources (Denno et al. 1980, Prestidge and McNeill 1982). Indeed, when such synchrony does occur, and if natural enemies are not an important countering force, outbreaks of planthoppers can be severe (Denno and Roderick 1990).

Prestidge and McNeill (1982) argue that nitrogen requirements can be satisfied by two distinct life history styles in sap-feeding insects. First, there are highly mobile (macropterous) species that meet nitrogen requirements by actively dispersing to the most nutritious stands of plants that change spatially over the course of the year. Second, there are sedentary (brachypterous) species that meet their nitrogen demands by compensatory feeding during times of impoverished plant nitrogen. These species tend to be more tolerant of fluctuating levels of host plant nitrogen. In fact, for delphacids, there is evidence for a possible trade-off between mobility (presence of wings and flight muscles) and the ability to compensate for low plant nitrogen by increased feeding (enlarged cibarial muscles). For instance, the cross-sectional area of the cibarial muscles (those that influence the rate and volume of food ingestion) of the volant *P. marginata* is significantly less than that for its brachypterous congener *P. dolus* (R.F.D., unpublished data). If such a trade-off generally prevails, mobility may diminish a species' ability to withstand bouts of low plant nitrogen because of the constraints it places on the enlargement of cibarial musculature.

This difference in the way nitrogen requirements are met may explain why mobility is associated with strong population responses to elevated plant quality such as mass colonization followed by rapid population growth (Denno 1994). Moreover, be-

cause mobility in planthoppers is associated strongly with the exploitation of temporary habitats, habitat persistence not only underlies the dispersal strategies of planthoppers (Denno et al. 1991, 1996) but may also constrain the way they are able to meet their nitrogen requirements. Thus, mobile planthoppers should selectively exploit only those temporary habitats characterized by nitrogen-rich host plants. For our assessment, habitat persistence and plant quality were confounded to some extent with highly nutritious plants occurring mostly in temporary habitats such as agricultural crops and low marsh habitats that receive either artificial or natural nitrogen subsidy. However, nutrient enrichment experiments show that indeed highly mobile planthopper species seek out the most nitrogen-rich plants within a temporary habitat (Hu et al. 1986; Denno, unpublished data).

Planthopper Mobility and Escape from Natural-Enemy Control

Natural enemies influenced the populations of mobile and sedentary planthoppers differently as well (Table 1). Enemies, usually invertebrate predators, exerted strong control or inflicted heavy mortality in populations of all five sedentary delphacids, whereas strong enemy effects occurred in only two of the eight mobile planthopper cases ($\chi^2 = 6.96$, $P = 0.008$). In sedentary grassland species (*P. dolus, C. anceps*, and *S. minutus*), spiders and heteropteran predators accounted for heavy mortality (Rothschild 1966, May 1978), and in *P. dolus* exclusion of spiders promoted population outbreak (Döbel and Denno 1994). Similarly, with the introduction of a predaceous mirid, populations of the sedentary *T. colocasiae* remained suppressed, but the experimental removal of this egg predator led to rapid population growth (Matsumoto and Nishida 1966, Waterhouse and Norris 1987).

A highly mobile life style appears to promote escape from natural enemy control. A classic case of predator escape is provided by the highly mobile *N. lugens*, which migrates annually from central China across the East China Sea to colonize the rice fields of Japan and Korea (Kisimoto and

Fig. 11. By colonizing robust stands of the cordgrass *Spartina alterniflora* in low marsh habitats (foreground), the salt marsh-inhabiting planthopper *Prokelisia marginata* encounters both a nitrogen-rich host plant and a habitat devoid of many predator species.

Rosenberg 1994). Natural enemies, which effectively suppress this planthopper in insecticide-free paddies in southeastern Asia, are left behind to a great extent when this planthopper colonizes temperate rice (Kisimoto 1981). Although *N. lugens* colonizes in low numbers, its populations grow rapidly under these enemy-reduced conditions, often to outbreak proportions (Kisimoto 1981, Perfect and Cook 1994). An analogous situation occurs with *P. marginata* in the intertidal marshes of North America. This planthopper, by migrating annually to low marsh habitats, not only encounters a more nutritious host plant but it leaves behind most spider predators, which are unable to persist at this regularly-flooded elevation (Denno 1983, Döbel et al. 1990; Fig. 11). As might be expected, populations of *P. marginata* frequently erupt under these rather ideal conditions (Denno et al. 1985; Fig. 12). Outbreaks of several other mobile pest planthoppers including *J. pellucida* on cereals, *P. maidis* on corn, and *P. saccharicida* (Australia) and *S. saccharivora* on sugarcane are not deterred by enemies, even though natural enemies can impose high mortality at times (Raatikainen 1967; Metcalfe 1971, 1972; Napompeth 1973; Bull 1981).

Mobility, however, does not preclude necessarily effective suppression by natural enemies. An introduced mirid, *Tytthus mundulus* (Breddin), almost eliminated *P. saccharicida* from Hawaiian sugarcane, and, as mentioned above, populations of *N. lugens* in southeast Asia are suppressed effectively by predators if insecticides are not used frequently (Kenmore et al. 1984, Perfect and Cook 1994). What factors contribute to the variation in natural enemy control among mobile delphacid species?

The answer apparently lies in the extent to which mobility uncouples interactions between delphacid planthoppers and their important predators. Both hunting spiders and mirid egg predators alike have the potential to effect strong aggregative responses, and, when they do, these predators often suppress their planthopper prey effectively (Döbel and Denno 1994). However, if predators colonize habitats late or in low numbers relative to their delphacid prey, they are unlikely to inflict sufficient mortality to suppress populations (Döbel and Denno 1994). Poor life-cycle synchrony between mirid egg predators and their delphacid prey has been cited as the primary reason for ineffective suppression (Napompeth 1973, Osborn 1974, Manti 1989).

It is not surprising that all of the delphacid planthoppers involved in these cases of predator escape via life-cycle asynchrony are the highly mobile species (e.g., *P. maidis* and *N. lugens*), those that we scored as having only weak or moderate top-down control. By contrast, life-cycle synchrony between the mirid *T. mundulus* and its mobile prey, *P. saccharicida*, is cited as a major reason for the success of this biocontrol agent (Williams 1931, Rothschild 1966). Similarly, for *N. lugens* in southeast Asian rice, habitat continuity promotes the synchronous colonization of new fields by both planthoppers and predators, a situation that in-

creases the effectiveness of natural enemies (Perfect and Cook 1994, Yu et al. 1996). In general, however, our analysis suggests that natural enemies are able to track sedentary species better than mobile ones. More often than not, a mobile life history is likely to promote asynchrony with predators and diminish the likelihood for top-down control.

Outbreaks and the Interplay Between Bottom-Up and Top-Down Forces

Mobile planthopper species exhibited a greater propensity for frequent population outbreak than sedentary species (χ^2 = 6.96, P = 0.008; Table 1; Fig. 12). Six of the eight mobile species experienced frequent outbreaks, whereas outbreaks were rare or occasional in all five sedentary species. The average proportion of macropters in populations of species exhibiting frequent outbreaks was 0.86 ± 0.06, a proportion that differed significantly from that (0.33 ± 0.12) for species experiencing only rare or occasional outbreaks (t = 3.698, P = 0.004 when comparing angular-transformed proportions). Thus, mobility does seem to promote outbreaks in delphacid planthoppers.

We argue that mobility fosters outbreaks because it allows planthoppers to seek out and locate highly nutritious host plants, and, at the same time, it tends to uncouple interactions with natural enemies. The relatively strong influence of bottom-up forces and the diminished impact of natural enemies on populations of mobile compared with sedentary delphacids (Table 1) is consistent with this assertion. The wing-dimorphic life history of delphacid planthoppers further enhances rapid population growth because colonization and reproduction can be maximized by the partitioning of these two functions between two adult wing forms.

Just how outbreaks are encouraged by a wing-dimorphic life history is illustrated by the typical population-dynamic scenario that occurs repeatedly for mobile species exploiting temporary habitats (e.g., *N. lugens* on rice and *Peregrinus maidis* on corn) (Denno and Roderick 1990). In a newly developing crop, macropters colonize at very low densities, mate soon after arrival, leave offspring that develop mostly into brachypterous adults, and rapid population growth ensues (Raatikainen 1967, Fisk et al. 1981, Kisimoto and Rosenberg 1994). In the generations following colonization, nymphs molt increasingly more into macropterous adults that escape deteriorating conditions by dispersing to other habitats (Fisk et al. 1981, Kisimoto 1981). This progression of wing-form change is mediated largely by increasing density and deteriorating plant quality (Denno 1994). Thus, the dimorphic life history exhibited by many delphacids allows for effective colonization of the most favorable host plants by macropters and enhanced establishment in the new habitat by the more prolific brachypters.

That outbreaks of pest planthoppers (*N. lugens* on rice and *P. saccharicida* on sugarcane) often arise from local concentrations of brachypters

Fig. 12. Outbreaks of the salt marsh-inhabiting planthopper *Prokelisia marginata* frequently occur in low marsh habitats where their cordgrass host plant *Spartina alterniflora* is more nutritious and their natural enemies are less abundant.

(Zimmerman 1948, Kisimoto 1965) demonstrates how effectively a population can become established from just a few highly fecund females. A dimorphic life history especially encourages outbreaks when macropters either colonize *en masse* (Denno 1983) or when the ambient densities of natural enemies are low at the time of their arrival (Kisimoto 1981). Both of these circumstances can swamp natural enemies and lead to eruptive population dynamics.

Implications for the Management of Pest Planthoppers

So, are we at a loss to manage effectively these mobile planthopper pests? Most certainly not, but the quick-strike capability of pest planthoppers certainly continues to present a formidable challenge to pest managers (Matteson et al. 1994, Settle et al. 1996). The key to improved planthopper management will lie undoubtedly with enhancing the effectiveness of the natural enemy complex (Fig. 13) and in developing more durable and effective crop varieties. Both altered habitat management practices and a better understanding of the interactive effects of bottom-up and top-down forces will contribute toward this end.

First let us examine habitat management and how modified efforts in this arena might enhance enemy impact. Clearly, the selective use of insecticides will help conserve natural enemies and deter outbreaks of *N. lugens* in tropical rice (Gallagher et al. 1994). Moreover, implementing practices that provide spatial refuges for natural enemies and encourage their early colonization of new crops are vital (Yu et al. 1996). Many predators and parasitoids of planthoppers have the inherent capability of effecting a strong numerical response and colonizing crops along with their planthopper prey (Döbel and Denno 1994, Perfect and Cook 1994, Yu et al. 1996). These are not new ideas, although much more research is necessary to learn how planting strategies (e.g., synchronous versus asynchronous cropping), the presence of reservoir vegetation, and the dynamics of alternative nonplanthopper prey can be managed to promote the early colonization of crops by natural enemies (Yu et al. 1996, Settle et al. 1996).

Our understanding of how host plant-related factors might legislate the effectiveness of natural enemies in crop systems is woefully inadequate. Historically, great emphasis has been placed on the development of crop varieties resistant to delphacid attack, despite the often rapid breakdown of resistance (Hare 1994). However, much less is known concerning how crop variety mediates interactions between delphacid planthoppers and their enemies, or how natural enemies influence the durability of resistant cultivars (Gould et al. 1991, Hare 1994). Moreover, vegetation structure can dictate the effectiveness of natural enemies. For example, spiders effectively suppress populations of planthoppers (*P. dolus* and *P. marginata*) in salt-marsh habitats rich in leaf litter, whereas populations virtually explode in simple habitats devoid of such litter (Döbel and Denno 1994). In the same salt-marsh system, evidence suggests that cannibalism among spiders is diminished significantly in complex habitats (G. A. Langellotto and R.F.D., unpublished data), which may explain their enhanced ability to suppress planthoppers in such habitats (Döbel and Denno 1994).

Another important factor that can diminish or promote top-down regulation is the occurrence of high-order interactions among the various natural enemies that attack herbivorous insects (Rosenheim 1998). In most insect communities, including delphacid-dominated ones, there is a complex of predators that feeds collectively on the same prey species (Settle et al. 1996, Schoenly et al. 1998), but these predators may exhibit intraguild predation by attacking each other as well (Polis et al. 1989, Fagan et al. 1998, Rosenheim 1998). In such antagonistic cases, interactive predator effects cascade down through the food web, and prey populations actually can increase (Rosenheim et al. 1993). Substantial intraguild predation occurs among the predators attacking planthoppers (Fagan et al. 1998), but little is known concerning how this phenomenon influences the collective impact of the predator complex. Moreover, even less is known concerning how vegetation structure or plant architecture alters intraguild predation. Exciting new findings in the salt marsh system suggest that habitat complexity can diminish intraguild predation between spiders and mirids and increase their combined ability to reduce delphacid populations (D. L. Finke and R.F.D., unpublished data). Thus, lessons can be learned from natural systems regarding how bottom-up factors mediate top-down forces. These findings may point the way to the development of more effective management practices and new crop varieties that will maximize both the presence and the effectiveness of the natural

Fig. 13. Enhancing the effectiveness of natural enemies, such as the wolf spider *Pardosa pseudoannulata* (Boesenber & Strand), holds the key to the improved pest management of planthoppers in Asian rice systems.

enemy complex that attacks these severe, mobile agricultural pests. 🐝

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