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Effects of nitrogen-enriched rice plants on ecological fitness of planthoppers

Zhongxian Lu and K.L. Heong

Planthoppers are known to prefer nitrogen-enriched rice plants. When reared on high-nitrogen plants, they have higher feeding rates and honeydew secretion, probe less, and lay more eggs. These ecological fitness characters are quantified and their relationships with tissue nitrogen content were found to be linear. The linear models were coupled with a transfer function population model and simulation studies showed that planthopper densities increased 40-fold for every fold increase in nitrogen content. Crops with nitrogen-enriched plants tend to favor planthopper population development and the implications for nitrogen use and sustainable management of planthoppers are discussed.

The Green Revolution that began in the mid-1960s was characterized by the breeding and widespread adoption of new high-yielding varieties (HYVs), pesticides, and nitrogenous fertilizers. Food production, especially of rice, wheat, and maize, increased markedly. In the next three decades, excessive inputs of pesticides and fertilizers resulted in negative environmental effects, which Conway and Pretty (1991) called the "unwelcome harvest." In the last 45 years, world consumption of nitrogenous fertilizer increased by 30-fold (Fig. 1), whereas rice yields increased by only 2.2-fold (FAOSTAT 2008), suggesting that the use of nitrogen is excessive. Since 1960, flows of biologically available nitrogen doubled and those of phosphorus tripled. The use of synthetic nitrogenous fertilizer escalated; 50% of all that had been produced was used since 1985. The recovery efficiency of applied nitrogen in most cases is less than 50% and for rice less than 35% (Witt 2003). The differences in nitrogen content between animal and plant tissues may be an important reason why most herbivores have an ability to seek out host plants with high nitrogen content (Southwood 1973). Heavy applications of nitrogenous fertilizer may not affect insect biology directly, but they bring about changes in host-plant morphology, biochemistry, and physiology, which can improve nutritional conditions for herbivores (Bernays 1990, Simpson and Simpson 1990), thus playing a key role in modifying and reducing host resistance to herbivores (Barbour et al 1991). Rice crops with high nitrogenous fertilization become favorable habitats to more than 200 species of insect herbivores, some of which are important pests. The excessive use of nitrogen fertilizer promoted by the Green Revolution had been

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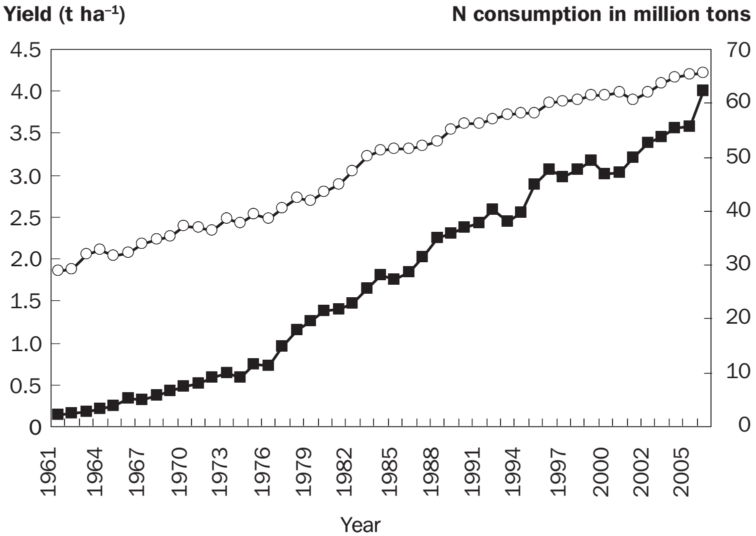

Fig. 1. World trends in nitrogen consumption (■) (million tons) and rice yields (○) (t ha^{-1}) between 1961 and 2006.

considered a key driver in the shift of brown planthopper (BPH) *Nilaparvata lugens* from a minor to a major insect pest in the 1970s (Dyck et al 1979). In this chapter, we provide further evidence and quantification of the effects of nitrogen-enriched rice plants on various planthopper ecological fitness characters.

The two important planthopper species in tropical Asia are the BPH and the whitebacked planthopper (WBPH) *Sogatella furcifera*. They are monophagous phloem feeders that invade maturing rice crops from other rice areas, sometimes being displaced by wind over long distances (see Otuka et al, this volume). Since phloem is poor in nutrients, the planthoppers need to filter large quantities of phloem sap and thus have low efficacy of conversion rates of only 5% to 7% compared with other herbivores' conversion rates of 40% to 90% (Slansky and Scriber 1985).

Planthoppers' preference for nitrogen-enriched rice plants has been documented (Cheng 1971, Lu et al 2005, Wang and Wu 1991) and BPH on high-nitrogen plants had been found to have higher feeding rates and honeydew excretion (Cheng 1971, Sogawa 1970). Planthoppers also probe less (Lu et al 2005, Sogawa 1970), have higher survival rates, and have greater population buildup (Cheng 1971, Preap et al 2001). They also produce more eggs (Preap et al 2001, Wang and Wu 1991) and have a higher tendency for outbreaks (Hosamani et al 1986, Li et al 1996, Uhm et al 1985). Kanno et al (1977) found that BPH on nitrogen-enriched plants consumed 3–7 times more, excreted 7 times more honeydew, and had 2–3 times higher body nitrogen. Both water content (WC) and relative water content (RWC) of BPH on high-nitrogen plants increased significantly (Lu et al 2004a). Similar responses to nitrogen fertilization were found in WBPH (Hu et al 1986, Ma and Lee 1996, Wu and Zhu 1994). Nitrogen enrichment

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in plants can alter BPH on some resistant varieties. For instance, on resistant varieties IR26 and Utri Rajapan, BPH growth rates increased proportionately with nitrogen applied (Cheng 1971, Heinrichs and Medrano 1985). In these experiments, applied nitrogen was used as a treatment and tissue nitrogen was not measured.

Effects of plant tissue nitrogen on ecological fitness characters of planthoppers

Ecological fitness is the measure of how well an individual or a population adapts to a specific niche.[1] The characters used for measurement are survival rates, longevity, and fecundity under the different nitrogen enrichment regimes of rice variety IR64, which has the *Bph1* resistance gene and several QTLs rendering field resistance to BPH (Cohen et al 1997). Plant tissue nitrogen content was determined by converting chlorophyll meter readings using a calibration model (Lu et al 2004b). Planthopper nymphal survival rates were positively related to nitrogen content, whereas nymphal duration decreased with an increase in nitrogen content (Fig. 2A and B). Female progenies were heavier, lived longer, and laid more eggs (Fig. 2C, D, and E). The increase in prey size can have negative effects on predation as it can affect predator handling time. Egg hatchability also increased with nitrogen content (Fig. 2F), resulting in more hoppers produced and higher dry weights (Fig. 2G and H). Between generations, BPH reared on plants receiving 200 kg N ha^{-1} lived 3 times longer and produced 10 times more eggs than those plants reared with no nitrogen applied. Using a transfer function population model coupled with the predicted parameters from the linear equations in Figure 2, simulations of population densities for nitrogen application rates of 100 to 400 kg ha^{-1} showed that, for every fold increase in nitrogen application, planthopper densities can increase by 40-fold (Fig. 3).

WBPH were reared on Shanyou 63 (hybrid), Xiushui 63 (japonica), and Zhe 733 (indica) plants with low (0 N input) and high nitrogen (200 kg N ha^{-1} input) over three generations. Females reared on low nitrogen over three generations had decreasing trends in dry weight and egg oviposition (Fig. 4). On high-nitrogen plants, dry weights and oviposition increased with generations. Similarly, in BPH, fitness variables gradually increased when BPH were fed successively on high-nitrogen regimes, whereas, with successive low-nitrogen regimes, the variables gradually declined (Lu et al 2004a). The increase in eggs laid by WBPH females in low- and high-nitrogen plants was 267%, 163%, and 158% for Shanyou 63, Xuishui 63, and Zhe 733, respectively. This provides further support to reported population shifts in planthoppers. WBPH in China in the 1980s and 1990s had shifted due to the abnormal susceptibility of the Chinese hybrids to WBPH compared with japonica varieties (Sogawa et al 2003). However, for indica variety Zhe 733, the two fitness parameters were higher, indicating that this variety was more susceptible.

Populations of planthopper are known to have high fecundity of more than 1,000 eggs per female (Li et al 1996) and a rapid increase of about 500 times in three

[1]Further discussions on ecological fitness can be found in *The Standard Encyclopedia of Philosophy*, http://plato.stanford.edu/entries/fitness/.

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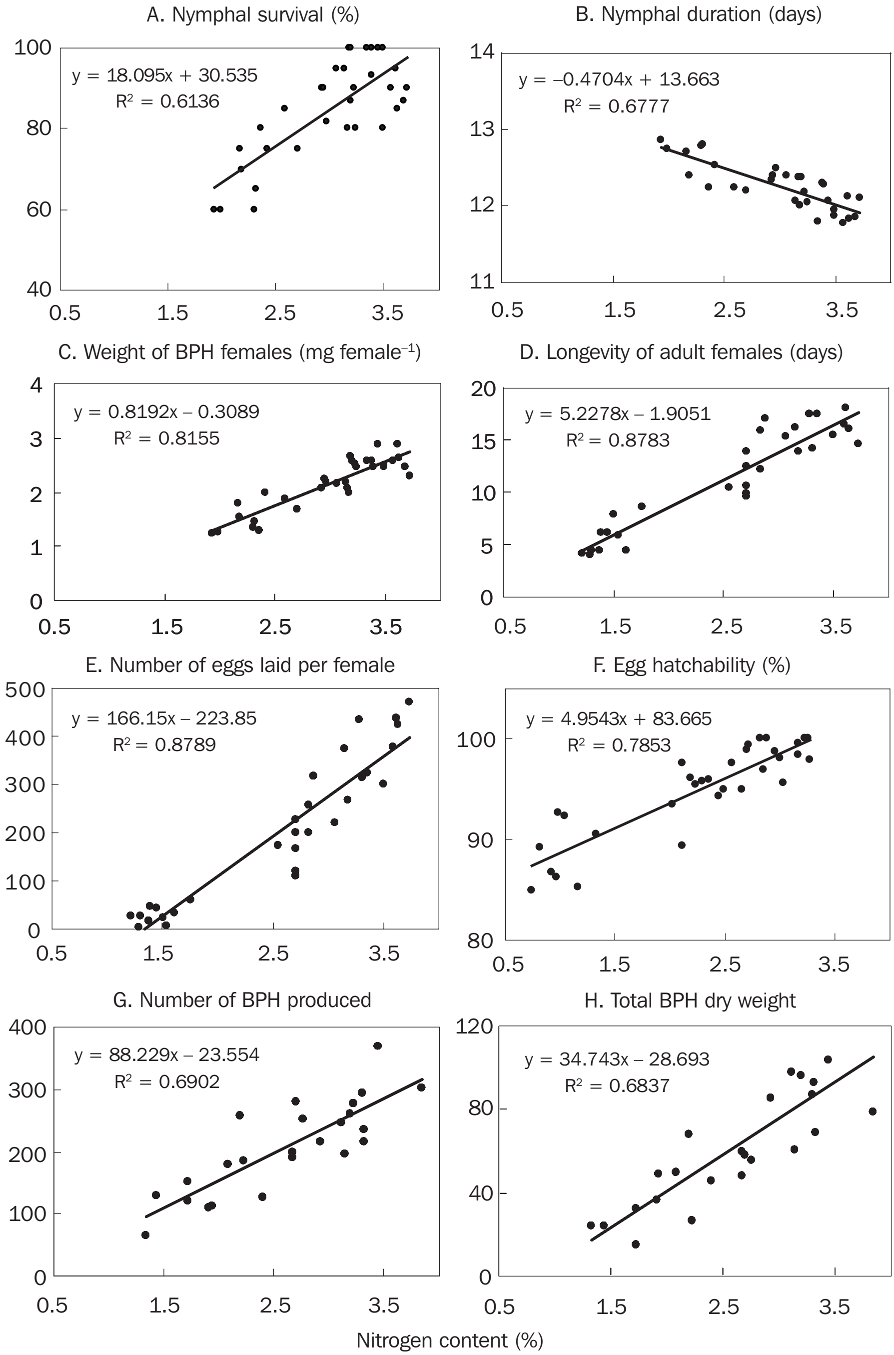

Fig. 2. Relationships between fitness variables of the brown planthopper and nitrogen content (%).

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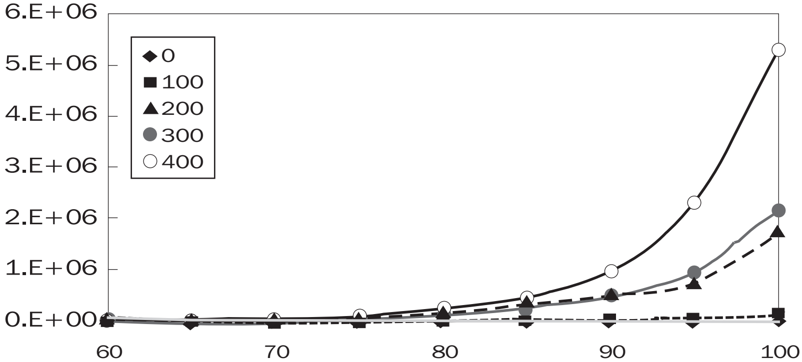

Fig. 3. Simulation of population development from 5 pairs of brown planthoppers using a transfer function population model (Heong 1988) and fitness parameters at nitrogen regimes of 0, 100, 200, 300, and 400 kg ha^{-1}.

generations (Kuno 1984), from a low initial density of less than 0.001 per hill. This is true in temperate regions or in environments with low naturally occurring biological control. In the tropics, such high increases were reported in fields sprayed with insecticides. Most of these studies also relied on data collected from the immediate generation after recruitment. When exposed to successive generations of nitrogen-enriched plants, the cumulative planthopper populations might even be fitter.

On nitrogen-enriched plants, planthoppers tend to increase their feeding rates. This may be because of the increase in host phloem amino acids such as aspartic and glutamic acids, which are feeding stimulants (Sogawa 1982). Planthoppers also tend to select nitrogen-rich over nitrogen-poor plants (Sogawa 1970, Lu et al 2005). The combined effects of increased colonization, increased stimulation for feeding, and increased fitness generally result in rapid population growth.

Plant injury and yield loss caused by BPH populations in paddy fields in temperate regions are dependent on the initial immigrant and high population parameters (Li et al 1996). BPH recruitments in these areas are apparently displaced by Asian monsoon winds from Southeast Asian areas where BPH reproduce around the year (Sogawa 1995). In the tropics, however, initial recruitments are lower (Yu et al 1997) and population suppression by natural enemies (Heong et al 1992, Way and Heong 1994) is high. Thus, high fitness potentials may be neutralized by strong natural biological mechanisms. In temperate rice, however, population abundances may be more dependent on fitness components and coupled with high nitrogen, high pesticide applications, and low natural biological control, which make these areas more vulnerable to BPH outbreaks.

It is clear that planthoppers in high-nitrogen application regimes have significantly higher fitness, as discussed by other authors (e.g., Cook and Denno 1994). And, after successive generations of high-nitrogen regimes, population increases might even be greater. Although ecological fitness is increased in high-nitrogen regimes, it does not completely explain the low planthopper outbreaks in many rice-growing

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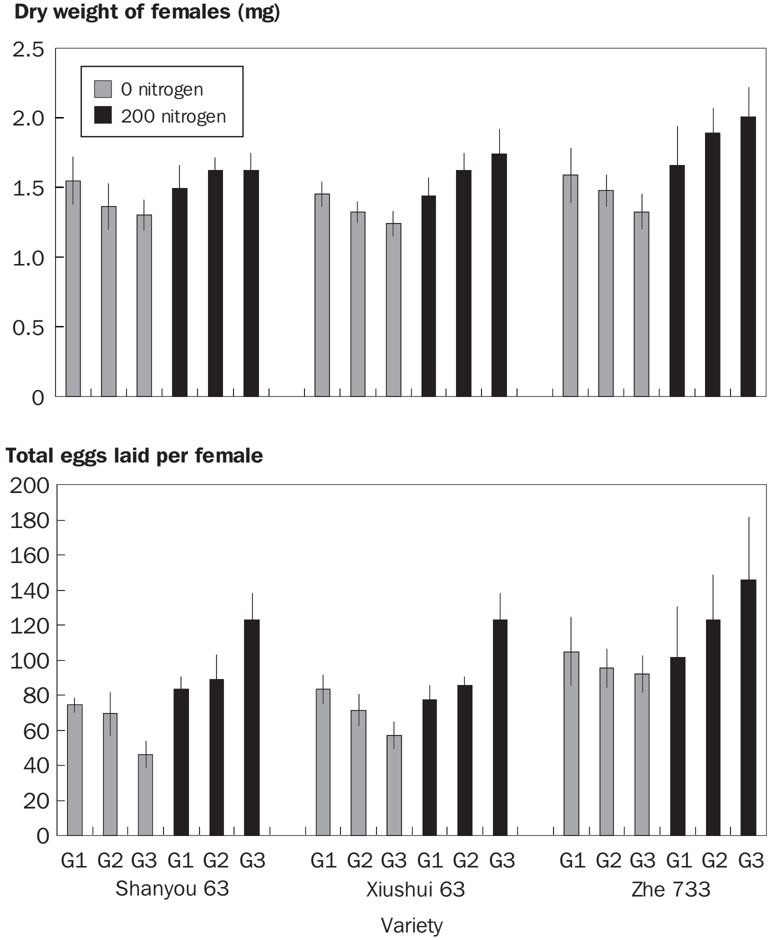

Fig. 4. Female weights and eggs laid per female of whitebacked planthoppers reared successively for 3 generations in 0 N and 200 kg N ha^{-1} regimes.

areas and fields, in both tropical and temperate regions, with high nitrogen use. Way and Heong (1994) attributed the stability of pest populations in tropical rice to natural biological control. It has been argued that the diversity and effectiveness of natural biological control in the temperate region are relatively low due perhaps to weather conditions coupled with high insecticide use. On some occasions when insecticides were suddenly stopped, crops suffered high BPH attacks mainly from recruitments from neighboring fields. Thus, in intensive areas with nitrogen applications, sudden stoppage of insecticide may render higher risks of BPH outbreaks. A gradual reduction in unnecessary sprays followed by a gradual spread of such practices may thus be a more practical and acceptable way to reduce insecticide use in these areas, as was done in Vietnam (Heong et al 1998).

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Implications for fertilizer and planthopper management

Nitrogenous fertilizer is important to sustain and meet the world's food demand and food security in the foreseeable future. The world needs an additional 50 million tons of rice annually or 9% of current production to meet demand in the near future (IRRI 2006). However, fertilizer management in irrigated rice in Asia is characterized by inefficient and unbalanced use of inorganic fertilizers and the amount of grain yield produced per unit fertilizer N applied is low (Witt 2003). In addition, the excess N in plant tissues contributes significantly to pest and disease problems. Nutrient management methods that will improve efficiency (Witt et al 2005) will also improve the management of planthoppers. Excess nitrogen in rice generally causes excess vegetative growth, lower harvest index, proneness to lodging, and susceptibility to disease and insect pests and often results in an asymptotic or parabolic relationship between crop yield and nitrogen dose (Sinclair 1998, Srivastava and Singh 1999). In a 5-year test at the Missouri Rice Farm at Glennonville, rice yields were greatest when the recommended N fertilizer rate was applied, and yields decreased when N fertilizer was applied at 150% of the recommended amount.

Rice production must increase by about 65% more than today to meet the demand projected for 2025. If the technologies that affect nutrient use by the rice crop remain unchanged, that production increase will require almost 300% more than the present application rate of N alone in irrigated environments. This is an undesirable amount economically and environmentally. It is obvious that nutrient-use efficiency needs to be improved, along with the yield potential of new rice cultivars (Fischer 1998). In China, the consumption of nitrogen increased by 44-fold in the past 40 years, an average yearly increase of 10.5%. In 1998, China consumed three times more nitrogen than the rest of the world, 181 kg nitrogen per ha compared with the world's consumption of 60 kg per ha (Zhu and Chen 2002). High rice yields might be attributed to the high average nitrogen rate of 180 kg per ha. However, the partial factor productivity (PFP) of nitrogen fertilizer is much lower, implying low nitrogen fertilizer-use efficiency. The excessive use of nitrogenous fertilization may be due to low prices, high seed costs, and farmers' attitude of maximizing tillers and labor (Peng et al 2002). These practices, coupled with prophylactic spraying regimes of 5 to 10 sprays of multiple active ingredients of insecticides, might be the main causes of unstable planthopper populations and frequent outbreaks. Heavy insecticide use is not only masking the effects of natural biological control but is stimulating the development of insecticide resistance (see Matsumura et al, this volume). Thus, management of planthoppers will need to focus on reducing prophylactic insecticide applications, especially in the early crop period, and improving fertilizer efficiency.

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Notes

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