

Effect of Nitrogen Fertilizer on Herbivores and Its Stimulation to Major Insect Pests in Rice

LU Zhong-xian¹, YU Xiao-ping¹, Kong-luen HEONG², HU Cui³

¹Institute of Plant Protection and Microbiology, Zhejiang Academy of Agricultural Sciences, Hangzhou 310021, China; ²International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippine; ³Institute of Applied Entomology, Zhejiang University, Hangzhou 310029, China)

Abstract: Nitrogen is one of the most important factors in development of herbivore populations. The application of nitrogen fertilizer in plants can normally increase herbivore feeding preference, food consumption, survival, growth, reproduction, and population density, except few examples that nitrogen fertilizer reduces the herbivore performances. In most of the rice growing areas in Asia, the great increases in populations of major insect pests of rice, including planthoppers (*Nilaparvata lugens* and *Sogatella furcifera*), leafroller (*Cnaphalocrocis medinalis*), and stem borers (*Scirpophaga incertulas*, *Chilo suppressalis*, *S. innotata*, *C. polychrysus* and *Sesamia inferens*) were closely related to the long-term excessive application of nitrogen fertilizers. The optimal regime of nitrogen fertilizer in irrigated paddy fields is proposed to improve the fertilizer-nitrogen use efficiency and reduce the environmental pollution.

Key words: nitrogen fertilizer; herbivore; insect pests; rice; fertilizer-nitrogen use efficiency

The 'Green Revolution' initiated in the mid 1960s and characterized by the successful breeding and widespread adoption of new high yield varieties, pesticides and nitrogen fertilizers, has doubled the production of many crops, such as rice, wheat and maize. Meanwhile, the continuous and excessive inputs of pesticides and fertilizers have resulted in some negative effects, 'unwelcome harvest', on environments and resources, as well as the considerable disturbances to plant and animal communities^[1-2]. Crop losses caused by insect pests gradually increased in spite of the effective technological development in insecticide synthesis and application for pest management^[3].

The large differences in nitrogen contents between animal and plant tissues may be the major reason that most herbivores have an ability to seek the host plants with high nitrogen content^[4]. The heavy application of nitrogen fertilizer rarely affects insect directly, however, it can alter or change morphological, biochemical and physiological characters of host plants and improve nutritional conditions for herbivores^[5-6]

by playing a key role in insect population dynamics through host selection and ecological fitness, such as survival, growth, fecundity and reproductive capacity and significant reduction of host resistance against herbivores^[7]. In this paper, the effects of nitrogen fertilizer on herbivores and its stimulation for major insect pests in rice, and the optimal regime of nitrogen fertilizer in irrigated paddy fields were discussed.

Nitrogen fertilizer affects ecological fitness of herbivores

Selection to host plants

Feeding for survival and development of immature herbivores is the first step in all physiological activities, while oviposition is considered as the life end of female adults^[5, 8]. The behavior characteristics of feeding and oviposition activities reflect the suitability and acceptance of herbivores to host plants, as well as the attractive capacity and nutritional value of host plants to herbivores, so the study on this field is anchored as the foundation of insect physiology and ecology^[5, 8-9]. Herbivores need proper selection on appropriate host plant to feed and lay eggs during their life cycle. Several features of host plants, such as color, size,

Received: 28 September 2006; **Accepted:** 22 December 2006

Corresponding author: LU Zhong-xian (luzxmh2004@yahoo.com.cn)

This paper was translated from its Chinese version in *Chinese Journal of Rice Science*.

shape, sound, texture and toughness, play important roles in an insect's host selection.

Nitrogen may influence semiochemicals and nutritional values of plants and also behavioral characteristics of herbivores^[10-11]. In host-plant the nitrogen content is generally considered as an indicator of food quality and a factor affecting host selection by herbivores^[12]. It has been noted that a high rate of nitrogen fertilizer significantly increased the number of egg masses deposited by Asian corn borer, *Ostrinia furnacalis*, on maize leaves^[13]. Nitrogen was found to modify the plant nutrition and reduce the resistance against aphids in cotton^[14] and coleopterans and lepidopterans in tomato^[7]. Bentz et al^[10-11] found that the protein-nitrogen content of the leaves linearly increased with the increase in level of nitrogen applied to plants, and the number of eggs of *Bemisia argentifolii* laid on poinsettia, which also increased linearly with the increase of plant nitrogen content. During the experiment, more *B. argentifolii* females were found on young and fully expanded mature leaves than on non-senescence old leaves, which is correlated with the high nitrogen content of those leaf types. Similar results were found in sweet potato whitefly, *B. tabaci* on poinsettia and the greenhouse whitefly *Trialeurodes vaporariorum* on chrysanthemum^[15-16]. The reason may be that females may assess the physiological or biochemical conditions of plants by probing the plant cuticle and underlying tissues while moving among plants, and this assessment may influence the choice of whether to stay or to leave. After landing on a plant, the greenhouse whitefly was found to reject unsuitable host plants after probing the apoplast in the mesophyll layer for a few minutes^[17].

The host selection and oviposition frequency of *T. vaporariorum* were correlated with the suitability of plant to support survival and development of whitefly progenies^[16]. This may be due to the different available choice situations that the increased plant nitrogen content can increase adult survivorship of whiteflies. Jauset et al^[17-18] suggested that the internal chemical properties of plant were responsible for site selection by *T. vaporariorum* which can adjust its feeding site based on the leaf nitrogen content from older leaves to younger leaves, since the younger

leaves have a higher content of soluble nitrogen as well as protein nitrogen compared with the older ones.

The selection of feeding and oviposition of herbivores on host plants with higher nitrogen content can be induced by rearing previously on plants with high nitrogen. Herbivorous fly, *Liriomyza trifolii* exposed to tomato plants with high nitrogen content preferred to feed and oviposit on high nitrogen plants, whereas flies exposed to plants with low nitrogen content showed no preference^[19]. This result is consistent with the hypothesis that a preference is induced as the result of contact with high-nitrogen plants. The inexperienced flies may have a low acceptance threshold for nitrogen content of plants and therefore show no preference, and this threshold is not altered by exposure to plants containing low nitrogen. The threshold may be set by gut situation, assimilation of particular nutrients, and/or oviposition after having encountered a host plant^[20].

Although most herbivores are limited in low nitrogen concentrations in food with positive performance related to the increase in nitrogen of foliage, but some are not in agreement with the nitrogen limitation hypothesis^[21]. Fischer and Fiedler found that female butterflies *Lycaena tityrus* did not discriminate between leaves with high and low nitrogen contents^[22]. Fox and Eisenbach found that female diamondback moth *Plutella xylostella* (L.) laid more eggs on low nitrogen-fertilized plants than on high nitrogen-fertilized plants^[23]. In a laboratory trial, the significantly more leafhopper *Carneiocephala floridana* loaded on the salt marsh *Borrchia frutesce* without nitrogen fertilizer application, while the total number of eggs laid was not significantly affected by the application of fertilizer^[24]. These findings undermine the general applicability of the nitrogen limitation hypothesis^[21].

Food quality and utilization

It is necessary for herbivores to obtain and utilize the nutritional foods for growth, development and reproduction. The amount, rate and quality of food consumed by immature herbivores influence their fitness, growth rates, developmental duration, final body weights, dispersal abilities and probabilities of

survival. Similarly, the amount, rate and quality of food consumed by adults influence their performance in mating success as well as timing and extent of reproduction and disposal ability^[8]. The host plant quality relevant to herbivore fitness may be physical attributes, allelochemicals and nutritional composition. The composition of food includes both absolute and relative amounts of proteins, amino acids, lipids, fatty acids, carbohydrates, water, minerals and vitamins. In order to attain the ideal growth, developmental and reproductive performance, herbivores must obtain adequate amounts of the necessary nutrients in a suitable host plant. Among the above contents, nitrogen content in host plants is considered to be the most important and limited factor for herbivores^[21].

Data from several hundred experiments with 25 species of Lepidoptera and 4 species of Hymenoptera (sawflies) clearly indicated that the performance values of larvae tend to decrease with a decline in leaf water and nitrogen contents. The indices of food consumption and utilization increase significantly with the increase of nitrogen content in host plants. The relative consumption rate (RCR) increased from 0.5 to 5.49 mg/(mg · day) when the nitrogen content in host plants increased from 1% to 5%, and the efficiency of conversion of ingested food (ECI) raised from 5.14% to 64.00% as the nitrogen content in host plants from 1% to 6%^[8]. However, the feeding behavior of herbivores is regulated by chemical compositions in host plants^[25]. The nitrogen including amino acids and protein, and sugar are two major kinds of herbivore feeding regulators in adjustment of feeding rate on different host plants^[8, 22]. The nitrogen as feeding regulator can positively or negatively affect the feeding amounts of herbivores on host plants with high nitrogen content in two ways. It has been noted that most herbivores increase feeding significantly on high nitrogen host^[8, 26]. Some herbivore species consume food faster, utilize food less efficiently with a higher nitrogen use efficiency on low nitrogen plants than on high ones^[27-28].

In plants with low nitrogen content, herbivores might take more food to meet their needs as nitrogen is one of the critical nutritional element. The aphids, chinch bugs, lepidopterous larvae, scale insects and mites all benefited either directly or indirectly from an

increase in nitrogen content in their food. Many insects alter the food consumption rate in response to variation in food nutrient content, especially on low nitrogen content plants^[28-31]. Blua and Toscano^[29] found that the whitefly, *B. argentifolii*, generated less honeydew on high nitrogen plants than on low or medium ones. The feeding compensation of herbivores on low nitrogen plants can be utilized in biological control of weed. For example, the weed biological control specialist *Spodoptera pectinicornis* fed on the floating aquatic plant *Pistia stratiotes*. Wheeler and Center^[31] found that the larvae *S. pectinicornis* compensated for low nitrogen leaves by increasing fresh weight consumption threefold when feeding on *P. stratiotes*.

It has been reported that many homopterans generally rely on symbiotes to supply certain essential nutrients, lacking in phloem and xylem fluid^[32]. The phloem sap contains only about 0.03–1% amino acids, so homopterans depend on symbiotes to recycle nitrogen^[33]. The microbial recycling of nitrogen is of great nutritional value in animal, because it increases the efficiency of the animals to utilize dietary nitrogen, enabling them to survive and grow on low nitrogen input. However, nitrogen recycling has not been demonstrated unequivocally in any association, though there is strong evidence that the mycetocyte symbiotes are important in cockroaches, yeasts in planthoppers, and gut bacteria in termites^[34].

Survival, growth and development

The present review listed at least 115 studies in which insects grew better in plants with higher nitrogen content, indicating the positive effects of nitrogen on growth and development of herbivores. Moreover, the herbivores on high nitrogen plants showed longer survival rate, greater developmental rate and relative growth rate^[22, 28, 36-38] with bigger body sizes^[36-37, 39], shorter developmental time^[22, 37, 40] and fewer instars^[28]. In plants with low nitrogen content, the soybean looper developed slowly and displayed the increases in number of larva instar and duration of larval development^[28].

On the other hand, a decrease or no obvious changes in herbivore performance on host plants with high nitrogen content were observed in at least 44

studies. In cotton plant the bollworm growth and development was accelerated with the increase of plant nitrogen content in a certain extent, but it will decrease over the extent [41-42]. Rossi et al [24] found the survival rate of leafhopper *Carneocephala floridana* from first instar to adult was lower in two nitrogen fertilized groups of both herbs *Borrchia frutescens* and *Salicornia virginica*. Previous studies showed that the plant nitrogen content had no effects on the performance of growth and development of *Bemisia tabaci*, on the body size of *B. argentifolii*, or on the immature survival rate of *A. woglumi*, *Dendranthema grandiflora* and *B. argentifolii* [29, 43]. Casey and Raupp [44] reported that the survival rate, development time, age to 1st reproduction and clutch size of azalea lace bug, *Stephanitis pyrioides* had no significant relationship with the levels of nitrogen fertilization.

Fecundity and population dynamics

The plant nutrient status is an indicator of host plant quality, which plays an important role in the population dynamics of many herbivores. In highly nitrogen fertilized agro-ecosystems, nitrogen may not be the limiting nutrient for herbivores. In these agricultural settings, phytophagous arthropods that respond positively to plant nitrogen content may be more likely to reach pest status after a certain nitrogen concentration within the host plant is reached. The positive effects on population dynamics, which contribute to higher survival rates, longer adult longevity and reproductive periods [45], shorter pre-oviposition period [46], greater rate of eggs laid per day [37, 46] and fecundity [37,46-47] of herbivores, are attributed to the increasing of the soluble protein content and specific free amino acids to change the morphology of host plant. The results are increase in intrinsic rate of increase (r_m) [37, 39, 47], and high population densities [14, 35, 40, 48-55].

Nitrogen is taken up by plants in two different forms, nitrate or ammonium. The amino acid compositions were different among plants with different nitrogen treatments, and amino acid content and carbohydrate-to-amino acid ratios are linked to changes in aphid development [56]. In a single-clone experiment, *Borrchia* spp. in fertilized- and

shaded-only plots developed more *Asphondylia* galls than those in non-manipulated control plots, and plants that received both shading and fertilizer developed the most galls. The shade and fertilization produced an additive increase in plant nitrogen content, but their effects resulted in a synergistic decrease in carbohydrate-to-amino acid ratios [40]. In sugar cane, the fiber content is an important factor to resist the damage by the stem borer *Eldana saccharina*, Coulibaly [57] reported that the increasing application of nitrogen fertilizer reduced the fiber content in sugar cane and resulted in increased damage by the stem borer.

Recently, most attention has been paid on the relationship between nitrogen content in host plants and changes in performances of herbivores. However, the herbivore performances may be controlled by other factors, which are not measured [22]. The changes in nitrogen level of plant tend to be accompanied by changes in the level of many other nutrients, water and numerous allelochemicals [12]. The importance of nitrogen compared to other resources should be evaluated, while the performance of herbivore population dynamics may be the comprehensive result of nitrogen and others factors [58]. It is also dependent on the predominant factors such as nitrogen, carbohydrates or the carbohydrate-to-amino acid ratios, which might explain the results from previous studies that there exist negative effects or no effects of the sole nitrogen content in plants on herbivore performances [35-36, 43, 49, 59-60]. Scriber [3] reported that 25% of 179 studies indicated that population parameters were negatively correlated with nitrogen concentrations. The part of this discrepancy may be attributed to the effects of nitrogen fertilization on foliar concentrations of allelochemicals and nitrate nitrogen that trend to reduce the insect fitness.

Herbivorous community

The human activities have greatly altered the global nitrogen cycle by increasing the rate and magnitude of nitrogen deposition. Among these factors, long-term nitrogen application decreases plant species richness, increases crop biomass, and shifts plant composition to a few dominant species [61]. Such plant community responses to nitrogen loading may

impact the food chain. The responses of terrestrial food chains to nutrient loading may be similar to responses of aquatic food chains, where phosphorus loading increases algal productivity and shifts algal, zooplankton, insect and fish community compositions^[62]. The effects of nitrogen addition on insect diversity may be complicated due to the changes in the plant community by opposing effects on insect species richness. At high nitrogen rate the resulting lower plant species richness might decrease the insect species richness due to the lower diversity in food resources for insect specialists^[63]. Nitrogen inputs should also increase plant productivity, which should increase the availability of insect resources, the number of insect individuals and possibly the number of insect species^[63].

The long-term nitrogen loading of grasslands decreased plant species richness and increased plant biomass. Haddad et al^[62] found that the total insect species richness and effective insect diversity, as well as herbivore and predator species richness, negatively related with nitrogen rate in 54 plots that had been maintained at various rates for 14 years. There was also variation in trophic responses to nitrogen. Insect abundances, measured as the number of insects and insect biovolume, were positively related to nitrogen rate, as were the abundances of herbivores and detritivores. This study demonstrated that long-term nitrogen loading affects the entire food chain, simplifying both plant and insect communities.

Prestidge^[54] studied the influence of nitrogen fertilizer on the grassland *Auchenorrhyncha* and found that fertilizer addition reduced the leafhopper species diversity by disproportionately increasing the total number of individuals which effectively reduced the equitability index. Moreover, delphacids were more abundant in plots receiving nitrogen fertilizer whereas cicadellids were more abundant in unfertilized areas. Leafhoppers were more abundant on plots with a 'preferred' leaf nitrogen level. Adult aggregation and female reproductive successes were greater at the 'preferred' leaf nitrogen level.

Nitrogen stimulates insect pests of rice

Rice leaffolders

de Kraker^[64] reviewed 15 published papers on field trials and found that in a large number of trials

the increase in nitrogen fertilization led to higher injury levels by leaffolders. In a previous laboratory experiment the use of nitrogen fertilizer affected several biometric characteristics of rice leaffolder, including the increase in larval survival rate, leaf area consumed, pupal weight, moth longevity, fecundity, and preference of oviposition^[65-69].

The effects of nitrogen fertilization on population dynamics and natural control of rice leaffolder were studied in an irrigated rice area by de Kraker et al^[64]. They found that the average density of leaffolder larvae at the highest nitrogen level was eight times more than that at the zero nitrogen level, while the injured leaves ranged from 5% to 35%. The severe increase in larval density was due to the positive effect of nitrogen fertilization on egg recruitment and survival of medium-sized larvae. Moreover, the significant effect of nitrogen fertilization in the present small-scale experiment was attributed mainly to an oviposition choice of the moths in plots with different nitrogen levels. However, such effects would be less pronounced when implemented over a large area.

Planthopper and leafhoppers

Sap-sucking leafhoppers and planthoppers are the most common pests in rice ecosystems. Among the 22 species of Delphacidae and 34 of Cicadellidae in rice fields in Asia, the planthoppers, brown planthopper (BPH) *Nilaparvata lugens* (Stål) and white backed planthopper (WBPH) *Sogatella furcifera* (Horvath), and green leafhoppers (GLH) *Nephotettix virescens* (Distant), are the most important economic insect pests^[70]. The nutrients content such as amino acids in rice sap were so low that BPH have to suck more sap, which resulted in lower conversion efficacy of digested food (ECD) in BPH (ranged from 5% to 7%)^[71-75] than that in other sucking herbivores on forb, grass and seed (ranged from 40% to 90%)^[8]. The increase in amino acid content of rice sap and more succulent plants by the application of nitrogen fertilizer could improve the nutritional conditions for sap-sucking hoppers and elevate their population^[76].

The rice plants supplied with nitrogen were preferred to feeding and oviposition by BPH^[71-73]. The BPH on plants with high nitrogen content had high feeding rates and honeydew excretion^[71, 74], less

probing behavior^[74-75], higher survival rates, and population built-up^[71, 75, 77], fecundity and oöytes production^[73, 77], and high tendency for outbreak^[78-80]. Kanno et al^[81] monitored the feeding activity of BPH using the isotope mark of ³²P and found that the feeding amounts, honeydew excretion and nitrogen content in body of BPH on high nitrogen plants were increased by 3-7, 7 and 2-3 times, respectively. At various rice growth stages, the BPH populations were affected more by the nitrogen application in earlier season, whereas the plant density seemed to be more affected in later season^[80]. The water content (WC) and related water content (RWC) significantly increased, while the amount of sap flowed reduced statistically with the increase in nitrogen content of rice plants. However, the RWC in rice treated with high nitrogen fertilizer drastically decreased due to injury by BPH nymphs, while the reduced survival duration with the increase of nitrogen content was recorded. This might be one of the key factors for enhancing the susceptibility to BPH damage in rice plants supplied with nitrogen fertilizer^[82].

The responses of BPH to nitrogen differed on rice varieties with different resistance levels. Little differences in honeydew excretion, survival rate and population built-up of BPH were found on resistant rice varieties at 320 kg/ha and 160 kg/ha nitrogen rates. The damages on resistant variety IR26 by BPH were not affected apparently by nitrogen applications, but on susceptible variety Kaoshenyu 12 the damages was obvious^[71]. The BPH weights, feeding rates and population growth increased with nitrogen application on IR26, Utri Rajapan and Triveni. Population growth of BPH increased threefold on resistant varieties IR26 and Utri Rajapan, and twofold on moderately resistant variety Triveni, without antibiosis^[83]. At the same rate of nitrogen fertilizer, more BPH adults were located on susceptible varieties than on resistant ones^[73]. The interaction between nitrogen levels and light intensity was found in feeding preference, survival rate, development and probing frequency of BPH on rice varieties with different resistance levels^[84]. On susceptible rice TN1 with different rates of nitrogen fertilizer, the honeydew excreted by BPH fluctuated with the increase in nitrogen. Kumar and Pathak^[85]

found that increase in nitrogen fertilization up to 100 kg/ha resulted in the increase of honeydew excretion, while the further increasing in nitrogen dose reduced honeydew excreted by BPH.

Nitrogen fertilization also significantly increased the populations of WBPH^[86-89], GLH^[86-87], and small brown planthopper^[87]. However, Ma and Lee^[87] have found that GLH population did not increase with higher nitrogen levels in fields at later transplanting times.

Stem borers

The stem borers of the families Pyralidae and Crambidae such as the yellow stem borer (YSB) *Scirpophaga incertulas*, striped stem borer (SSB) *Chilo suppressalis*, white stem borer (WSB) *S. innotata*, gold-fringed stem borer *C. auricilius*, dark-headed stem borer *C. polychrysus*, and pink stem borer *Sesamia inferens* are among the major insects of rice. Among them, YSB is the most dominant species in the tropical regions of Asia, while SSB is the major species in temperate countries. The young stem borer larvae feed within the leaf sheath, and older larvae feed inside the stem and sever vascular tissues^[90]. Infestations by different species of rice borers had been reported to be influenced by nitrogen fertilization. The dead hearts and white heads caused by YSB increased with higher nitrogen levels^[91]. Similar effects of nitrogen on the incidence of SSB had also been observed^[87, 92, 93]. The application of nitrogen fertilizer can increase the succulence in stems and leaves, which can lead to greater stem borer attack, higher larval weights and shorter the developmental time. The higher incidence of stem borer was clustered within the area in FFP (farmers' fertilizer practice) than that in SSNM (site-specific nutrient management) plots based on the data from 137 Reversing Trends of Declining Productivity (RTDT) Project monitoring farms^[94]. Liu and Qin^[95] reviewed the population of YSB and SSB in China and found that the rates of damage, densities, and the weight and sizes of larval body of SSB increased significantly with the increase in nitrogen, while the nitrogen content of rice plant was a key factor affecting the diapause of YSB larvae.

Optimum regime of nitrogen fertilizer applying in rice fields

Nitrogen is the most essential mineral nutrient for plant growth and development and proper nitrogen management is essential in intensive agriculture for plant production. Plants respond quickly to available nitrogen in soil and the adequate absorption of nitrogen can increase photosynthesis, vegetative growth and eventually high yield. However, if there is a continuous increase in nitrogen application, the uptake rate tends to fall rapidly with no further increase in yield. It has been noted that the excessive application causes massive vegetative growth and lower harvest index, plant lodging and susceptibility to disease and insect pests, resulting in an asymptotic or parabolic relationship between crop yield and nitrogen dose [96-97]. During a 5-year test at the Missouri Rice Farm in Glennonville, USA, the yields were the greatest at recommended nitrogen fertilizer rate, and reduced when nitrogen fertilizer was applied at 150% of the recommended amount. Moreover, there was no difference in rice yield between the fields with 100 and 200 kg/ha both in dry season and wet season (Lu Z X et al, unpublished data). On the other hand, nitrogen use efficiency generally declined with the increase in nitrogen application. The application of nitrogen in excess resulted in higher accumulation in soil, predominantly in inorganic forms, and caused serious environmental problem, such as groundwater pollution, eutrophication of streams and lakes, destruction of the stratospheric ozone layer, greenhouse effects, soil acidification, etc [1]. Therefore, an optimal supply of nitrogen is essential to maintain throughout the crop growth for better yield and production.

To meet the food demand of world population in 2025 the rice production must increase to 65% more than today. If the technologies affecting the nutrient utilization in rice crop remained unchanged, the increase in production will require almost 300% more than the present application rate of nitrogen alone in irrigated environments, which is an undesirable amount not only economically but also environmentally. The nutrient-use efficiency of rice

cropping systems must be improved along with the yield potential of rice cultivars, since the modern high-yield rice varieties depended on the nitrogen fertilizer and water supply [98-99]. Assessing nitrogen status in a quick and reliable fashion is considered to be a critical aspect in rice production. The methods that estimate leaf area-based nitrogen concentration of rice using the SPAD meter (Chlorophyll meter) and the Leaf Color Chart (LCC) have been adopted widely in paddy field in guiding nitrogen application to increase the nitrogen use efficiency [100-101]. In an experiment applying 30 kg N/ha each time the SPAD value fell below the critical value of 37.5 resulting in application of 90 kg N/ha, which produced rice yields equivalent to those with 120 kg N/ha applied in three splits. Using a SPAD value of 35 was inadequate for the two rice cultivars because it resulted in application of only 60 kg N/ha and, thus, low yields. Limited experimentation with LCC indicated that nitrogen management based on LCC shade 4 helped to avoid over-application of nitrogen to rice. Results showed that plant need-based nitrogen management through chlorophyll meter reduced nitrogen requirement of rice from 12.5 to 25.0%, with no loss in yield [100]. According to this field experiment, the application rate of 100 kg N/ha is probably adequate. However, the rate might be reduced slightly in wet season based on the nutrient status of fields.

In China during the past 39 years, the consumption of nitrogen increased by 43.8 times with average yearly increase of 10.5%, while all over the world the increase was 6.4 times. During 1999, China consumed about one third of total world nitrogen with 9% world arable land, while 13% arable land was applied the same proportion nitrogen in the USA [102]. Among all nitrogen fertilizer consumed during 1995-1999 in China, 37% of which was applied in rice field with 21% planting area of total arable land, and with 35% production in total food yield. The high rice yield may be attributed to the huge average nitrogen rate of 180 kg/ha, which was much higher than the average rate of 103 kg/ha in the world. However, the partial factor productivity (PFP) of nitrogen fertilizer was much lower, implying the low nitrogen fertilizer use efficiency (NFUE). Unfortunately, the farmers in China are continuously increasing the amount of

nitrogen fertilizer over 200 kg/ ha despite the decrease in yields at nitrogen application rate more than 100 kg/ha was detected in some tested provinces. The excessive use of nitrogen fertilizer might be stimulated by the low price of nitrogen fertilizer, with the purpose to maximize tillers number of hybrid rice to decrease the costs of expensive seeds, to supply nitrogen as nitrogen loss in mid-season drainage as well as to save the labor cost in China^[103].

Therefore, there is the need to develop optimized management practices for increasing nitrogen fertilizer use efficiency in rice production, which could reduce the input of fertilizer, and decrease the application of pesticides as lower occurrence of pests, finally reduce loss of yield and increase farmers' income. To increase nitrogen fertilizer use efficiency is beneficial for increasing farmers' income, but for improving resources use efficiency and protecting environment to sustainable development of rice production.

ACKNOWLEDGEMENT

This study was supported by the National Natural Science Foundation of China (Grant No. 30471170).

REFERENCES

- Conway G R. The Doubly Green Revolution: Food for all in the 21st Century. New York: Cornell University Press, 1997.
- Conway G R, Pretty J N. Unwelcome Harvest: Agriculture and pollution. London: Earthscan Publications Ltd, 1991.
- Scriber J M. Nitrogen nutrition for plants and insect invasion. In: Hauch R D. Nitrogen in Crop Production. Wisconsin: ASA-CSSA-SSSA, USA, 1984: 441-460.
- Southwood T R E. The insect/plant relationship – an evolutionary perspective. In: Emden F V. Insect-plant Relationship. Symposia of the Royal Entomological Society of London. No 6. Oxford: Blackwell, 1973: 3-30.
- Bernays E A. Insect-plant Interactions VII. Florida: CRC Press, 1990.
- Simpson S J, Simpson C L. The mechanisms of nutritional compensation by phytophagous insects. In: Bernays E A. Insect-plant Interactions, Vol. II. New York: CPC Press, Inc, 1990: 111-160.
- Barbour J D, Farrar R R, Kennedy G G. Interaction of fertilizer regime with host plant resistance in tomato. *Entomol Exp Appl*, 1991, **60**: 289-300.
- Slansky F J, Scriber J M. Food consumption and utilization. In: Kerkut G A, Gilbert L I. Comprehensive Insect Physiology, Biochemistry, and Pharmacology, 4. Pergamon: Oxford, 1985: 87-163.
- Bernays E A, Chapman R F. Host-plant Selection by Phytophagous Insects. New York: Chapman and Hall, 1994.
- Bentz J A, Reeves J III, Barbosa P, Francis B. Within-plant variation in nitrogen and sugar content of poinsettia and its effects on the oviposition pattern, survival, and development of *Bemisia argentifolii*. *Environ Entomol*, 1995, **24**: 271-277.
- Bentz J A, Reeves J III, Barbosa P, Francis B. Nitrogen fertilizer effect on selection, acceptance and suitability of *Euphorbia pulcherrima* as a host plant to *Bemisia tabaci*. *Environ Entomol*, 1995, **24**: 40-45.
- Mattson W J. Herbivory in relation to plant nitrogen content. *Ann Rev Ecol Syst*, 1980, **11**: 19-61.
- Chu Y I, Horng S B. Effect of slag and nitrogen fertilizer on the damage of Asian corn borer to field corn. *Mem Coll Agric, Natl Taiwan Univ*, 1994, **34**(1): 45-53.
- Cisneros J J, Godfrey L D. Midseason pest status of the cotton aphid in California cotton: Is nitrogen a key factor? *Environ Entomol*, 2001, **30**: 501-510.
- Bentz J A, Reeves J III, Barbosa P, Francis B. Effect of nitrogen fertilizer source and level on ovipositional choice of poinsettia by *Bemisia argentifolii*. *J Econ Entomol*, 1995, **88**: 1388-1392.
- Bentz J A, Larew H G. Ovipositional preference and nymphal performance of *Trialeurodes vaporariorum* on *Dendranthema grandiflora* under different fertilizer regimes. *J Econ Entomol*, 1992, **85**: 514-517.
- Noldus L P, Xu R, van Lenteren J C. The parasite-host between *Encarsia formosa* Gahan and *Trialeurodes vaporariorum* XIX. Feeding-site selection by the greenhouse whitefly. *J Appl Entomol*, 1986, **101**: 492-507.
- Jauset A M, Sarasua M J, Avilla J, Albajes R. The impact of nitrogen fertilization of tomato of feeding site selection and oviposition by *Trialeurodes vaporariorum*. *Entomol Exp Appl*, 1998, **86**: 175-182.
- Minkenberg O P, Fredrix M J. Preference and performance of a herbivorous fly, *Liriomyza trifolii*, on tomato plants differing in leaf nitrogen. *Ann Entomol Soc Am*, 1989, **82** (3): 350-354.
- Papaj D R, Rausher M D. Individual variation in host location by phytophagous insects. In: Ahmad S. Herbivorous Insects: Host seeking behavior and mechanisms. New York: Academic, 1983: 77-124.
- White T C R. The Inadequate Environment: Nitrogen and the abundance of animals. Berlin: Springer, 1993.
- Fischer K, Fiedler K. Response of the copper butterfly *Lycaena tityus* to increased leaf nitrogen in natural food plants: Evidence against the nitrogen limitation hypothesis. *Oecologia*, 2000, **124**: 235-241.
- Fox L R, Eisenbach J. Effects of experimental design and nitrogen on cabbage butterfly oviposition. *Oecologia*, 1989, **80**: 211-214.
- Rossi A M, Brodbeck B V, Strong D R. Response of xylem-feeding leafhopper to host plant species and plant quality. *J Chem Ecol*, 1996, **22**(4): 653-671.

- 25 Qin J D, Wang C Z. The relation of interaction between insects and plants to evolution. *Acta Entomol Sin*, 2001, **44**(3): 360-365.
- 26 Hattenschwiler S, Schafellner C. Opposing effects of elevated CO₂ and nitrogen deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia*, 1999, **118**: 210-217.
- 27 Slansky F J, Feeny P. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecol Monographs*, 1977, **47**: 209-228.
- 28 Wier A T, Boethel D J. Feeding, growth, and survival of soybean looper in response to nitrogen fertilization of nonnodulating soybean. *Environ Entomol*, 1995, **24**: 326-331.
- 29 Blua M J, Toscano K. *Bemisia argentifolii* development and honeydew production as a function of cotton nitrogen status. *Environ Entomol*, 1994, **23**: 316-321.
- 30 Rausher M D. Host plant selection by *Battus philenor* butterflies: The roles of predation, nutrition, and plant chemistry. *Ecol Monographs*, 1981, **51**: 1-20.
- 31 Wheeler G S, Van T K, Center T D. Herbivore adaptations to a low nutrient food: Weed biological control specialist *Spodoptera pectinicornis* fed the floating aquatic plant *Pistia stratiotes*. *Environ Entomol*, 1998, **27**: 993-1000.
- 32 Douglas A E. Nutritional interactions in insect-microbial symbioses: Aphids and their symbiotic bacteria *Buchnera*. *Ann Rev Entomol*, 1998, **43**: 17-37.
- 33 Douglas A E. Reproductive failure and the free amino acid pools in pea aphids lacking symbiotic bacteria. *J Insect Physiol*, 1996, **42**: 247-255.
- 34 Sasaki T, Kawamura M, Ishikawa H. Nitrogen recycling in the brown planthopper, *Nilaparvata lugens*, involvement of yeast-like endosymbionts in uric acid metabolism. *J Insect Physiol*, 1996, **42**: 125-129.
- 35 Jansson R K, Smilowitz Z. Influence of nitrogen on population parameters of potato insects: Abundance, population growth, and within-plant distribution of green peach aphid, *Myzus persicae*. *Environ Entomol*, 1986, **15**: 49-55.
- 36 Kaneshiro L N, Johnson M W. Tritropic effects of leaf nitrogen on *Liriomyza trifolii* (Burgess) and an associated parasitoid *Chrysocharis oscinidis* (Ashmead) on bean. *Biol Control*, 1996, **6**: 186-192.
- 37 Minkenbergh O P, Ottenheim J J. Effect of leaf nitrogen content of tomato plants on preference and performance of a leafmining fly. *Oecologia*, 1990, **83**: 291-298.
- 38 Prestidge R A. Instar duration, adult consumption, oviposition and nitrogen utilization efficiencies of leafhoppers feeding on different quality food. *Ecol Entomol*, 1982, **7**: 91-101.
- 39 Jauset A M, Sarasua M J, Avilla J, Albajes R. Effect of nitrogen fertilization level applied to tomato on the greenhouse whitefly. *Crop Prot*, 2000, **19**: 255-261.
- 40 Liu S, Wang Y Z. The preliminary study on the effects of different amounts of nitrogen fertilizers on cotton bollworm. *J Hebei Agric Univ*, 1989, **12**(1): 81-87
- 41 Gong P Y, Li X Z. Effects of diet nitrogen on the development and fecundity of cotton bollworm. *Acta Entomol Sin*, 1992, **35**: 46-46
- 42 Xia J Y, Ma Y, Wang C Y. Effects of host plant with different nitrogen fertilizer on the development and reproduction of cotton bollworm. *Acta Entomol Sin*, 1997, **40**(suppl): 95-102.
- 43 Bethke J A, Redak R A, Schuch U K. Melon aphid performance on chrysanthemum as mediated by cultivar, and differential levels of fertilization and irrigation. *Entomol Exp Appl*, 1998, **88**: 41-47.
- 44 Casey C A, Raupp M J. Supplemental nitrogen fertilization of containerized azalea does not affect performance of Azalea lace bug. *Environ Entomol*, 1999, **28**: 998-1003.
- 45 Bi J L, Ballmer G R, Hendrix D L, Henneberry T J, Toscano N C. Effect of cotton nitrogen fertilization on *Bemisia argentifolii* population and honeydew production. *Entomol Exp Appl*, 2001, **99**: 25-36.
- 46 Metcalfe J R. Studies on the effect of the nutrient status of sugar cane on the fecundity of *Saccharosydne saccharivora*. *Bull Entomol Res*, 1970, **60**: 309-325.
- 47 Nevo E, Coll M. Effect of nitrogen fertilization on *Aphis gossypii* variation in size, color, and reproduction. *J Econ Entomol*, 2001, **94**: 27-32.
- 48 Ali A G, Ahmed A. Effect of plant density and nitrogen fertilization on the infestation in wheat plants with cereal aphids. *Assiut J Agric Sci*, 1996, **27**: 119-124.
- 49 Archer T L, Onken A B, Matheson R L, Jr Bynum E D. Nitrogen fertilizer influence on greenbug dynamics and damage to sorghum. *J Econ Entomol*, 1982, **75**: 695-698.
- 50 Bowdish T I, Stiling P. The influence of salt and nitrogen on herbivore abundance: Direct and indirect effects. *Oecologia*, 1998, **113**: 400-405.
- 51 Duffield S J, Bryson R J, Young J E, Sylvester-Bradley R, Scott R K. The influence of nitrogen fertilizer on the population development of the cereal aphids *Sitobion avenae* and *Metopolophium dirhodum* on field grown winter wheat. *Ann Appl Biol*, 1997, **130**: 13-26.
- 52 Fox L R, Letourneau D K, Eisenbach J, van Nouhuys S. Parasitism rate and sex ratios of a parasitoid wasp: Effects of herbivore and plant quality. *Oecologia*, 1990, **83**: 414-419.
- 53 Moon D C, Rossi A M, Stiling P. The effects of abiotically induced changes in host plant quality (and morphology) on a salt marsh planthopper and its parasitoid. *Ecol Entomol*, 2000, **25**: 325-331.
- 54 Prestidge R A. The influence of nitrogenous fertilizer on the grassland auchenorrhyncha. *J Appl Ecol*, 1982, **19**: 735-749.
- 55 Su J W, Men X Y, Ge F, Liu X H, Li H D, et al. Effect of nitrogen fertilizer on pest population and cotton production. *Chinese J Appl Ecol*, 2003, **14**(10): 1735-1738. (in Chinese with English abstract)
- 56 Ebert T A. Aphids and Plant Nitrogen. Poway: Welton Ln, 1996.
- 57 Coulibaly R. Effect of nitrogen fertilizer on the damage of *Eldana saccharina* Walker to sugar cane. *Sugar Cane*, 1990(Suppl): 18-20.
- 58 Joern A, Behmer S T. Impact of diet quality on demographic attributes in adult grasshopper and the nitrogen limitation hypothesis. *Ecol Entomol*, 1998, **23**: 174-184.

- 59 Chau A, Heinz K M, Davies F T. Preliminary study on the effect of nitrogen fertilization on cotton aphid, *Aphis gossypii*. *IOBC/wprs Bulletin*, 2002, **25**(1): 53-56.
- 60 Vos J G M, Frinking T F. Nitrogen fertilization as a component of integrated pest management of hot pepper under tropic lowland conditions. *Intl J Pest Manag*, 1997, **43**: 1-10.
- 61 Inouye R, Tilman D. Convergency and divergence of old field vegetation after 11 years of nitrogen addition. *Ecology*, 1995, **76**: 1872-1887.
- 62 Haddad N M, Haarstad J, Tilman D. The effects of long-term nitrogen loading on grassland insect communities. *Oecologia*, 2000, **124**: 73-84.
- 63 Siemann E, Tilman D, Haarstad J, Ritchie M. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am Nat*, 1998, **152**: 738-750.
- 64 de Kraker J. The potential of natural enemies to suppress rice leaffolder populations. [PhD thesis]. Wageningen: Wageningen Agricultural University, 1996.
- 65 de Kraker J, Rabbinge R, Huis A V, Lenteren J C V, Heong K L. Impact of nitrogenous-fertilization on the population dynamics and natural control of rice leaffolder (Lep: Pyralidae). *Intl J Pest Manag*, 2000, **46**: 225-235.
- 66 Dan J G, Chen C M. The effects of feeding condition on the growth, development and reproduction of rice leaffolder. *Acta Phytophyla Sin*, 1990, **17**: 193-199. (in Chinese with English abstract)
- 67 Liang G W, Luo G H, Li C F. Effects of fertilizer application on the adult and egg density of the rice leaffolder. *Guangdong Agric Sci*, 1984, **14**(2): 34-35. (in Chinese)
- 68 Swaminathan K, Saroja R, Raju N. Influence of source and level of nitrogen application on pest incidence. *IRRN*, 1985, **10**(1): 24.
- 69 Zhang G F, Lu C T, Shen X C, Wang W X. The synthesized ecological effect of rice density and nitrogen fertilizer on the occurrence of main rice pests. *Acta Phytophyla Sin*, 1995, **22**(1): 38-44. (in Chinese with English abstract)
- 70 Wilson M R, Claridge M F. Handbook for Identification of Leaffolder and Planthoppers of Rice. Wallingford: CAB International, 1991.
- 71 Cheng C H. Effect of nitrogen application on the susceptibility in rice to brown planthopper attack. *J Taiwan Agric Res*, 1971, **20**(3): 21-30.
- 72 Lu Z X, Heong K L, Yu X P, Hu C. Effects of nitrogen nutrient on the behavior of feeding and oviposition of the brown planthopper, *Nilaparvata lugens*, on IR64. *J Zhejiang Univ: Agric & Life Sci*, 2005, **31**(1): 62-70. (in Chinese with English abstract)
- 73 Wang M Q, Wu R Z. Effects of nitrogen fertilizer on the resistance of rice varieties to brown planthopper. *Guangdong Agric Sci*, 1991 (1): 25-27. (in Chinese)
- 74 Sogawa K. Studies on feeding habits of brown planthopper: I. Effects of nitrogen-deficiency of host plants on insect feeding. *Japan J Appl Entomol Zool*, 1970, **14**: 101-106.
- 75 Lu Z X, Heong K L, Yu X P, Hu C. Effects of plant nitrogen on ecological fitness of the brown planthopper, *Nilaparvata lugens*, in rice. *J Asia-Pacific Entomol*, 2004, **7**(1): 97-104.
- 76 Balasubramanian P, Palaniappan S P, Gopalan M. The effect of carbofuran and nitrogen on leaf folder incidence. *IRRN*, 1983, **8**: 13-14.
- 77 Preap V, Zalucki M P, Nesbitt H J, Jahn G C. Effect of fertilizer, pesticide treatment, and plant variety on the realized fecundity and survival rates of brown planthopper, *Nilaparvata lugens*, generating outbreaks in Cambodia. *J Asia-Pacific Entomol*, 2001, **4**: 75-84.
- 78 Hosamani M M, Jayakumar B V, Sharma K M. Sources and levels of nitrogenous fertilizers in relation to incidence of brown planthopper in Bhadra Project. *Curr Res*, 1986, **15**: 132-134.
- 79 Li R D, Ding J H, Hu G W, Shu D M. The Brown planthopper and Its Population Management. Shanghai: Fudan University Press, 1996. (in Chinese)
- 80 Uhm K B, Hyun J S, Choi K M. Effects of the different levels of nitrogen fertilizer and planting space on the population growth of the brown planthopper. *Res Report RDA: P M & U*, 1985, **27**(2): 79-85.
- 81 Kanno H, Kim M, Ishii S. Feeding activity of the brown planthopper on rice plants manured with different levels of nitrogen. *Japan J Appl Entomol Zool*, 1977, **21**(2): 110-112.
- 82 Lu Z X, Villareal S, Yu X P, Heong K L, Hu C. Effect of nitrogen on water content, sap flow and tolerance of rice plants to brown planthopper. *Rice Sci*, 2004, **11**(3): 129-134
- 83 Heinrichs E A, Medrano F G. Influence of nitrogen fertilizer on the population development of brown planthopper. *IRRN*, 1985, **10**(6): 20.
- 84 Liu C M, Wu R Z. Influence of light intensity and nitrogen fertilizer on resistance to brown planthopper in rice. *J South China Agric Univ*, 1992, **13**(2): 27-33. (in Chinese with English abstract)
- 85 Kumar P, Pathak P K. A simple and accurate method of quantifying honeydew excretion in brown planthopper. *Indian J Entomol*, 2001, **63**: 208-210.
- 86 Hu J Z, Lu Q H, Yang J S. Effects of fertilizer and irrigation on the population of main insect pests and the yield of rice. *Acta Entomol Sin*, 1986, **29**(1): 49-54. (in Chinese with English abstract)
- 87 Ma K C, Lee S C. Occurrence of major rice insect pests at different transplanting times and fertilizer levels in paddy field. *Korean J Appl Entomol*, 1996, **35**(2): 132-136.
- 88 Prasad J, Misra D S. Influence of different levels N, P and K on the population of leaffolder and planthoppers. In: Chelliah T, Balasubramanian M. Pest Management in Rice. Coimbatore: Tamil Nadu Agricultural University, 1983: 245-254.
- 89 Wu L H, Zhu Z R. The relationship between rice leaf color and occurrence of rice diseases and insects and its mechanism. *Chinese J Rice Sci*, 1994, **8**(4): 231-235. (in Chinese with English abstract)
- 90 Alinia F, Ghareyazie B, Rubia L, Bennett J, Cohen M B. Effect of plant age, larval age, and fertilizer treatment on resistance of a *cry1Ab*-transformed aromatic rice to Lepidopterous stem borers and foliage feeders. *J Econ Entomol*, 2000, **93**: 484-493.

- 91 Yein B R, Das G R. Effect of spacing and nitrogen levels on the incidence of insect pests of rice. *Pesticide*, 1988, **22**: 37-40.
- 92 Tan Y C. Preliminary study on relationship of nitrogen fertilizer with population of stripped stem borer. *Entomol Knowl*, 1986, **23**(3): 101-102.
- 93 Swaminathan K, Saroja R, Raju N. Influence of source and level of nitrogen application on pest incidence. *IRRN*, 1985, **10**(1): 24.
- 94 Sta Cruz P C, Simbahan G C, Hill J E, Dobermann A, Zeigler R S, Du P V, dela Peña F A, Samiayyan K, Suparyono, Tuat V N, Zheng Z. Pest profiles at varying nutrient input levels. In: Peng S, Hardy B. Rice Research for Food Security and Poverty Alleviation. Manila: IRRI, 2001: 431-440.
- 95 Liu G J, Qin H G. The advance in rice stem borer research in China. *Entomol Knowl*, 1997, **34**: 171-174. (in Chinese)
- 96 Sinclair T. Historical changes in harvest index and crop nitrogen accumulation. *Crop Sci*, 1998, **38**: 638-643.
- 97 Srivastava H S, Singh R P. Nitrogen Nutrition and Plant Growth. Enfield: Science Publishers Inc, 1999.
- 98 Fischer K S. Toward increasing nutrient-use efficiency in rice cropping systems: The next generation of technology. *Field Crops Res*, 1998, **56**: 1-6.
- 99 Panda N, Khush G S. Host Plant Resistance to Insects. Wallingford: CAB International, 1995: 67-103.
- 100 Singh J, Singh Y, Ladha J K, Bronson K F, Balasubramanian V, Singh J, Khind C S. Chlorophyll meter- and leaf color chart-based nitrogen management for rice and wheat in Northwestern India. *Agron J*, 2002, **94**: 821-829.
- 101 Peng S, Laza R C, Garcia F V, Cassman K G. Chlorophyll meter estimates leaf area-based nitrogen concentration of rice. *Comm Soil Sci Plant Anal*, 1995, **26**: 927-935.
- 102 FAO. Statistical databases. <http://www.FAO.org>. 2001.
- 103 Peng S B, Huang J L, Zhong X H, Yang J C, Wang G H, Zou Y B, Zhang F S, Zhu Q S, Buresh R, Witt C. Challenge and opportunity in improving fertilizer-nitrogen use efficiency of irrigated rice in China. *Agric Sci China*, 2002, **1**(7): 776-785.