

Effect of Nitrogen Fertilizer on the Intrinsic Rate of Increase of *Hysteroneura setariae* (Thomas) (Homoptera: Aphididae) on Rice (*Oryza sativa* L.)

GARY C. JAHN,¹ LIBERTY P. ALMAZAN, AND JOCELYN B. PACIA

International Rice Research Institute, Entomology and Plant Pathology Division, DAPO Box 7777, Metro Manila, Philippines

Environ. Entomol. 34(4): 938–943 (2005)

ABSTRACT We studied the intergenerational effects of nitrogen (N) fertilizer applications to rice plants on the size, fecundity, and intrinsic rate of increase (r_m) of *Hysteroneura setariae* (Thomas). Treatments consisted of rearing aphids on rice plants receiving 0, 50, 100, and 150% of the standard N fertilizer rates. Adult females produced on the 0 and 150% treatments were transferred to new plants at 0 or 150% N levels to create a matrix of four treatments: 0–0, 0–150, 150–0, and 150–150%. Second-generation aphids produced on 150% N plants had significantly higher survivorship, fecundity, and r_m regardless of the N treatment of plants that parents fed on. N levels had no observed effect on head width. Aphids reared on 0% N plants whose parents were also reared on 0% N plants had significantly shorter body lengths than aphids on all other treatments, including the 150–0% treatment, indicating that the effect of a high N diet was expressed in a second generation of aphids. Results are discussed in the context of aphid population outbreaks in rice fields and in greenhouses.

KEY WORDS *Hysteroneura setariae*, nitrogen fertilizer, intrinsic rate of increase, fecundity, rice

RUSTY PLUM APHID, *Hysteroneura setariae* (Thomas), distribution is virtually worldwide (Thomas 1878, Yano and Miyake 1983, Heie et al. 1996, Stoetzel and Miller 2001, CSIRO 2004). Outbreaks of *H. setariae* in nonirrigated lowland rice fields have been reported from Sierra Leone, Nigeria, and India (Dale 1994). As with other phloem-feeding pests, *H. setariae* outbreaks on rice are associated with drought (Akinlosotu 1977). Heavy rains apparently reduce aphid populations (Dale 1994). *Camponotus compressus* (Fabricius) and other ant species have been observed tending *H. setariae* on rice (David et al. 1967, Akibo-Betts and Raymundo 1978). *H. setariae* occurs on all stages of rice, feeding on the leaves and unripened grains, aggregating on rice panicles and at the juncture of the leaf sheath and leaf lamina. Brown necrotic spots appear on the outside of the grain where *H. setariae* has fed. In addition to rice, *H. setariae* is a pest of wheat, sugarcane, and soybean. It is a vector of six plant viruses including sugar cane mosaic virus (Ingram and Summers 1936, Chan et al. 1991), but is not known to transmit any viral diseases of rice. In the Philippines and the rest of Southeast Asia, it is a minor pest of rice in fields but a common pest of rice and wild rice grown in greenhouses for research. *H. setariae* feeds on milk stage rice grains, i.e., when the grain endosperm is in a liquid state, resulting in empty grains (Akibo-Betts and Raymundo 1978, Barrion and Litsinger 1991). *H.*

setariae was first observed on rice in the Philippines in 1961 (Baltazar 1965). The alternate grass hosts of *H. setariae* in the Philippines include 14 species of Gramineae and at least 1 species of Poaceae (Baltazar 1965, Barrion and Litsinger 1991).

Hysteroneura setariae has four nymphal instars. Each instar lasts 2–3 d. It takes 10 d on average to reach the fourth-instar stage. Adults live 8–15 d (Garg and Sethi 1978). *H. setariae* are parthenogenetic and viviparous. Unfertilized eggs produce female offspring (Shepard et al. 1995).

Nitrogen (N) application rates are known to affect the individual size, survival, and intrinsic rate of increase (r_m) of several species of rice pests (Preap et al. 2001, Jahn 2004, Lu et al. 2004). The ease of rearing *H. setariae* in greenhouses and the large body of literature on aphid response to N levels on other host plants (e.g., van Emden 1996, Cisneros and Godfrey 2001) makes *H. setariae* an ideal species to use in N response studies. If N levels are found to affect r_m of aphids on rice, it may be possible to use nutrient management to indirectly mitigate aphid damage to rice, at least in greenhouses. Nevo and Coll (2001) discovered that the N rates applied to cotton plants on which the first generation fed had a stronger effect on the fecundity, r_m , and body size of second-generation cotton aphids, *Aphis gossypii* Glover, than the N rates applied to the cotton plants that the second generation fed on. In this study, we examined the effects of N fertilizer on the size, survival, fecundity, and r_m of *H.*

¹ Corresponding author, e-mail: g.jahn@cgiar.org.

setariae. In particular, we wanted to determine the cumulative effect of N fertilizer applications on aphids over two consecutive generations. We tested the hypothesis that the fecundity, r_m , and body size of second-generation *H. setariae* would be more greatly affected by the N rates applied to rice host plants of the first generation than the N levels of their own food plants.

Materials and Methods

Experiments were conducted in a greenhouse at the International Rice Research Institute (IRRI) in Los Baños on the island of Luzon, Philippines, to determine the effect of N applications to rice (*Oryza sativa* L.) on the size, population growth, r_m , and fecundity of *H. setariae*. The mean temperature was 36.3°C and the mean relative humidity was 28.7% in the greenhouse.

To examine the cumulative effect of N rates over two consecutive generations, we adopted the technique that Nevo and Coll (2001) used to study aphid reproduction on cotton. Aphids were reared on rice cultivar IR72, grown under 0, 50, 100, and 150% of the standard nitrogen rate of 0.090 g N/pot for transplanted rice. The 50 and 100% treatments were included to establish the nitrogen, phosphorus, potassium (N-P-K), and chlorophyll response of plants to N treatments. Aphids produced on the 0% N treatments were transferred to new rice plants grown under 0 and 150% N; aphids produced on the 150% N treatments were also transferred to new rice plants grown under 0 and 150% N.

Aphid Colony. Aphids were collected from wild rice grown in IRRI's plant breeding greenhouses in Los Baños and multiplied in another greenhouse on IR72. Rice cultivar IR72 is commonly grown in the irrigated lowlands of the Philippines. Rice was sown in clay pots (15 cm high, 10 cm base diameter, 15 cm surface diameter) at 40 seeds per pot in 1,200 g of Aquandic Epiacquoll soil (Dobermann et al. 2000, USDA Soil Survey 1994) collected from lowland rice fields at IRRI. No fertilizer was added to the soil used for direct seeding. After 1 wk, rice seedlings were transplanted into clay pots at three plants per pot in 1,200 g of Aquandic Epiacquoll soil. Each pot received a total of 0.587 g urea (46% N) = 0.270 g N, i.e., 0.090 g N per plant, split over three applications at maximum tillering, panicle initiation, and flowering. Pots of sown rice were individually watered; pots of transplanted rice were kept on a flood table with water maintained just above the edge of the pots.

Experiment. For the experiment, rice seeds were sown as described above. After 1 wk, they were transplanted at one plant per clay pot (7 cm high, 9 cm base diameter, 12 cm surface diameter) containing 600 g Aquandic Epiacquoll soil fertilized with 0.060 g N, 0.081 g phosphate, and 0.025 g potassium. This initial application of fertilizer before transplanting is known as the basal application and is important for helping the plants overcome transplant shock and establish themselves in the new soil. We chose to keep the basal

application the same for all treatments so that N levels, and not establishment rates, were the main treatment difference. After transplanting, 0% N treatments received no additional N, 50% N treatments received 0.045 g N/pot, 100% N treatments received 0.090 g N/pot, and 150% N treatments received 0.135 g N/pot split over four applications. Potted plants received N at the four treatment levels replicated four times in a completely randomized design (CRD), in the form of urea (46% N). At the rice milk stage, ten 1- to 2-d-old aphids were placed on the unripened grain of each plant. Each rice panicle was contained in a mylar cylinder (5 cm diameter by 30 cm high) with fine mesh nylon netting tied shut on top and around the stem. After 8 d, a total of 160 newly emerged adult female aphids were transferred from the 0 or 150% N treatments to 16 new milk stage plants grown under 0 and 150% N at 10 aphids per plant. After 8 d on the new plants, the number of aphids from each plant was recorded. Cages were large enough that food and space were not limited resources, as indicated by the absence of any alates throughout the experiment.

Measurements. The body length and head width of adult aphids was recorded for 10 aphids per plant. Population growth of aphids over two successive generations was measured as the intrinsic rate of increase, or $r_m = \ln(N_t/N_0)/t$ (Dixon 1987), where N_t = the population count at time t , and N_0 = the initial population size. Fecundity was measured as the mean number of offspring produced per individual per day.

The N-P-K content of the soil is not necessarily an indication of the N-P-K content of the plant, because N, P, or K can be present in the soil but in a form unavailable to the plant. To ensure that there were actual differences between treatment groups, we measured the N-P-K content of plants rather than soil. Total N content of leaves was measured by the dry combustion method (Smith 1980) with a spectrophotometer (Roboprep-TCO, Europa Scientific, Cambridge, United Kingdom). Because N applications can affect the overall health of the plant, different N application rates could affect the plant's ability to absorb P and K. The P and K content of the plant could influence aphid r_m , e.g., soybean aphids exhibit greater r_m on K-deficient soybean plants (Myers et al. 2005). Total P and K contents of leaves were measured by a modified wet ashing procedure (Miller 1998) with a Thermo Jarrell Ash Trace Analyzer (Thermo Elemental, Franklin, MA). An electronic chlorophyll meter (SPAD-502; Minolta Camera Co., Osaka, Japan) was used to measure chlorophyll readings.

Analysis. Correlation analysis was used to estimate the relationship between N application rates and the chlorophyll and N-P-K contents of leaves, as well as the relationship between fecundity and body length or head width. Data on aphid cohort populations, r_m , body length, and head width were tested for homogeneity of variances with Bartlett's test (Gomez and Gomez 1984). Variances were homogenous; therefore, data were not transformed and were analyzed by two-way factorial analysis of variance (ANOVA) at 5% significance. Means were separated by Tukey honestly

Table 1. Chlorophyll meter reading and NPK leaf content (% dry weight) of rice plants treated with four levels of nitrogen fertilizer

N application rate	n	Chlorophyll	N	P	K
0%	4	31.3c	1.3c	0.10c	1.71a
50%	4	37.4b	1.8b	0.12bc	1.74a
100%	4	44.0a	2.9a	0.15a	1.88a
150%	4	46.5a	2.9a	0.14ba	1.75a
SE for comparison		0.93	0.14	0.01	0.06
Critical value for comparison		2.76	0.42	0.02	0.20
F computed		109	68.8	12.6	2.46
F tabulated (df = 3,12)		3.49	3.49	3.49	3.49
P value		<0.01	<0.01	<0.01	0.12

Values in each column followed by the same letter are not significantly different at the $\alpha = 0.05$ level according to ANOVA and Tukey HSD mean comparison procedures.

significant difference (HSD). Analysis was conducted with Statistix (2003) software.

Results

Chemical Analysis. N application rate was correlated with the chlorophyll ($r = 0.95, P < 0.0001$), N content ($r = 0.96, P < 0.0001$), and P content ($r = 0.79, P < 0.0001$) of leaves, but not K content ($r = 0.28, P = 0.12$). The 0, 50, and 100% N application treatments had significantly different chlorophyll meter readings and leaf N content. However, the chlorophyll readings and leaf N contents of the 100 and 150% N application rates were not significantly different. The 0% N treatments had significantly less leaf P content than the 100 and 150% N treatments. The leaf K contents of the four N treatments were not significantly different (Table 1).

Effects on Population and Size. Population data from the parental generation of aphids could not be used because of a high coefficient of variation (culti-

var = 70.77). High N plants had significantly higher second-generation aphid populations than low N plants (Fig. 1). Second-generation aphids feeding on high N plants had significantly higher r_m , fecundity, and survivorship (Table 2). The mean body length of aphids reared on low N plants for two consecutive generations was significantly less than that of aphids produced on other treatments (Table 2). First- and second-generation interactions were not significant for any dependent variables except body length ($P = 0.045$). Aphid fecundity was positively correlated with body length ($r = 0.85, P = 0.002$) but not with head width ($r = 0.59, P = 0.2$).

Discussion

Nevo and Coll (2001) found that the effects of N fertilization of cotton plants on the morphology, fecundity, and r_m of *A. gossypii* could be detected across generations and that the N levels of the parental food plant had a stronger effect on these factors than the

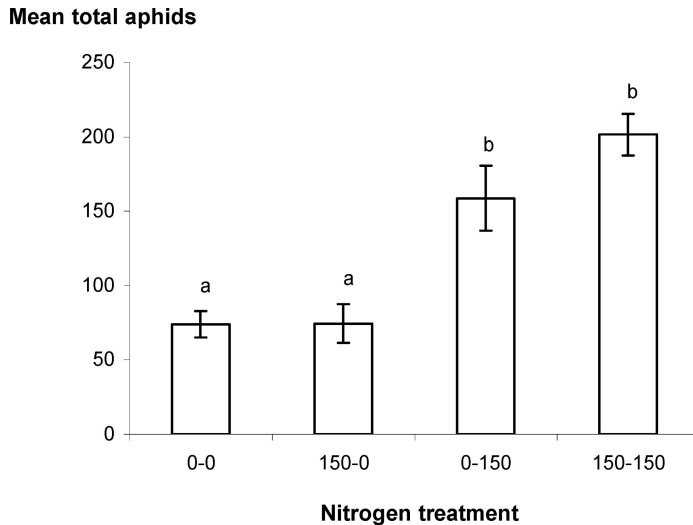


Fig. 1. Cumulative effects of N fertilizer on aphid populations on IR72 rice (means \pm SE). Treatments: 0-0, first and second generation of aphids raised on 0% N; 150-0, first generation raised on 150% N and second generation on 0% N; 0-150, first generation raised on 0% N and second generation on 150% N; 150-150, first and second generations raised on 150% N. Bars with the same letter are not significantly different at the 5% level (Tukey HSD test). ANOVA ($P < 0.01$; $F = 17.3$; treatment df = 3; error df = 12).

Table 2. Cumulative effects of nitrogen fertilizer on intrinsic rate of increase (r_m), fecundity body length, and head width of aphids on rice

Percent N (first generation)	Percent N (second generation)	Mean $r_m \pm SE$	Mean fecundity $\pm SE$	Mean percent survival $\pm SE$	Mean adult body length $\pm SE$ (mm)	Mean adult head width (mm) $\pm SEM$
0	0	0.248 \pm 0.014a	0.801 \pm 0.112a	56.75 \pm 6.73a	0.883 \pm 0.020a	0.296 \pm 0.002a
150	0	0.245 \pm 0.024a	0.810 \pm 0.164a	57.25 \pm 11.58a	0.969 \pm 0.013b	0.296 \pm 0.002a
0	150	0.341 \pm 0.020b	1.860 \pm 0.274b	78.5 \pm 2.63ab	1.025 \pm 0.019b	0.300 \pm 0.000a
150	150	0.375 \pm 0.008b	2.394 \pm 0.177b	88.5 \pm 2.25b	1.030 \pm 0.020b	0.316 \pm 0.018a

Values in each column followed by the same letter are not significantly different at the $\alpha = 0.05$ level according to ANOVA and Tukey HSD mean comparison procedures.

quality of cotton aphids' own food plants. In contrast, we found that additional nitrogen in the parental diet of *H. setariae* on rice had no apparent effect on aphid survivorship, fecundity, and r_m , whereas the N levels of their food plant strongly affected these factors. Unlike *A. gossypii* on cotton (Nevo and Coll 2001), N levels had no effect on the head width of *H. setariae* on rice. Body length was affected by N levels of the food and the parental food plant, although no cumulative effect was detected. Given that plants receiving higher N applications absorbed more P, it is not possible from this experiment to separate the effects of N and P at the physiological level. We can, however, conclude that higher application rates of N fertilizer increases survivorship, fecundity, r_m , and body length of *H. setariae*.

The increased survivorship, fecundity, and r_m exhibited by *H. setariae* feeding on rice treated with high N applications could partially explain the observation that aphid outbreaks on rice occur primarily during droughts. Drought conditions change the metabolism of rice plants so that proteins are broken down more quickly and more soluble N is available to sucking insects (Wiggins and Williams 1955, Mattson and Haak 1987, Dale 1994). A further consideration is that aphids on high N diets are larger, so predators would consume fewer aphids to obtain the same biomass, as observed in some other predator-prey relations (Roger et al. 2000, Hoddle 2003, Aljetlawi et al. 2004). The increased fitness of aphids on high N diets, combined with decreased predation, could contribute to aphid population increases. In addition, during droughts, ants are able to enter fields and protect aphids from natural enemies. Ants are well known to tend homopterans, and in many cases, protect them from natural enemies (e.g., Way 1963, Tedders et al. 1990, Queiroz and Oliveira 2001, Kaplan and Eubanks 2002, Jahn et al. 2003). Of the 62 species of ants associated with rice fields, many are known to tend aphids (Way 1963, Way et al. 1998). Indeed, the absence of natural enemies is generally thought to be the reason that population eruptions of aphids are common on greenhouse rice but rare in rice fields.

Possibly high N applications also contribute to higher aphid survivorship by interfering with the rice plants' natural defense mechanism. Orozco-Cardenas and Ryan (1999) discovered that a wide variety of plants, including rice, produce hydrogen peroxide when wounded, presumably as a defense against further damage by phytophagous pests. Of 18 plant spe-

cies from six families tested, only legumes did not produce hydrogen peroxide. They speculated that this may be related to some characteristic of the legume's nitrogen-fixing systems. Perhaps excess N interferes with rice's ability to produce hydrogen peroxide, leading to increased aphid feeding and survivorship. Nitrogen deficiency increases production of defensive chemicals in a variety of plant species, e.g., tobacco (Ohnmeiss and Baldwin 1994) and maize (Schmelz 2003). In celery, the addition of high levels of mineral and/or organic nitrogen fertilizers significantly decreases the production of volatiles that may be associated with plant defense (Van Wassenhove et al. 1990).

Given the association of aphid outbreaks with drought in rice fields, it is unrealistic to expect that reducing N applications would be sufficient to prevent explosive increases in aphid abundance. Urea is only applied to paddy rice when there is standing water in the field. If rain ends a drought, this usually ends aphid outbreaks as well. For rice grown in greenhouses, however, avoiding excessive urea applications could prevent or mitigate aphid outbreaks.

The strong effect of parental nutrition on cotton aphids may serve to dampen the effect of short-term fluctuations in host quality on aphid performance (Nevo and Coll 2001). For *H. setariae* on rice, we observed that host plant N levels, but not parental nutrition, affected r_m and fecundity. This may be because the *H. setariae* populations around rice fields in Luzon move primarily between wild rice and domestic rice. Wild rice is found on uncultivated land and would tend to have fairly stable nutritional value at a given location. It would be important for *H. setariae* to respond rapidly to high N levels when they find themselves on domestic rice. If this explanation is correct, aphid subpopulations living on plants subject to short-term N fluctuations should be more likely to exhibit the effects of parental nutrition on r_m and fecundity.

Acknowledgments

We thank R. Aquino, E. Rico, and R. Abuyo for maintaining aphid colonies and rice plants; N. Bunyi for secretarial support; R. Buresh for confirming the soil type used in this experiment and recommendations on fertilizer rates; V. Bartolome for advice on statistical analysis; S. Peng for advice on measuring N; R. Chavez and M. C. Ong for spectrophotometry; and Y. Chen, R. Velasco, and K. L. Heong for helpful comments.

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Received for publication 9 December 2004; accepted 10 May 2005.
