



Scirpophaga incertulas (Walker) (Lepidoptera: Pyralidae) and deepwater rice – an integrated view

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The role played by the lepidopteran yellow stem borer, *Scirpophaga incertulas* (Walker) in the life cycle of deepwater rice (*Oryza sativa*) is controversial. The major question is whether or not larval feeding in the elongated stems is damaging and if so, although no visible symptoms can be observed, leads to loss of yield. Drawing on evidence from entomological and agronomic studies, especially in Bangladesh and Thailand, this paper shows that there is little or no correlation between early- or mid-season borer infestation and yield; that stem density always declines from a pre-flood maximum, irrespective of borer infestation; how late-season infestations can lead to serious crop loss; and, how a promising concept for strategic timing of insecticide application was developed and tested. Copyright © 1996 Elsevier Science Ltd

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Deepwater rice, *Oryza sativa*, is grown in a vast area (over 5.5 million ha) of South and South-East Asia, where seasonal flooding of 1–3 m depth occurs, and is the staple food for many millions of people. It has the remarkable characteristic of being able to respond to rising flood waters by rapid stem elongation. During the past 18 years, there has been considerable research into the cultivation of this unique crop and the constraints which affect its yield. Important among the production constraints is the feeding activity of larvae of the yellow stem borer *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae). There is controversy, however, about how serious an impact this pest has upon the crop and when during the growing season (approximately March to November) that impact is greatest. On one hand is the belief that *S. incertulas* is the key pest with severe impact throughout the crop life cycle (Catling and Islam, 1995, *et ante.*). On the other hand is the wider approach taken in this paper, where all available evidence from entomological and agronomic research in Bangladesh and Thailand, has been reviewed and an alternative, integrated conclusion reached. It is shown that while *S. incertulas* can contribute to the annual decline in tiller numbers, from a peak around the time of onset of flooding, the decline takes place even in seasons when the pest is effectively absent, and is a wholly normal event emanating from primarily agronomic factors. Late season infestation, when larval feeding affects the terminal, panicle-bearing internode, however, can lead to major crop loss.

Evidence from entomological studies

All researchers agree that larval feeding in deepwater rice can be differentiated into three plant growth phases. Two phases, in the young plants before the onset of the seasonal flooding and in the uppermost internodes of the post-flood flowering plants, show the attack symptoms common to ordinary paddy rice. These are deadhearts and, only at maturity, whiteheads (unfilled panicles). The early-season numbers of stem borers are usually low and significant loss of tillers at that time is uncommon. The late-season infestation in some years can be very high and can cause serious crop loss, up to 80% of the yield (Taylor, 1988).

It is the effect of *S. incertulas* larval feeding on the middle, elongation phase, when the plant is growing very rapidly in response to inundation, that is controversial. From studies of stem borers in deepwater rice in Bangladesh, Catling considered that feeding by *S. incertulas* larvae within elongated stems must cause yield loss (Catling, 1979). This view was further expressed by Catling, Islam and Rahman (1988), who decided that as evidence of *S. incertulas* activity (frass, exit holes, feeding damage and pupal skins) can be found in up to 40–50% of submerged elongated stems and because those stems commonly are found to have decayed there must be associated yield loss.

The assumption underlying that decision was that larval feeding causes 'damage'. This, however, was not accepted by van Emden *et al.* (1979), who commented on the failure to demonstrate 'what would appear to be

self-evident – that panicle weights of affected stems should be lower than those of unaffected stems' and emphasised the need to establish 'the true host-plant relationship leading to yield loss'. Resolution of the issue has added importance because of the modern practice of producing simple guidelines to enable pest and disease symptoms to be identified, incidence to be assessed, and, that incidence to be used to predict potential yield loss as a basis and justification for implementing control procedures. Thus, a research programme specifically targeting the 'damage' issue was started in 1981 (Taylor, Alam and Razzaque, 1982).

Damage to individual stems

The question of actual physical damage due to the larval feeding had been investigated by Catling (1981), who considered that most of the stem damage is not evident in the form of deadhearts or whiteheads. Preliminary investigation had revealed that *S. incertulus* larvae chew into the parenchyma intermittently along the stem lumen but the damage is seldom deep enough to reach the inner ring of vascular tissue. Greater importance was attached to the destruction of the nodal septum as the larva moves from one internode to another. It was noted that 2–4 septa may be destroyed and that this destruction was thought to affect the normal functioning of the vascular system, probably by interfering with the translocation of assimilates.

In 1983, in order to make a direct evaluation of the impact of larval feeding, some 200 externally healthy stems were taken from the field in Bangladesh. The bases of the stems were immersed in a weak solution of aniline blue dye for 2–3 days and then the stems were longitudinally or transversely sectioned and examined with a stereomicroscope. First, the observations showed that at each node the vascular tissue forms a dense continuous ring connecting all the incoming and outgoing vascular bundles, and that the septum is made up solely of undifferentiated pith. In the hollow internodes the conducting system is made up of two rings of vascular bundles. In several instances, *S. incertulus* larvae were found actively feeding within the fourth and fifth internodes down from the stem apex. Most of the feeding was upon undifferentiated ground tissue and it was only the inner ring of vascular bundles which was notably affected. It appeared that the nodal ring of vascular tissue ensures that there is no interruption of vascular conduction above internodes in which a larva has been feeding and, thus, it was felt that the passage of a larva through the septum has no discernible detrimental effect on translocation. Moreover, as the pith clearly is soft tissue, the septum is unlikely to contribute to the physical strength of the node; which, moreover, has the properties of a cylinder. In a number of stems evidence of earlier larval feeding in lower internodes was seen, in all these cases the dye had been taken up by nodal roots above the damaged internodes and the upper stem conduction seemed wholly normal. Finally, in two stems with deadhearts, it was seen that feeding in the narrow terminal internode, with no significant lumen, had resulted in almost all the tissue,

including both rings of vascular bundles, being eaten (Taylor 1984, 1988).

Further work in Bangladesh was undertaken by Islam (1990), who decided to investigate the fate of tillers right through the period of inundation. Field findings were that about 44% of tillers marked before flooding failed to elongate successfully and an *in vitro* experiment using pot grown plants placed in metal tanks, with flooding up to only 100 cm (the lower limit for true deepwater rice), gave results indicating that stems infested with *S. incertulus* larvae were less likely to elongate successfully. Islam decided that larval feeding equates with 'damage', claiming that there is a negative effect of stem damage on the panicles of apparently healthy stems, and also that, 'In elongating and elongated rice stems, *S. incertulus* larvae mainly concentrate their activities in the hollow internodes and usually not at the growing point, therefore damage symptoms are seldom visible. For this reason the past importance of this pest was underestimated.'

Reverting to the anatomical question, but without providing further experimental evidence, Catling (1992) has since described the lumen itself as 'the preferred feeding site of the yellow stem borer' and has written that 'the lumen is interrupted at the nodes by a plug of undifferentiated tissue'. Thus, it seems clear that he has drawn back from believing that the destruction of the nodal septum could affect the vascular system. Catling and Islam (1995) have additionally commented that there was at all times an overabundance of soft stem tissue for larval feeding.

Damage to the whole crop

In Bangladesh in 1982, and with the co-operation of agronomists, an exhaustive assessment of 84 separate field trial treatments, involving dissection of over 25,000 deepwater rice stems taken at harvest, showed that there was no consistent correlation between the level of infestation of elongated deepwater rice stems and the yield of the crop. The range of field trials included factorial layouts (2 fertilizer levels \times 2 planting methods \times 2 varieties \times 8 randomised complete blocks, at each of 5 sites), transplanted variety tests (9 varieties \times 4 randomized complete blocks \times 3 sites) and fertilizer response tests (range of agronomic practices and varieties at each of 4 sites). Twenty-five stems were taken at harvest, from each of the many replicates, and dissected to determine the levels of borer infestation. Infestation ranged widely, being anywhere from 16–72%, with a CV of around 40% between the replicates of any one treatment. The CV for yield, tended to be somewhat lower, around 25% being typical. The correlation coefficients between yield and infestation were calculated for all the various treatments and on both a between-treatments and within-treatments basis. From the results of the factorial trials only one variety at one site gave a significant correlation, and that was positive, indicating higher infestation leading to higher yield ($r = 2.169$, t at 5% level = 2.04, d.f. = 30). From the variety trials, one variety showed a significant negative correlation between the collective data for infestation and yield at all three sites, indicating higher infestation led to lower

yield ($r = -0.69$, $t = 3.018$, t at 5% level = 2.23, d.f. = 10). Testing the individual site results for each variety (27 in total) gave six negative correlations and three positive correlations; of these two were significant, one positive and one negative ($r = -1.00$ and $r = 0.99$ at 5% level, $t = 4.30$, d.f. = 2). Finally, forty correlation coefficients were calculated from the fertilizer trials and only two were significant, both being positive. Clearly, no genuinely consistent link could be shown between infestation level determined on a whole stem basis and yield (Taylor, 1988).

On a smaller scale, examination of every plant in field plots of two rice varieties revealed that significantly greater grain sterility occurred only when the terminal (panicle-bearing) internode was infested in one variety (terminal node infested on 132 stems, with 51% grain sterility; 122 other stems with 28.5% grain sterility), and only when an infestation was in the top four internodes in the second variety (47 stems with 36.2% grain sterility [top internode only 21 stems with 55.7%]; 547 other stems with 16.0% grain sterility). In both varieties whiteheads were almost wholly restricted to stems with infestation of the terminal internode. A specific examination of whitehead-bearing stems ($n = 205$) showed that almost all of the grain loss was associated with infestation of the terminal internode (94%), or of, at least, one of the top six internodes (Taylor, 1988). Very similar results were obtained in 1985 by Islam (1990).

By recording from flood peak through to crop maturity, Islam (1990) further demonstrated the vulnerability of the crop to attack at this late stage, when most elongation was complete. The major losses caused by stem borers were deadhearts and whiteheads (combined loss being 8% for one variety and 24% for another). Although he noted that there was some loss on 'damaged but apparently healthy stems', the data show that this was true of one variety (3% reduction in panicle weight) but not of a second (0.7% greater panicle weight).

In season-long studies (in 1982–1985), Islam (1990) made weekly records of stem density and borer infestation. He interpreted graphs of the data from peak flooding to crop maturity in each of the years as appearing to show some negative relationships between borer damage and stem densities. Except for the year 1984, however, the infestation levels were generally low (most being less than 3.0%) and arsenic transformations were used in plotting the infestation. The calculated correlations, R^2 , also were low and, thus, the level of accuracy may have been too low to be reliable (Gomez and Gomez, 1976). Moreover, given that the population of *S. incertulas* larvae is finite in any one brood and that a larva will attack only one stem, the higher the number of stems the lower the proportion that can be infested. This was found to be problem in reverse in the early-season trials in 1981, where the number of stems was increasing and so masked any beneficial effects of insecticides (Taylor, Alam and Razzaque, 1982).

Despite the contradictory evidence, Islam (1990) wrote, 'About half the stems damaged by *S. incertulas* showed visible damage symptoms (deadhearts) before flooding and only 10% following flooding', and, later, 'In the field 58% of the stems decomposed in flood

water, of which direct losses due to stem borer as deadhearts and whiteheads (5%) and rats (4%) were low. A significant proportion of the remaining 49% loss was probably due to the loss of borer damaged but apparently healthy stems in floodwater.' Referring to his season-long studies, he claimed that — 'Monitoring of stem densities and borer damage levels for 4 years also revealed that borer damage was the major and consistent factor in stem loss'. He did not explain how the decline from 300–400 stems/m² down to around 200 stems/m² in 1982, and from 200–300 stems/m² down to around 100 stems/m² in 1985, could be due to infestation levels of only 3–11%.

Evidence from insecticide experiments

A summary of some trials in which several methods of application and timing of insecticides in farmers' fields were tested in Bangladesh and Thailand, was given by Islam, Catling and Pojananuwoong (1988).

Whole-season spraying

The earliest attempts were field experiments in Bangladesh in 1978 and 1979, in which an insecticide, diazinon, was applied at regular intervals throughout the season in the expectation that an insect-free crop would result, and so a direct determination of crop loss could be achieved (Catling, 1981; Catling, Islam and Patrasudhi, 1987). This work was accompanied by various unsuccessful small-scale experiments (Islam, Catling and Pojananuwoong, 1988). In summary, Islam, Catling and Pojananuwoong (1988) described the results as 'unexpectedly poor'. This negative view appears to contradict that expressed previously by Catling, Islam and Patrasudhi (1987) and examination of the original data (in Catling, 1981) shows that a yield saving of 21.1% was achieved in 1978, and 2.8 and 13.8% in 1979. This yield saving was of the same order as that achieved by spraying solely in the late-season (see below).

The term 'yield saving' is favoured by the present author as more realistic than 'yield increase' when the results of crop protection measures are expressed. For instance, while the use of a fertilizer may well promote grain production; with very few exceptions, insecticides do not act to stimulate yields but only prevent grain loss due to the action of a pest. Thus, results are better expressed from the formula:

$$\left(\frac{\text{yield in insecticide treated} - \text{yield in untreated}}{\text{yield in treated}} \right) \times 100 = \text{yield saving \%}$$

Early-season spraying

An entirely separate study examined the possibility of spraying at different times in the season. First was an investigation of the use of early-season (pre-flood) insecticide sprays. In 1981, eleven insecticides were used in a field trial, with four applications of each (during May and June). Several insecticides clearly reduced the incidence of deadhearts but the reduction was not reflected in the yields obtained from the various treatments. The experiments and a parallel trial

in a deepwater tank, however, contributed to the development of a population dynamics model (Taylor, Alam and Razzaque, 1982). In 1982, very low early-season moth populations led to abandonment of plans to include insecticide spraying among the treatments in multi-factorial trials of a package of otherwise agronomic practices.

Further work on early-season spraying, also in Bangladesh, was undertaken in 1983, when one half of each of two fields in a stem borer hot spot area was sprayed with monocrotophos at 250 g ai/ha with a knapsack sprayer. The unsprayed half of each field served as a check treatment. Stem population density and deadhearts were assessed by quadrat counts, and stems were dissected for borer damage. Field 1 was sprayed at basal tillering stage, on 8 June at the time of peak moth activity. One week later, the spray had reduced deadhearts from 9.2 to 1.8/m², but the number of damaged stems was not affected (21 and 23%). Field 2 was sprayed on 15 June, one week before flooding, when deadheart density was 12–13/m². Three weeks later, at a water depth of 100 cm, the two halves of the field did not differ in stem population or damage (Islam, Catling and Pojananuwong, 1988).

Late-season spraying

The development of a population dynamics model (Taylor, Alam and Razzaque, 1982) led to the evaluation of late-season sprays, applied from a boat, in 1982. Plots 10 m wide in farmers' fields were matched for plant stand and condition and then sprayed 1–3 times from August to October according to the peaks of moth activity, as monitored by using light traps. Monocrotophos at 250 g ai/ha was sprayed with a motorized mistblower from a boat. Both stem infestation and whitehead numbers were reduced significantly, and yield estimates showed significant savings (7.3 and 10%). The latter was similar to the reduction in whitehead numbers, which in one instance was achieved with a single strategically-timed application. Moreover, the yield saving was of the same order as had been achieved by the 1979 series of 20 applications, see above (Taylor and Islam, 1984; Taylor 1988).

In 1983, the late-season tests were repeated by Islam, this time using five fields of different genotypes. Again, one or two sprays significantly reduced the percentage of stem damage, whiteheads and grain sterility, and increased the panicle density, grains per panicle, and yield. One spray was associated with a reduction in stem damage from 48 to 37%, a yield increase of 8%, and a cost:benefit ratio (C:B) of 1.85; whereas with two sprays the stem damage was reduced to 22% and there was a C:B of only 1.30. The results led Islam, Catling and Pojananuwong (1988) to conclude that, 'It appears that one well-timed spray was better than two or three poorly timed ones. Thus, in Bangladesh, a single spray in the critical period from late August to early September at the time of the fifth seasonal moth peak can be tried.'

Summary of spraying experiments

Overall, it seems that Islam, Catling and Pojananuwong (1988) may not have appreciated the real significance of

the studies on critical timing. For instance, they described the results from the season-long spraying trials as 'unexpectedly poor', but this remark seems to have been made in hindsight, as it was not what was reported originally (see above). Actually, the yields from the sprayed fields were better than the unsprayed but by no more than was achieved with the critically-timed sprays (Taylor, 1988). The very fact that the latter spraying schedule yielded results which could not be bettered by season-long applications is strong evidence that the mid-season, elongation phase is not affected in any crucial manner by *S. incertulus* larvae.

Other entomological evidence

Singh *et al.* (1988) reported studies on stem borers in deepwater rice in Bihar, India. Field surveys showed stem infestation averaging 51.2% (range 36–64%) and whiteheads averaging 10.3% (range 10–44%). They did no statistical analysis, but (by extrapolation from their detailed table) there was no correlation between stem infestation and whiteheads (e.g. infestation 56% and whiteheads 4%; infestation 52% and whiteheads 44%; infestation 60% and whiteheads 4%; infestation 64% and whiteheads 25%). Screening of 92 DWR land races in 1985 did show some increase in the average number of larvae and average whitehead incidence with increasing infestation; but even 81–100% infestation gave only 10.2% whiteheads, whereas 21–40% infestation gave 6.8% whiteheads.

Shepard (1990) described attempts to simulate damage by *S. incertulus* in the high yield conventional rice variety, IR36, by cutting and removing 15 and 30% of the tillers at 50, 69 and 84 days after seeding. The early-season detilling had little or no effect on resulting yields but detilling at high levels during panicle initiation and grain-fill stages significantly reduced yields. Similar work on another high yielding variety, IR64, also showed that early season defoliation did not affect yield. In these varieties, however, there is no growth stage which is directly comparable to the mid-season elongation stage of deepwater rice.

Evidence from crop biology studies

A study of factors affecting crop yield cannot be effective unless all aspects are taken into consideration, and entomologists need to pay close attention to the biology of the crop itself. This need for an integrated approach has drawn considerable recent support from Trumble, Kolodny-Hirsch and Ting (1993).

Taylor (1988) tabulated data for 6 years (1977–1982) on the overall growth pattern of deepwater rice, notably the normal changes in tiller numbers as the season progresses. The data showed that, whereas the drop in tiller numbers was consistent in all 6 years, the level of stem borer infestation was very low until the late season (when elongation was complete) in 1979 and 1982. Catling and Islam (1995), apparently drawing on the earlier report by Catling (1981), show the borer populations in 1977–80, commenting specially on the very low larval numbers in 1979 and how only 5% of stems were damaged. However, they gave no informa-

tion on numbers of healthy tillers apart from mentioning that 'there is a normal decline in plant stand during the flooding period'. Islam (1990) had presented further data from 1983 to 1985, showing the usual pattern of decline in tiller numbers, and stated also that stem borer damage was low up to September except in 1984.

Although Taylor (1988) gave some information gleaned from agronomic studies, research by Akita on the effect of plant population density in rice has recently come to light (published in Japanese but reviewed by Squire, 1990). The key and crucial fact is that total above-ground dry-matter, vegetative dry-matter and grain dry-matter all reached a maximum at around 30 plants/m², with grain dry-matter actually declining somewhat from the peak at that population density. As Squire writes, 'At a higher population, when some mingling occurs, more of the resources are used, but each plant "competes" with its neighbours, and uses a smaller fraction of the resources.'

Other deepwater rice agronomists have now examined aspects of the plant populations. In Bangladesh, Haque and Hossain (1988) presented various graphs of changes with time, including a decline from 10 tillers/hill at flooding to 4 tillers/hill at 90 days, then remaining unchanged to maturity. Nodal tillers increased from almost nil to 6/hill at 90 days, dropping to 4/hill at maturity but many did not produce panicles. Hoque and Nasiruddin (1988) examined the effect of population density on yield and agronomic traits of deepwater rice under field conditions in both pure and mixed stands. The initial densities were 50, 100, 150, 225 and 350 plants/m². A linear increase in tillering occurred at all densities up to the pre-flood stage. The increases were 6 tillers/plant (88% increase) for the low density, 4 tillers/plant for the medium density and 1-2 tillers per plant (11.42% increase) for the high density. Optimum initial density for DWR was 100-120 plants/m². Tiller number decreased at peak flooding by 13.6% at low, 21.4% at medium and 20.2% at high density, but they remarked that it was not clear from this study which tillers died during flooding. They concluded that, 'Although the initial pre-flood and peak-flood population densities varied significantly, panicle densities showed insignificant differences and stabilised at around 200 in each density at maturity. Therefore, yield differences among densities were insignificant. The indication is that initial densities of 50-350 seedlings/m² have no effect on yield.' Jupp and Rahman (1988) studied the seasonal growth and yield of fertilized deepwater rice at two floodplain sites. They examined a wide range of growth components and factors in farmers' fields in 1986. Basal tiller density peaked at the end of June (being highest, >400 tiller/m², with both high levels of fertilizer, 90 kg N/ha and 60 kg N/ha) but by mid-September (maximum flood) had dropped to around 180 tillers/m², and then there was no further decline, except for a small drop in the unfertilized plot. A late flood resurgence affected all yields and for all treatments these were around 1.7 t/ha. They commented that 'the normal decline in tiller density over the season was also apparent' (Vergara 1985).

In Thailand, Kupkanchanakul *et al.* (1988) carried out a study of growth patterns in different depths of water (150 and 20 cm). Initial tiller levels at 30 DE

(days after emergence) were around 430/m² in both depths, declining steadily until at 170 DE tiller numbers were 167 and 134/m² respectively, and then remaining steady. Grain yield was 2.3 t/ha in the shallow water and 2.1 t/ha in the deep water. Deep water tended to reduce panicle numbers/m², because tiller number was reduced, but had no other effects on yield components. Kupkanchanakul, Vergara and Robles (1988) and Kupkanchanakul, Kupkanchanakul and Roonun (1990) studied the effect of time and frequency of leaf cutting for herbage on grain yield of deepwater rice. Leaves were cut at the collar of the last fully developed leaf at different times after emergence. Comparison with an uncut control showed there was no effect on yield when leaves were cut at 40 and 70 days after emergence. The cutting of leaves at 100 days after emergence, however, led to a significantly higher yield. This the authors attributed to an increased panicle number, possibly due to an observed reduction in plant height.

Conclusions

It is clear that the deepwater rice crop reaches a peak plant population level, measured by tiller numbers, at around the time of the onset of flooding. The peak is reached as a combination of favourable levels of temperature and moisture (the pre-monsoon rains) and of relatively low plant heights, with little competition between tillers for light. The subsequent decline in plant population is primarily a natural phenomenon inherent in the biology of the crop itself.

Tiller numbers *always decline* because of normal competition between plants, and in deepwater rice the optimum at maturity seems to be around 150 tillers/m². When higher numbers of panicles are attained the panicle size is lower and no improvement in yield is achieved. The rotting of the submerged parts of elongated stems is a normal feature which does not affect nutrient uptake (nodal roots are a feature of deepwater rice) and does not affect crop anchorage (the stem is fibrous); additionally, even if the stems do break free from the lower parts, yields are little affected (Taylor, 1988).

There is evidence that when larval numbers of *S. incertulas* are high in the period of early flooding the decline in tiller numbers may be accelerated, but the emphasis should be on the term 'accelerated'.

In view of all the foregoing, there seem to be good grounds for the argument that in the elongation phase the relation between *S. incertulas* and deepwater rice is that of a near perfect host-parasite relationship. Feeding activity of the borer larvae within elongated stems does not cause damage which can be translated into crop loss. This view gains support from Litsinger (1991), who reviewed most aspects of yield loss and crop loss in rice. He dealt mainly with conventional paddy rice and did not have much on either deepwater rice or yellow stem borer, but it is significant that he remarked 'the principal effect of early stem-borer attack is to kill tillers, but as these are produced in excess, considerable compensation by the crop is possible', and, also, 'there has been a tendency to equate crop injury with crop loss or to base crop loss assessments on untested

assumptions, making no allowance for compensatory growth'.

The counter argument that 'larval feeding equals damage' stems from Catling (1979), who found from surveys of 320 farmers' fields in 1977 and 1978 that 60% of all fields had outbreaks at harvest. This was confirmed by Catling, Islam and Patrasudhi (1987), who further stated – 'it is generally accepted that YSB is the major pest of DWR in the region because it consistently causes heavy stem damage every year (Catling, Islam and Patrasudhi, 1984/5)' and concluded 'but despite many attempts, there is no control measure in sight for the severest pest of them all – YSB'. Catling and Islam (1995) note that their work in 1977–1980 led to 'a series of further investigations over the last 15 years which were reviewed by Catling (1992)'. In that review, it was claimed that the best results in Bangladesh were obtained with insecticides timed to control Brood 5 moths and applied with a motorized knapsack sprayer from a boat. This was credited to Islam, Catling and Pojananuwong (1988) and it has since been stated that use was made of 'a tentative action threshold of 10% damaged stems at the booting to flowering stage' (Catling and Islam, 1995).

However, Catling (1992) made no reference to the detailed and exhaustive crop loss studies in Bangladesh during 1981 and 1982 (Taylor, Alam and Razzaque, 1982; Taylor and Islam, 1984; Taylor, 1984, 1988). In fact, it was the population dynamics model developed in late 1981 (Taylor, Alam and Razzaque, 1982) which underlay the innovative approach in the 1982 experiment. In that, the time of spraying was determined by an upsurge in the numbers of female *S. incertulas* detected by light-traps (i.e. the emergence of Brood 4 adults) and the experiment did not involve any so-called 'action threshold'. The suggest that a threshold could be determined by stem dissection is misleading because most conventional insecticides have a contact action and thus are ineffective against internal parasites. Spraying, therefore, will not reduce any existing infestation. The level of stem infestation is a measure of past events and is not a reliable indicator of further attack, particularly as *S. incertulas* is a relatively strong flier and can be an invasive pest. Light traps can reveal that females are emerging or arriving and thus a spray directed at hatching larvae (from egg masses laid on the leaf surface) can be a technically effective control measure. This was demonstrated in 1982 and reported by Taylor and Islam (1984).

Finally, if correct, the status of *S. incertulas* as a successful parasite of deepwater rice has a broader significance for students of evolutionary ecology. Chowdhury and Zaman (1970) considered the deepwater rice varieties of *O. sativa* as being descendants of the most prevalent wild rice species of Bangladesh, *O. sativa* var. *fatua*. The good capacity of deepwater rice for ratooning, that is continued generation of tillers after the harvest of the first crop (shown in an investigation which started in 1983; Bene, 1988), also indicates an affinity with the ancestral, perennial, *rayada* varieties of floodplain rice. Ratooning could also enable the plant population to withstand high grain sterility caused by the larvae of the final *S. incertulas* brood of the normal deepwater rice season. Thus, the grain loss may be a major problem for the farmer but it

is not necessarily devastating for the deepwater rice. In a much earlier example of the pest problems which have faced the high-yield varieties of the 'Green Revolution', the historical selection of paddy rice varieties with shorter, narrower stems could have led to inherently greater damage to vascular tissues by larval feeding, and so led to deadhearts throughout the growth of the crop.

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