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Rice Insects: The Role of Host Plant Resistance in Integrated Management Systems

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ABSTRACT Insects are among the most important abiotic and biotic constraints to rice production. National rice research programs are in various stages in the development and implementation of integrated pest management (IPM) stratagies for rice insect control. Among the various control tactics, insect resistant cultivars are sought as the major tactic in rice IPM. Through the activities of interdisciplinary teams of scientists significant progress has been made in the development and release of insect resistant cultivars to farmers. Because of its compatibility with other control tactics insect resistance has proven to fit well into the IPM approach to rice insect control agents and minimize the need for insecticide applications. The development of biotypes which overcome the resistance in rice plants has been a significant constraint in the breeding of rice for resistance to insects. Most notable examples in Asia are the green leafhopper, *Nephotettix virescens*, brown planthopper, *Nilaparvata lugens* and the Asian rice gall midge, *Orseolia oryzae*. The current breeding stratege is to develop rice cultivars with durable resistance on which virulent biotypes cannot adapt. In spite of the significant progress made in the breeding of insect resistant cultivars there are still numerous important rice insect species for which host plant resistance as a control tactic has not been fully utilized. Advances in biotechnology provide promise of solving some of the problems that have limited the use of host plant resistance as a major tactic in the integrated management of rice insect pests.

KEY WORDS Rice insects, varietal resistance, integrated pest management, biological control, cultural control, chemical control

Rice is a crucial element in the staple food economies of many countries and serves as a major source of calories for 40% of the world's population. Rice is grown in divers environments from 530 N latitude in China to 40° S latitude in Central Argentina. The environmental conditions under which rice is cultivated consists of (1) irrigated, (2) rainfed lowland, (3) deepwater, (4) uplands, and (5) tidal wetlands (Khush 1984). Most of the world's rice is produced in tropical Asia where the human population is high and per capita income and rice yields are low. howere, demand for rice in Africa is increasing at a faster pace than production increases as a result of a dietary shift from conventional foods. Indeed, the index of per capita food production has been decreasing in sub saharan Africa while it has increased in Asia and Latin America(Fig. 1). Average rice yields vary from 1 ton/ha in

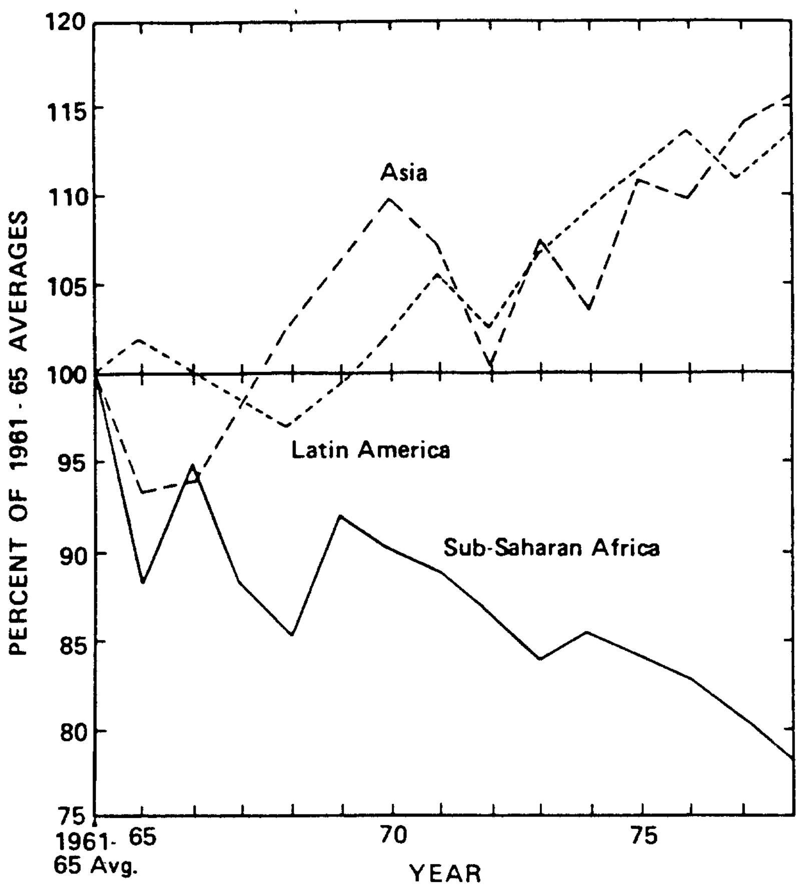

Fig. 1. Index of per capita food production (Heinrichs 1988a).

many West African countries to 6 tons/ha in Japan, South Korea, and the USA(IRRI 1988). Most of the world's rice production occurs in tropical Asia in irrigated and rainfed lowland fields.

There are numerous abiotic and biotic stresses that adversely affect crop yields (Heinrichs 1988a). In Asia typhons and floods are of importance while in West Africa adverse soils and drought are major factors. Rice pests are constraints throughout the rice growing world. Estimates of losses due to insects are certainly "estimates" at best as the losses vary greatly in space and time and are difficult to determine even under controlled conditions of experiment stations. Cramer (1967) and Panhak and Dhaliwal (1981) report that insects in Asia cause more than 30% yield losses. However, Shepard et al. (1990) consider this to be too high. Based on a survey of 50 rice entomologists in 11 Asian countries they estimate a yield loss of 19%.

The rice plant is attacked by more than 100 insect species throughout the world. However, within a given region only about 20 species occasionally cause economic damage (Pathak 1968). Major pest groups are the stem borers, leafhoppers and planthoppers, defoliators, and a complex of bugs that feed on developing grains. Figure 2 summarizes the relative importance of the major pests in several Asian countries.

In spite of the large number of insects that attack rice few insect outbreaks occur in tropical Asia, except where insecticides are indiscriminately used. Increased rice insect outbreaks, especially that of the brown plant hopper, *Nilaparvata lugens* are the result of the overuse of resurgence-inducing insecticides (Heinrichs & Mochida 1984). There is clearly a need to develop and implement effective, environmentally safe, and economically sound rice insect management systems. This is one of the greatest challenges facing rice scientists throughout the world. National rice research programs are in various phases of the development and implementation of IPM srategies. Management stratagies consist of various mixes of chemical control with insecticides, cultural controls, biological agents (parasites, predators and pathogens) and the planting of rice cultivars with genetic resistance to insects (Heinrichs 1992). Resistant cultivars are sought as the major tactic in the integrated management of insects. Resistance is essentially free to the farmer, is environmentally sound, and is generally compatible with other control tactics; chemical, cultural and biological control.

Because of their unique advantages, insect resistant cultivars are of special value under the conditions existing in developing countries and as a result have become an important component of most rice breeding programs. The major rice breeding objectives of Asian countries in order of priority are (1) yield potential, (2) grain quaility, (3) growth duration (4) disease resistance, and (5) insect resistance (Hargrove & Cabanilla 1985). Breeders in 10 Asian countries reported that 46% of the crosses made included insect resistance as a breeding objective. Interdisciplinary teams of entomologists working with plant breeders and problem area scientists have in certain regions of the world been successful in developing rice production systems with increased levels of resistance/tolerance to abiotic and stresses. The progress achieved in the breeding of high yielding cultivars with resistance to multiple stress has contributed greatly to the success of the green revolution. Resistant cultivars have increased the profitability of rice production, minimized the safety risks to farms, and contributed in a significant way to a more healthful environment.

The development of pest resistant cultivars has until recently been the "missing link" in integrated pest control. It is only since he 1960' that breeding for insect resistant rise cultibars has been a major component in rise research programs. Dr. M.D. Pathank, the first entomologist to be employed by IRRI is largely responsible for the tremendous progress in breeding for insect resistance that has occurred in rice in the last three decades. Dr. Pathak was recognized for his contributions to the field of host plant resistance at the Biennial Plant Resistance to Insects Workshop in Indiana, USA, in February 1992. Trained by the grand master of host plant resistance, Dr. R.H. Painter, Dr. Pathak is indeed the "father of host plant resistance in Asia" and it is with inspiration from him, during my 10 years at IRRI, that I write this paper. Dr. Pathak has laid foundation for most of the topics that I will review.

HOST PLANT RESISTANCE IN RICE IPM

Screening of rice cultivars for resistance to insects at IRRI began in 1962 shortly after Dr. Pathak returned to Asia after completing his PhD. under Dr. Painter at Kansas State University. Dr. Pathak took up the challenge given to him by IRRI's first Director General, Dr. R.F. Chandler, and the rest of the story is history.

Screening at IRRI began with an evaluation of a portion of the world collection of rice for resistance to the yellow stem borer *Scirpophaga incertulas* and the striped stem borer *Chilo suppressalis* . As is the general case with crop borers, only cultivars with moderate levels of resistance were identified.

In 1967 Dr. Pathak began the program of screening for resistance to the brown planthopper and the green leafhopper *Nephotettix virescens.* This screening identified a number of cultivars with high levels of resistance and their discovery created a great deal of interest and insect resistance became an important component in many rice breeding programs in Asia, one of which is the highly successful Korean rice breeding program.

Insect resistant cultivars have been integrated into rice pest management systems throughout the world but most effectively in Asia. A paradigm is that of Indonesia where the brown planthopper cre-

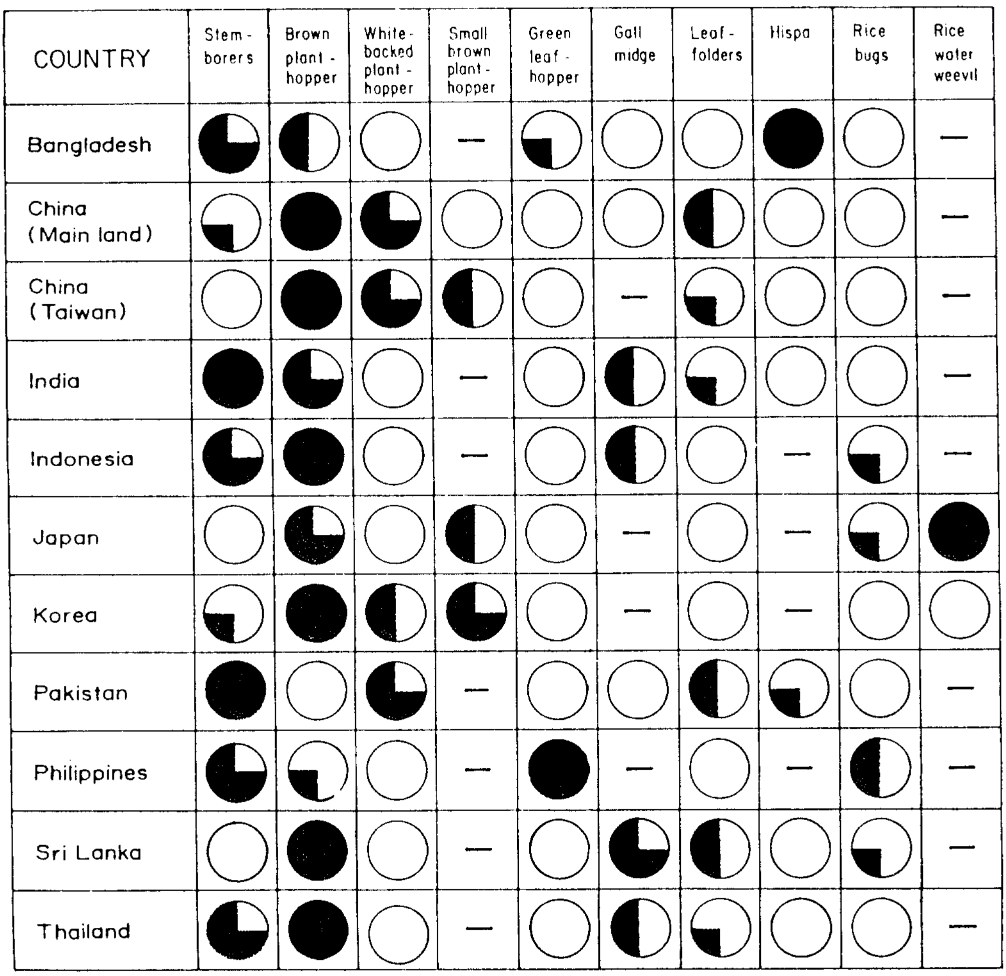

Fig 2. Status of insect pests of irrigated rice in Asia (compiled from data obtained from 50 rice entomologists in Asia). Shaded areas within the circles indicate the relative importance of the insect. A dash indicates the absence of the insect in a given country (From Shepard et al. 1990).

ated havoc for a number of years in the 1970's and 1980's. As a realization of the fact that the indiscriminate use of insecticides is the primary cause for brown planthopper outbreaks in tropical Asia, through insecticide-induced resurgence of populations(Heinrichs & Mochida 1984), the Government of indonesia took bold steps to put into effect a national policy of IPM. The policy was officially established through Presidential Instruction. No 3/1986 by President Suharto. The policy established the basis of a sound IPM approach to rice insect control in Indonesia which integrates the judicious use of insecticides based on ecological information, with insect resistant cultivars, biological controls and cultural practices.

Indonesia is concerned about its environment and has taken bold and innovate steps to preserve it. A cornerstone of the Indonesian rice IPM Program is the use of insect resistant cultivars in a mix with other control tactics.

This is certainly a means to minimize pest diversity and to maximize the effect of biological control agents.

Biological Control and Host Plant Resistance

Although insect resistant rice cultivars an adverse effect on natural enemis, because these cultivars lower the prey density, they are, for the most part, considered to be compatible with biological control. Insect resistant cultivars have a distinct positive effect on natural enemies, especially parasites and predators, by minimizing the need for the application of insecticides which are toxic to them.

Complexes of biological control agents have been identified for the major rice pests and they work effectively to regulate rice insect populations. IPM research is now beginning to determine the interactions between host plant resistance and biological control (Smith 1992).

The predaceous mirid bug, *Cyrtorhinus lividipennis* is extremely abundant in tropical Asian rice fields. Studies by Myint et al. (1986) have shown that combining of a resistant cultivar, and predation by *C. lividipennis* had a cumulative effect on the mortality of the green leafhopper *N. virescens*. Mortality of *N. virescens* attributed to the antibiosis in the resistant cultivar, IR 29, was 66% but with the addition of *C. lividipennis*, *N. virescens* mortality increased to 92 %. Mortality of *N. virescens* on TN 1, a susceptible cultivar, was only 41 % with *C. lividipennis* predation.

Host plant resistance enhances the predatory activity of certain natural enemies causing a synergistic effect. Predation rate of the spider, *Lycosa pseudoannulata* feeding on the brown planthopper, increased when feeding on resistant cultivars(Kartohardjono & heinrichs 1984). The mechanism involved is assumed to be the restless and subsequent extreme movement of the brown planthopper in the resistant cultivar which causes it to be more easily detected by the spider. Also, because of the adverse effect of resistant cultivars on brown planthopper populations the planthopper: spider ratio in the field is most favorable for biological control activity. The brown planthopper: spider ratio increased with the level of planthopper susceptibility from IR 36, a highly resistant cultivar, and IR 8 a brown planthopper susceptible cultivar (Fig. 3).

N. Lugens mortality as affected by resistant cultivars in combination with the predators, *C. lividipennis* and *L. pseudoannulata* is shown in Fig. 4 (Kartohardjone & Heinrichs 1984). Mortality was highest when *N. lugens* was exposed to both a predator and a resistant cultivar.

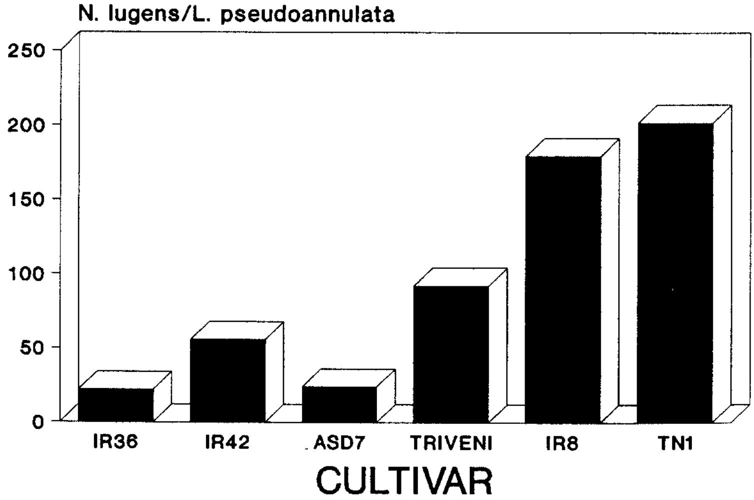

Fig. 3. Brown planthopper (*Nilaparvata lugens*): spider (*Lycosa pseudoannulate*) ratios at 40 days after transplanting of rice cultivars with varying levels of *N. lugens* resistance. IR36, IR42, and ASD7 are resistant, Triveni is moderately resistant, and IR8 and TN1 are susceptible (modified from Kartohardjono and Heinrichs 1984).

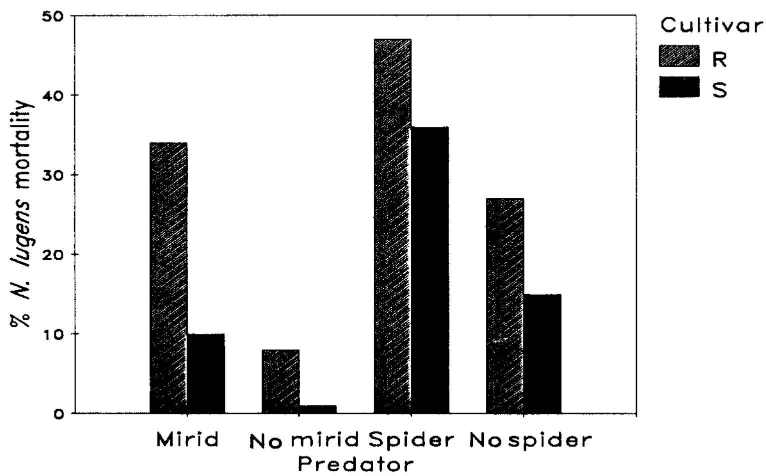

Fig 4. Predatory activity of the mirid bug, *Cyrtorhinus lividipennis* and the spider *Lycosa pseudoannulata* when feeding in the brown planthopper, *Nilaparvata lugens* reared on a *N. lugens* susceptible, and resistant rice cultivar (Kartohardjono and Heinrichs 1984).

Chemical Control and Host Plant Resistance

Insect pest problems have generally intensified with the expanded cultivation of the modern high yielding varieties and the simultaneous intensification of production. Depending on level of resistance and the insect pest complex, insecticides can enhance the yield of insect resistant cultivars. Insecti-

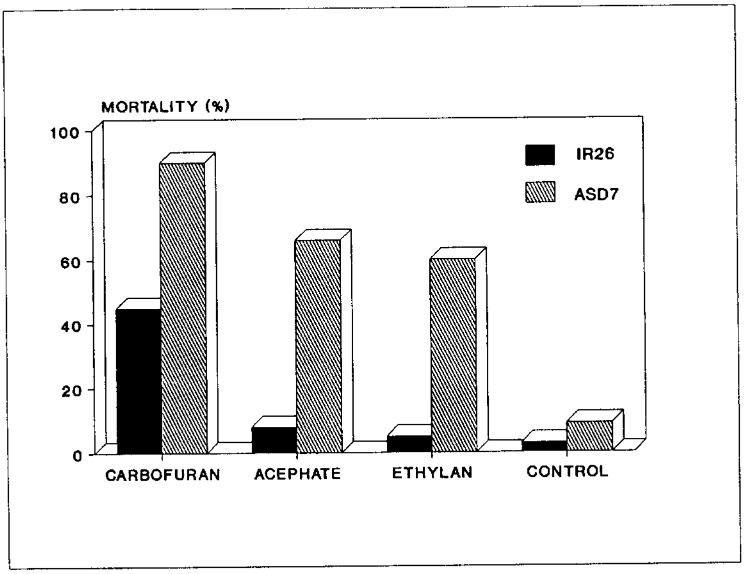

Fig 5. Contact toxicity of insecticides applied with a Potters spray tower against the brown planthopper *Nilaparvata lugens* biotype 2 when reared on susceptible (IR 26) and moderately resistant (ASD7) rice cultivars (modified from Heinrichs et al. 1984).

cides can enhance the yield of insect resistant cultivars. Insecticides are more effective and cause higher insect mortality when applied to insects feeding on resistant plants. Whitebacked planthoppers *Sogatella furcifera* and brown planthopper feeding on resistant or moderately resistant rice cultivars are killed at lower insecticide rates than those feeding on susceptible cultivars (Heinrichs et al. 1984). LD50 rates were two to three times as high on hoppers feeding on a susceptible cultivar TN1 as when feeding on a moderately resistant cultivar N22.

The increased toxicity of insecticides to the brown planthoppers feeding on moderately resistant cultivars was also reported in Heinrichs et al.(1984). Mortality rates of biotype 2 brown planthoppers reared on the moderately resistant cultivar ASD7 were 2 to 12 times that of those reared on susceptible IR 26 when sprayed with various insectcides (Fig. 5). The differences between IR 26 and ASD7 were especially large in the acephate and ethylan treatments.

Combining host plant resistance and insecticides can have a cumulative effect in the control of the green leafhopper *N. virescens* and the tungro virus for which it serves as an efficient vector. The extent of the cumulative effect depends on the level of host plant resistance in the cultivar. Cultivars with a high level of *N. virescens* resistance (IR 28) have a low *N. virescens* population and low incidence of tungro and those cultivars that are highly susceptible to *N. virescens* (IR 22) have a high level of tungro virus infection regardless of the number of insecticide applictions or the rate of insectcide applied (Fig. 6). Grain yields of highly resistant IR 28 were not affected by insectcide rate whereas yields of both the moderately resistant and susceptible cultivar increased with insecticide

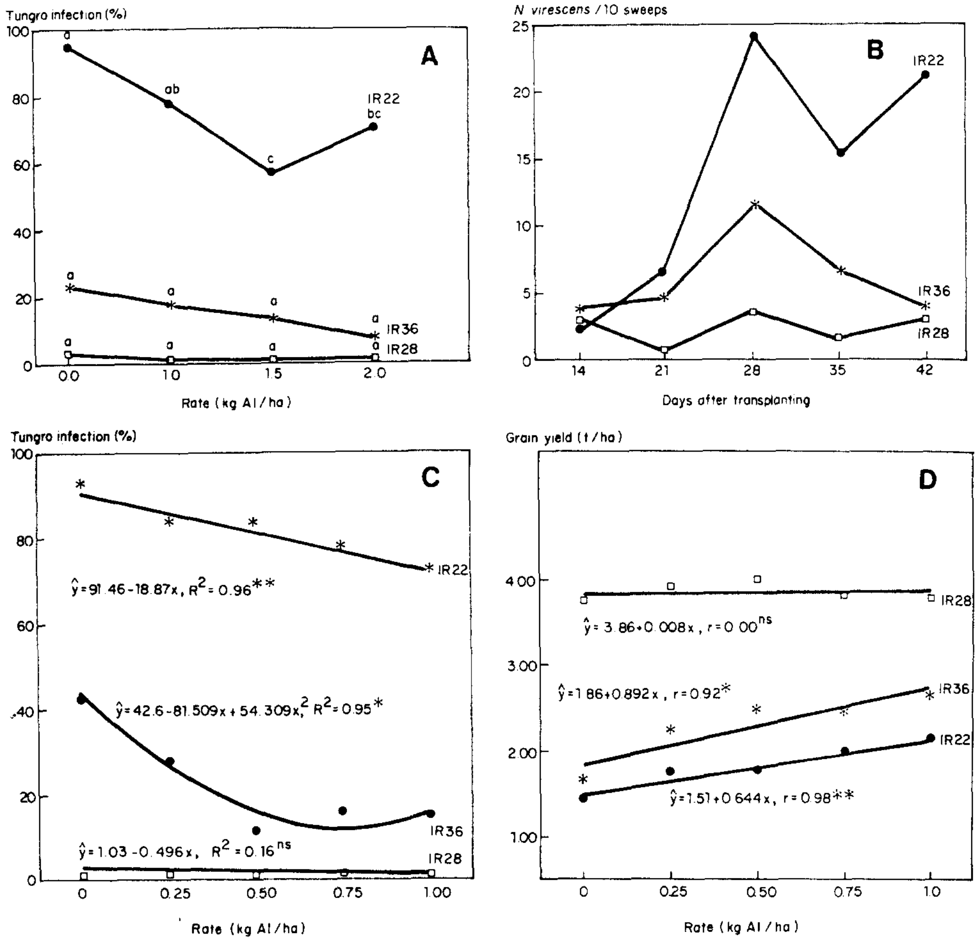

Fig 6. Percent rice tungro virus RTV infection, *N. virescens* populations, and grain yield of rice cultivars IR 22, IR 28, and IR 36 having different levels of *N. virescens* resistance as affected by rates of soil-incorporated carbofuran. (A) percent RTV infestion, Victoria, Laguna, 1983 wet season. For each cultivar, insecticide rates with the same letter are not significantly different (p=0.05 level; Duncan's 1951 multiple range test). (B) *N. virescens* populations per 10 sweeps, Victoria, Laguna, 1984 dry season. Data for soil-incorporated carbofuran rates (0, 0.25, 0.50, 0.75, and 1.00 kg [AI]/ha) were pooled and averaged across treatments. (C) Percent RTV infection, Victoria Laguna, 1984 dry season. (D) Grain yield, Victoria, Laguna, 1984 dry season. (Heinrichs et al. 1986).

rate.

Although brown planthopper resurgence occurs on both susceptible and resistant cultivars when resurgence-inducing insecticides are used host plant resistance mitigates the degree to which resurgence occurs. On studies conducted at IRRI brown planthopper populations on a resistant cultivar treated with a resurgence inducing insecticide were only 10 per hill while there were 1,100 brown planthoppers per hill on a treated susceptible cultivar (Aquino & Heinrichs 1979). Thus in fields where insects other than the brown planthopper regularly increase to populations above the economic threshold and require treatment with insecticide, brown planthopper resurgence can be minimized by the planting of a resistant or a moderately resistant cultivar.

A negative interaction between host plant resistance and insecticides which is of great concern involves the selection of brown planthopper biotypes that overcome the resistance factors in plants. Although biotype development on one hand allows planthopper populations to resurge on formerly resistant cultivars, on the other hand, resurgence-inducing insecticides accelerate biotype development. Even a low level of resurgence on resistant cultivars accelerates the selection of resistace-breaking planthopper biotypes by increasing the planthopper population size and thus the chance of selection. As a result, the number of seasons that a farmer can grow a particular brown planthopper resistant cultivar, before it becomes susceptible to a specific biotype and is replaced with another cultivar, is limited.

The presence of insecticide resistant strains is not easily detected when resistant cultivars are grown. However, when resistant cultivars " break down" through the selection of a virulent insect biotype the resistance (if present) of the brown planthopper to an insecticide is expressed because the cultivar resistance that masks the detection of insecticide resistance is removed. Thus, the planthoppers survive and multiply on the formerly resistant cultivar and because of resistance to insectcides chemical control is no longer effective. The loss of cultivar resistance and the decrease in the effectiveness of insecticides, because of the insects' adaptation, are often manifested in the phenomenon of insect resurgence with extremely high population densities (Heinrichs, in press).

Another interaction between host plant resistance and insecticides that is of concern is the apparent difference in the susceptibility of brown planthopper biotype to insecticides(Heinrichs & Valencia 1978). Studies at IRRI indicated that biotype 1 was the least susceptible to the commonly used insecticides. However, instead of an inherent genetic difference in the biotypes, the biotypic difference in susceptibility to insecticides may have been due to the quality of the host plant as each biotype tested (1,2 and 3) was reared on a different rice cultivar. In any regard, it goes without saying that the interactions between host plant resistance and biotypes is complex. To complicate matters, also consider the effect of insecticides on the nutritional quality and morphology of the rice plants, and on the natural enemies, and the management system for the brown planthopper becomes even more complex. It is certain that an ecologically oriented approach to the development of resistant rice cultivars and insecticides is necessary.

Cultural Control and Host Plant Resistance

The use of cultural practices to minimize insect damage is an ancient method of control. Over 2,000 years ago Chinese farmers adjusted planting dates to avoid pests and burned crop stubbles to reduce insect populations (Flint & Van den Bosch 1981 in Smith 1992). Litsinger (1992) has extensively reviewed the literature on the cultural control of rice insects and lists a number of agronomic practices that have been developed by farmers through observations and trial and error. Some of these practices have been handed down through many generations. However, the development and utilization of insect resistant cultivars is recent and there are few examples in the literature that document the integration of cultural practices with host plant resistance and the most important practices will be briefly discussed.

Four important cultural practices are covered under the general titles of (1) sanitation (2) water management, (3) fertilizer management, and (4) pest evasion. An important form of sanitation involves the removal of rice fields and from areas surrounding the fields. This practice works synergistically with insect resistant cultivars.

The management of water through the flooding of rice fields reduces the populations of some stem borer species. In China (Shin-Foon 1980) early spring flooding of rice stubble controls overwintering *Chilo suppressalis* larvae. Draining of water on the other hand, decreases populations of the rice water weevil, *Lissorhoptrus, oryzophilus* (Isley & Schwardt 1934). If effective insecticides for rice waterweevil are taken off of the market U.S. growers may have to resort to this method of control as there are no commercially released rice cultivars with resistance to the water weevil.

Although the use of increased amounts of nitrogen fertilizer has been a major ingredient in the profitable production of modern rice cultivars it has been shown that insect pest populations increase with increased levels of nitrogen fertilizer, even on insect resistant cultivars (Heinrichs & Medrano 1985). Splitting of nitrogen applications has been shown to be more beneficial to crop production than a single application.

A reduction in the amount of nitrogen applied at each application also mitigates insect pest bulildup during vegetative growth, a factor that will enhance the performance of moderately resistant cultivars. The combining of insect resistance with fertilizer responsiveness is most effectively accomplished by selecting cultivars with moderate levels of insect resistance that respond to fertilizer (Smith 1992).

Cultural practices used in rice production systems to evade insect pests are (1) synchronous planting, (2) planting date, and (3) the planting of early maturing cultivars. Synchronous planting of rice within an area that is related to the effective dispersal of the brown planthopper and the yellow stem borer *Scirpophoga incertulas* decreases the pest population on the crop(Loevinsohn et al. 1988). In Indonesia Oka(1979) suggested that the synchronized planting of rice fields in a given area would reduce the buildup of *N. lugens* populations. Planting of a legume between the two rice crops was suggested as a means of reducing pest incidence on synchronously planted fields.

Planting rice after emergence of the first generation of the yellow stem boror allows farmers to grow rice at a time of low borer pressure. Shifting planting dates has helped minimize damage by several borerspecies in India, Indonesia and Malaysia (Khan 1967).

Another method to avoid peak pest population is the planting of early maturing rice cultivars. The results of studies conducted by Heinrichs et al. (1986) indicated that the incorporation of brown planthopper resistance into early maturing cultivars would enhance the overall level of crop protection.

Breeding For Insect Resistance In Rice

There is a rich source of insect resistance germplasm in the world collection of rices. Systematic evaluation of the world collection at research stations throughout the world has identified numerous sources of resistance (Heinrichs et al. 1985). Table 1 gives the status of screening and breeding for

Table 1. Status of screening and breeding for varietal resistance to rice insect pests (modified from Heinrichs et al. 1985)

Insect		Status				
Common name	Scientific name	Screening methods developed	Resistance sources identified	Resistant breeding lines available	Resistant varieties released	Genes for resistance identified
Brown planthopper	*Nilaparvata lugens*	+	+	+	+	+
Whitebacked planthopper	*Sogatella furcifera*	+	+	+	+	+
Smaller brown planthopper	*Laodelphax striatellus*	+	+	+	+	−
Rice delphacid	*Sogatodes oryzicola*	+	+	+	+	−
Green leafhopper	*Nephotettix virescens*	+	+	+	+	+
Zigzag leafhopper	*Recilia dorsalis*	+	+	+	+	+
White leafhopper	*Cofana spectra*	+	+	−	−	−
Blue leafhopper	*Empoascanara maculifrons*	+	+	−	−	−
Rice striped borer	*Chilo suppressalis*	+	+	+	+	−
Yellow stem borer	*Scirpophaga incertulas*	+	+	+	+	−
Sugarcane borer	*Diatraea saccharalis*	+	+	+	−	−
African striped stem borer	*Chilo zacconius*	+	+	−	−	−
African white stem borer	*Maliarpha separatella*	+	+	−	−	−
Lesser cornstalk borer	*Elasmopalpus lignosellus*	+	+	−	−	−
African pink borer	*Sesamia calamistis*	+	+	−	−	−
S. A. white borer	*Rupela albinella*	+	+	−	−	−
Stalk-eyed fly	*Diopsis macrophthalma*	+	+	+	−	−
Rice stem maggot	*Atherigona oryzae*	+	+	−	−	−
Whorl maggot	*Hydrellia philippina*	+	+	+	+	−
Gall midge	*Orseolia oryzae*	+	+	+	+	+
Rice Seedling fly	*Atherigona exigua*	+	+	−	−	−
Armyworm	*Mychimna separata*	+	−	−	−	−
Thrips	*Stenchaetothrips biformis*	+	+	+	+	−
Rice bug	*Leptocorisa oratorius*	+	+	−	−	−
Black bug	*Scotinophara latiuscula*	+	+	+	+	−
Caseworm	*Nymphula depunctalis*	+	+	−	−	−
Leaffolder	*Cnaphalocrocis medinalis*	+	+	+	−	−
Rice water weevil	*Lissorhoptrus oryzophilus*	+	+	+	−	−
Hispa	*Dicladispa armigera*	+	+	−	−	−
Bloodworm	*Chironomus tepperi*	+	+	−	−	−
Rice weevil	*Sitophilus oryzae*	+	+	−	−	−
Maize weevil	*Sitophilus zeamais*	+	+	−	−	−
Lesser grain borer	*Rhyzopertha dominica*	+	+	−	−	−
Angoumois grain moth	*Sitotroga cerealella*	+	+	−	−	−

varietal resistance to insects. Major emphasis has been on leafhoppers and planthoppers in Asia, stalk-eyed fly in Africa, rice delphacid in South America, and the rice water weevil in the USA. The screening methods which have been employed in various rice breeding programs throughout the world are described in Heinrichs et al. (1985). Insect resistant cultivars selected from the world collection have been successfully used as doner parents by rice breeders in the development of multiple resistant cultivars.

Successful rice breeding programs consist of an interdisciplinary group of scientists that work together as a team. This is important because the degree to which a cultivar becomes a success depends on numerous factors which involve many disciplines. Agronomists, cereal chemists, biotechnologists, entomologists, pathologists, physiologists, and soil scientists must work closely with plant breeders. Such interdisciplinary programs have produced insect resistant cultivars with high yield potential. These cultivars are being used as a major tactic in the integrated management of rice insect pests in many regions of the world.

MECHANISMS OF INSECT RESISTANCE IN RICE

Host plant resistance to rice insects has been a successful tactic in integeated management programs in spite of the fact that knowledge of the mechnisms involved is often limited. However a more profound understanding of more efficient screening programs and provide guidance for the breeding program.

Plant resistant to insects is the result of a series of interactions between plants and insects that influences the degree of establishment on plants. Responses of insects to plants are influenced by plant chemical factors that alter the behavior and physiology of the insect and various plant physical characters that interface with insect vision, feeding, mating, and oviposition (Saxena 1986). Research on the physical and chemical factors in plants that are involved in resistance to rice insects is limited. Research has primarily concentrated of the rice stem borers, brown planthopper and green leafhoppers.

Stem Borers

Chaudhary et al.(1984) in their review suggested numerous morphological, anatomical, and biochemial factors that impart moderate levels of resistance to the striped stem borer and yellow stem borer. Among the morphological factors plant height, stem diameter and length of flag leaf were correalated with the number of eggs laid by moths (Patanakamjorn & Pathak 1967). Resistant cultivars possessed tight leaf sheaths that partially covered the internodes. Tight leaf sheaths were suggested as preventing newly hatched larvae from entering the stem.

Anatomical studies indicated that resistant cultivars had four to five layers of sclerenchymatous tissue that apparently prevented larvae from boring into the stem (Van & Guan 1959). Culivars with a narrow lumen were less susceptible to stem borers.

In biochemical studies oryzanone (p-methyl acetophenone) is attractive to ovipositing moths and larvae by its odor (Munakata et al. 1959). Non-preference in TKM6 is due to pentadecanal that inhibits oviposition and reduces egg-hatching, larval survival, and larval development (IRRI 1978). High silica content of stems reduced larval survival, apparently because of the effect of silica in wearing down the mandibles (Pathak et al. 1971). Studies on the chemical bases of resistance to stem borers have been limited. More knowledge of the chemical bases of resistance would lead to a more directed program of breeding for stem borer resistance.

Green Leafhoppers

Studies by Kawabe (1985) on the resistance of Japanese cultivars to *Nephotettix cincticeps* indicat-

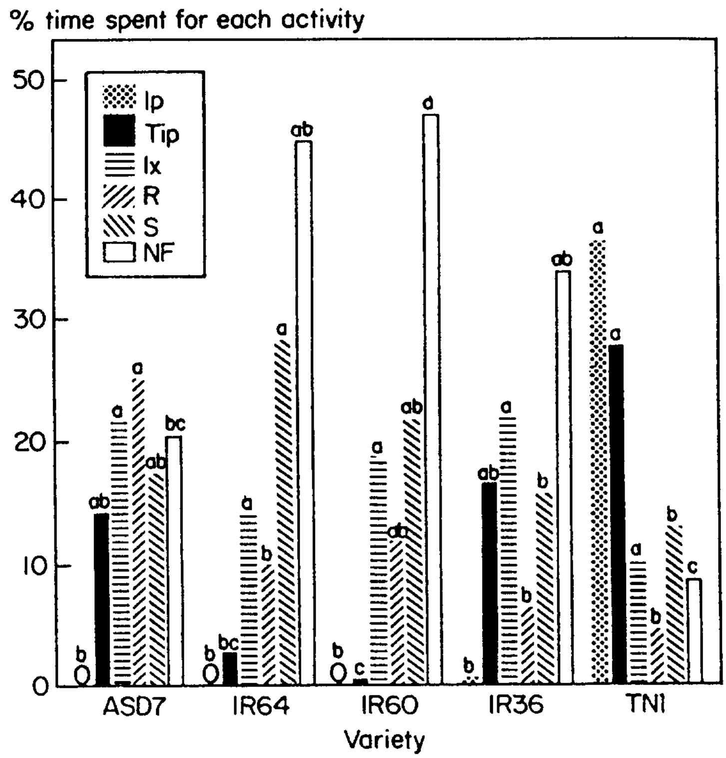

Fig. 7. Percentage of time spent for each activity (or waveform) on different rice varieties. Ip, phloem ingestion; TIp, trial ingestion from the phloem; Ix, xylem ingestion; R, rest; S, salaivation and NF, not feeding Bars of the same waveforms with the same letters are not significantly different at p=0.05, Duncan's (1995) multiple range test. (from Rapusas and Heinrichs 1990).

ed that the three components if resistance, antibiosis, antixenosis (non-preference), and tolerance were involved. His feeding studies demonstrated that the phloem of resistant cultivars contained a biological or physiological mechanism such as a phytoalexin or a mechanical barrier that inhibits phloem sap ingestion.

An electronic monitoring device and a video camera were used to study the feeding behavior of *N. virescens* (Rapusas & Heinrichs 1990). On a susceptible cultivar (TN 1) most of the feeding activity consisted of phloem ingestion. On resistance cultivars(ASD7, IR 64, IR 60) xylem ingestion was a major feeding activity even though the stylets were able to penetrate the phloem. On moderately resistant IR 36 a small amount of phloem ingestion occurred but most of the feeding time consisted of xylem ingestion(Fig. 7). There appeared to be a mechanism in the phloem seive elements that prevents *N. virescens* from ingesting phloem sap on resistant cultivars.

Plant age significantly affects the levels of *N. virescens* resistance in rice (Papusas & Heinrechs 1987). IR 36 plants at 10 days after sowing (DAS) were preferred by *N. virescens* over older plants. Insect survival, growth and weight were higher on 20 DAS plants than on plants at 40, 60, or 80 DAS. Phloem feeding was highest on young plants and tungro virus transmission efficiency increased with extent of phloem feeding. Detailed methods for studying the chemical bases of resistance to leafhoppers is described in Smith et al. (1991).

Brown Planthopper

Reduced feeding of the brown planthopper on resistant plants is attributed to the presence of antifeedants or the lack of sufficient phagostimulants (Saxena 1986). Resistance in the cultivar Mudgo was reported to be due to a low concentration of amino acids, especially asparagine, a sucking stimulant (Sogawa & Pathak 1970). Soluble silicic acid and oxalic acid were reported to be sucking inhibitors in resistant rice plants (Yoshihara et al. 1979, 1980). Kaneda (1982) reported beta sitosterol to be a sucking inhibitor.

Plant volatile chemicals affect the orientation response and feeding activity of the brown planthopper (Smith et al. 1991). In tests conducted by Saxena and Okech (1985) the planthoppers preferred susceptible plants sprayed with their own extract over plants of the same cultivar sprayed with the extract of a resistant cultivar. The identity of the allelochemics was not determined but it was assumed that the steam distillation method employed extracts of essential oils, terpenoids, aldehydes, fatty acids, esters, waxes etc.

Surface waxes have been shown to affect brown planthopper behavior (Woodhead & Padgham 1988). Cook et al. (1987) studied the effects of the plant surface on brown planthopper behavior using high resolution video equipment as described in Cook (1991). On resistant cultivars the hoppers did not commence probing, after exploration of the plant surface by the labial sensillae, as they did on susceptible cultivars. Instead, they moved away to another site on the leaf sheath to explore the surface again. This response was attributed to waxes. Woodhead and Padgham (1988) identified the active components of resistant cultivar IR 46 as the wax extracts, alkanes or carbonyl compounds.

VARIABLITY AND THE QUEST FOR DURABLE RESISTANCE

Biotypes

Variability in the levels of insect virulence on resistant cultivars has been a severe problem in Southeast Asia. Most notable examples are the green leafhopper, *N. virescens*, brown planthopper, *N. lugens* and the Asian rice gall midge, *Orseolia oryzae* (Heinrichs 1992).

These insects have a wide range of genetic variability that maximizes their fitness in the presence of genetic diversity of host plants. The planting of one or a few genetically related cultivars over large areas, as has been common since the release of "green revolution" cultivars, has greatly decreased the genetic diversity. Rice insects have developed virulence and cause severe damage to cultivars that were resistant when originally released for cultivation. These new forms of pests, called " biotypes" are populaltions of insects that are capable of damaging plant cultivars that are resistant to other populations of the same species (Heinrichs 1988b). Biotype selection enables the insect species to keep pace with changes in the defenses of its host plant that occur through plant breeding programs (Saxena & Barrion 1987). Among the various rice insect species, biotypes of the brown planthopper have been a major constraint to the breeding of resistant rice cultivars and have been extensively studied throughout Asia.

IR 26 with the *Bph* 1 gene was the first known planthopper resistant cultivar released by IRRI in 1974. On release it was resistant in the Philippines but after 2 to 3 years of cultivation brown planthopper outbreaks were observed in IR 26. Pathak & Heinrichs (1982) showed that, under laboratory conditions, high levels of virulence of *N. lugens* populations to resistant cultivars could be selected in 7 to 10 generations. Several *N. lugens* resistant cultivars have been released after IR 26 and most have also succumbed to biotype selection after being cultivated for a few years (Heinrichs 1988b). The extreme variability of virulence patterns was shown by Claridge et al. (1982) in *N. lugens* populations collected in Sri Lanka. When six populations collected from a wild rice species, traditional cultivars, and modern improved cultivars, were tested for virulence, they were most closely adapted to the cultivar, from which they were collected, even though all poputlations were collected within a 200 km area. Virulence is inherited as a polygenic or quantitative trait (den Hollander & Pathak 1981).

Breeding for Durable Resistance

In spite of the development of virulent biotypes plant resistance will remain a key tactic in the integrated management of rice insect pests. Several strategies have been developed to increase the value of resistance by increasing the level of stability or durability of insect resistant cultivars. Because of the tremendous amount of genetic diversity in the world collection of rice several strategies are available to mitigate the problems caused by biotypes.

Horizontal resistance is a type of resistance that is expressed equally to all biotypes. Tolerance is a form of horizontal resistance that is durable because it exerts no selection pressure on the population of insects. Tolerant plants have the ability to grow and reproduce and to repair insect injury in spite of supporting an insect population equal to one that damages a susceptible host plant (Painter 1951).

Tolerance is more difficult to assess than antibiosis and antixenosis and thus the number of rice cultivars indentified in screening programs has been few. Greenhouse and field methods have been developed to evaluate rice cultivars for brown planthopper tolerance (Heinrichs et al. 1985, Panda & Heinrichs 1983). Field studies identified Utri Rajapan, an Indian cultivar as having a high level of tolerance.

Advances in biotechnology provide the possibility of solving some of the problems that have limited the use of host plant resistance in insect management programs. Biotechnology has allowed wide hybridization where wild rices (*Oryza* spp.), with a rich source of genes for resistance, can be crossed with *Oryza sativa*. Tissue culture techiques such as another culture (Fig. 8) can be used to expedite the incorporation of resistance genes through hybridization and the acceleration of the development and homozygous lines.

Most of the wild rices in the IRRI collection have been screened and sources of resistance to the major insect pests of rice in Asia have been identified (Table 2) (Heinrichs et al. 1985, Wu et al. 1986, Romena & Heinrichs 1989). Wild rices may provide new genes which can provide a durable form of resistance.

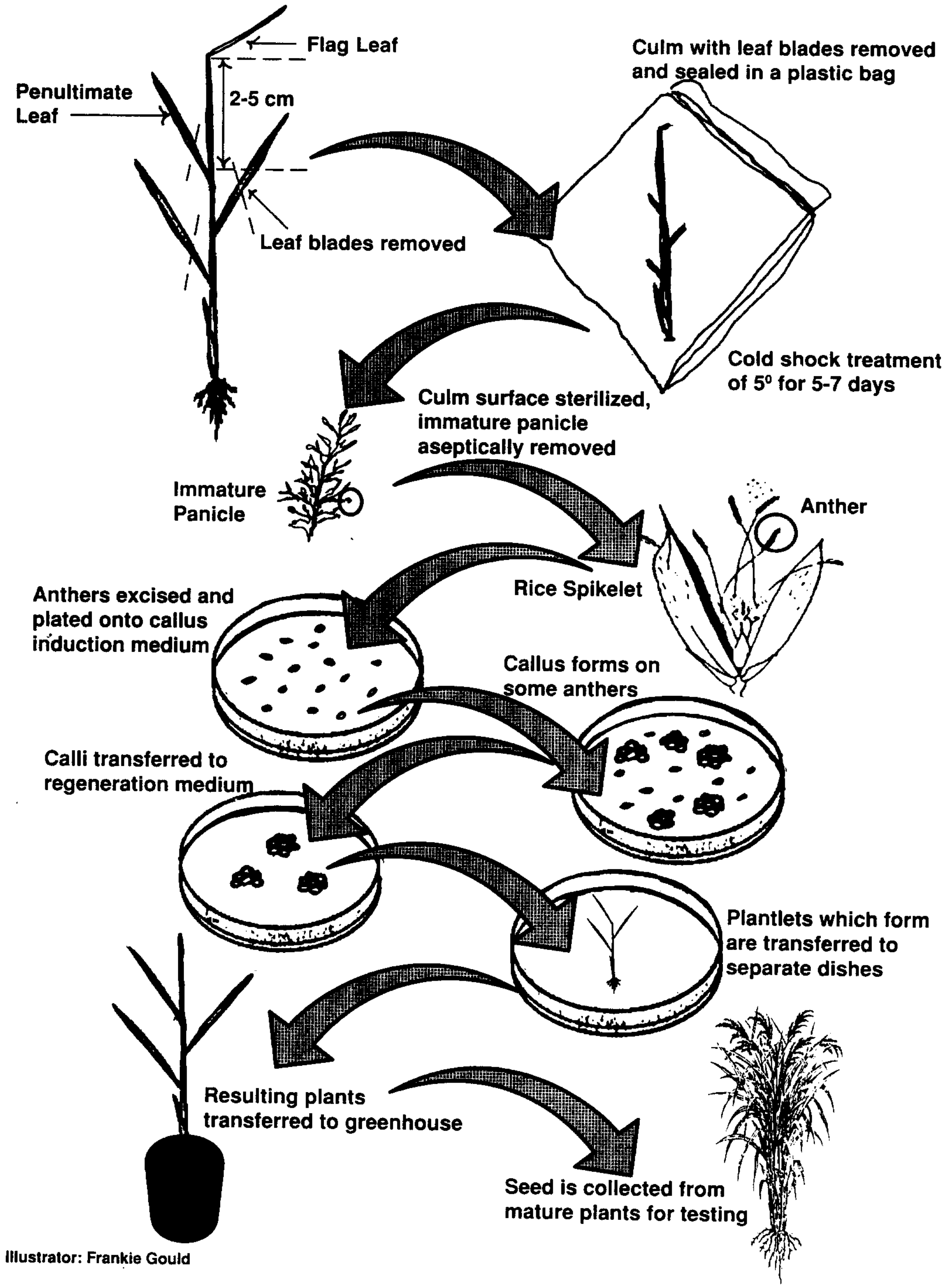

Fig. 8. Procedure for anther culture of rice (Croughan and Robinson 1991).

Table 2. Agronomically important characteristics identified among the wild *Oryza* species (from Toenniessen and Herdt 1989)

Species	2n	Genome	Characteristics
O. nivara	24	AA	Grassy stunt virus resistance
O. rufipogon	24	AA	Source of cytoplasmic male sterility, tolerance to stagnant flooding
O. glaberrima	24	AA	GLH resistance, early vegetative vigor
O. barthii	24	AA	Bacterial blight resistance
O. longistaminata	24	AA	Floral characteristics for outcrossing
O. punctata	24, 48	BB, BBCC	BPH, WBPH, GLH resistance
O. officinalis	24	CC	BPH, WBPH, GLH resistance
O. eichingeri	24	CC	BPH, WBPH, GLH resistance
O. minuta	48	BBCC	BPH, WBPH, GLH, blast, and bacterial blight resistance
O. australiensis	24	EE	BPH resistance, drought tolerance
O. brachyantha	24	FF	Whorl maggot and stem borer resistance
O. ridleyi	48	–	Whorl maggot resistance

CONCLUSION

Insect pests are one of several constraints that limit rice production. Throughout the history of rice production farmers have developed various forms of control strategies to mitigate the yield losses caused by insects, both in the field and in storage. With the recent development of a more scientific approach to rice insect control major emphasis has been placed upon insecticides in rice insect mannagement programs. However, because of the economic, ecological, and human health concerns, and because insect pests develop resistance to insecticides, there has been much interest in the development of alternative tactics for rice insect management.

Rice is an excellent example of the successful utilization of host plant resistance as a tactic in the management of insects. Much of the world collection has been evaluated for insect resistance and many cultivars have been used as donor parents in rice breeding programs throughout the world. These breeding programs have provided rice farmers with insect resistant cultivars that are playing an important role in the management of rice insect pests. However no one control tactic is a panacea and host plant resistance is no exception as is evident in the discussion on biotype development. Thus to increase the durability of host plant resistance it must be integrated with other control tactics, cultural, biological and chemical.

Significant progress has been made in the breeding and commercial utilization of insect resistant rice cultivars. However, there are still numerous important rice insect pests throughout the world for which host plant resistance as a control tactic has not been adequately utilized. Innovative conventional breeding techniques and molecular genetic approaches may provide means for more fully exploiting the world collection of *Oryza sativa* and wild rices (*Oryza* spp.) in the development and utilization of commercial rice cultivars with stability to variable rice insect populations.

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