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REVIEW ARTICLE

Induced resistance in rice against insects

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Abstract

Vaccinations are the mainstay of western preventive medicine, and they have been used to protect some crops against disease and insect pests. We consider rice as a model for protection using induced resistance since it is one of the most important staple crops and there have been significant new developments in: cross-resistance among rice insects, chemical pathways involved in induced resistance, sequencing the rice genome and expression of genes conferring resistance against rice insect pests. Insect attack has been found to cause lesions that kill planthopper eggs and early stages of gall midges. Damaged plants released volatiles that made them less likely to be chosen by planthoppers and more attractive to parasitoids. Chemical elicitors have been developed for dicotyledonous plants and these can induce resistance in rice, although rice does not fit models developed to explain signalling in dicots. For example, salicylic acid did not increase in rice after infection by pathogens and did not appear to be the mobile signal for induced resistance against pathogens although it was involved in induced responses to phloem-feeding insects. Jasmonic acid acted as a signal in some induced responses to pathogens as well as chewing insects. Many of the genes associated with induced resistance in rice have recently been mapped, and techniques are being developed to incorporate them into the genome of cultivated varieties. Attempts to control insect pests of rice will affect interactions with pathogens, predators and parasites, and other organisms in this agroecosystem.

Keywords: agriculture, cross-protection, gene expression, genetic engineering, jasmonic acid, pathogen, salicylic acid, signal, vaccination

Vaccinations in agriculture

Vaccinations are the mainstay of western preventive medicine, and there are many parallels between the use of vaccinations in medicine and agriculture. Plant pathologists have been aware that plants can become more resistant to pathogens following exposure to avirulent strains for over 100 years (Beauverie, 1901; Ray, 1901; Chester, 1933) although entomologists have discovered induced resistance much more recently (Green & Ryan, 1972; Haukioja & Hakala, 1975). The activity of the inducing agent is not due to antibiotic activity *per se* by killing or harming the attackers; rather, the inducing agent makes the plant more resistant to subsequent challenges (Kuc, 1982). Induced resistance in this review refers to changes in the host plant in response to attacks or treatment that cause the plant to become less preferred or less favourable for insects compared to an uninduced plant (Karban & Baldwin, 1997).

Vaccination techniques have been developed to protect crop plants against economically important diseases and arthropods, although these have been used commercially in only a small percentage of the plant systems where they

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seem effective (Campbell, 1989; Karban & Baldwin, 1997). As was true in medicine, early attempts to induce resistance in agriculture relied upon introducing mild, economically benign insects and mites to induce resistance against economically important arthropod pests. Although it is possible to achieve induced resistance in this way, this technique poses several hurdles.

The following characteristics will increase the feasibility of using induced resistance in specific agricultural systems (following Karban & Baldwin, 1997): (i) the pest must be destructive (costly) and difficult to control by other means; (ii) the inducer must not be a pest itself or cause significant losses in yield; (iii) it must be feasible to introduce the inducer into the system; (iv) the inducer should be sustainable (perhaps self-replicating); and (v) the plant must have some tolerance of the pest and of the inducer since vaccinations are unlikely to provide complete control, by themselves. All of these conditions contribute to the cost effectiveness of induced resistance. In many markets, use of vaccination techniques will also require that some corporation or governmental agency finds commercialization of the vaccine profitable, financially and politically (Kuc, 1995). In the past this has been the biggest hurdle to overcome in adopting induced resistance in commercial agriculture.

We envision three strategies that use induced resistance to protect crop plants.

1. Avirulent organisms can be introduced to protect crops against economically damaging pests. This is the most straight-forward method of vaccinating plants although it is also the most difficult to use effectively.
2. As we learn about the chemical pathways that lead to induced resistance, it may become feasible to use natural or synthetic chemical elicitors of induced responses.
3. Similarly, as we learn more about the genetics and molecular control of resistance, it may become feasible for us to selectively express resistance traits that are naturally inducible. By using genetic manipulations, we can overexpress or control the expression of genes conferring resistance traits that were naturally only expressed following attack. Genetic manipulations enable us to move induced resistance traits from resistant varieties and species into susceptible varieties that have desirable agronomic characteristics.

In the following sections, we will present rice (*Oryza sativa* L.) as a model system for work on induced resistance against insect pests. The sequencing of the rice genome has opened the door to a wealth of genomic and biochemical information about the resistance pathways of rice; the biology of the insects are well-studied, and unlike other models (e.g. *Arabidopsis*), rice is the most important staple for close to a quarter of the world's population. We will describe our current knowledge of the mechanistic basis of induced resistance in rice, strategies for increasing resistance in rice to insect pests, the relationship between induced resistance and other integrated pest management (IPM) strategies in rice, and finally prospects for the future.

Insect pests of rice

In this review, we focus on the insect pests found in Asia. While the majority of insects on rice cause very little damage (Dale, 1994), there are several widespread and abundant pests that attack rice throughout Asia. For induced resistance to be useful in an IPM context, it is important to understand the biology of rice insects, particularly when they attack, and the frequency and severity of attack. Detailed information about the timing, specificity and physiology of the organisms involved is critical if induced resistance techniques are to be successful.

The rice leaffolder, *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae), attacks the rice plant during the vegetative stage. Enclosed by a leaf, larvae scrape away at the surface of leaves. Leaffolders rarely cause significant yield loss, because the rice plant is capable of tolerating serious defoliation. For example, abnormally high infestation levels, or the loss of 67% of leaves, did not cause a significant yield loss (Miyashita, 1985). Leaffolders are normally controlled by a wide range of natural enemies (Khan *et al*., 1988; Barrion *et al*., 1991); however, outbreaks have been reported resulting from excessive fertilizer and pesticide use throughout Asia (Yadava *et al*., 1972; Chatterjee, 1979; Dhaliwal *et al*., 1979).

Lepidopteran borers are considered major pests of rice because they attack from seedling to maturity and are very destructive (Khan *et al*., 1991; Bandong & Litsinger, 2005). There are about fifty species that attack rice (Khan *et al*., 1991). The two most important in Asia are the striped stem borer, *Chilo suppressalis* (Walker) (Lepidoptera: Pyralidae), and the yellow stem borer, *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae). The insects tunnel into the stems and kill part of the plant. During the vegetative stage, stem borer damage results in dead hearts, or discoloured apical shoots. Feeding during the reproductive stage can result in white heads, or unfilled spikelets. Stem borers are difficult to control by existing methods.

Several important insect pests feed on phloem sap of rice. The brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae), is the most common of these species. It feeds on the phloem in leaf sheaths, causing wilting and drying of the leaves. Under severe infestations, planthoppers can kill entire plants. *Nilaparvata lugens* can be found at all stages of plant development (Dale, 1994). It became a major threat to rice production in the early 1970s, when new high-yielding varieties were introduced with insecticides. There is considerable evidence that *N. lugens* outbreaks are associated with overuse of insecticides (Kenmore *et al*., 1984; Gallagher *et al*., 1994).

The Asian gall midge, *Orseolia oryzae* (Wood-Mason) (Diptera: Cecidomyiidae), is found primarily in lowland irrigated rice. It attacks rice from the seedling stage until the end of the tillering stage. *Orseolia oryzae* is only found in cultivated rice near perennial wild rice, which provides an alternate habitat during the dry season (Shepard *et al*., 1995). Attack by this insect results in a profuse tillering and stunting of rice plants (Dale, 1994).

Mechanistic basis of induced resistance in rice

Early work on dicotyledonous plants revealed that induced resistance against pathogens and insects was systemic in some species, such that plant tissues on attacked plants distant from the site of attack were protected (Ross, 1961; Green & Ryan, 1972; Kuc, 1982; Karban & Carey, 1984). Plants use chemical signals to coordinate their responses to attack. Knowledge about these signals will allow us to understand and manipulate plant defences. Careful

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examination of the signalling events related to systemic-induced resistance revealed that chemical cascades involving salicylic acid (SA) were responsible for many induced reactions against pathogens (Malamy *et al*., 1990; Metraux *et al*., 1990), and cascades involving jasmonic acid (JA) were involved in many induced responses against wounding and insect attack (Farmer *et al*., 1992). Other signalling molecules have also been identified, such as abscisic acid and ethylene, although the important role of jasmonates in signalling responses to herbivory has been highly conserved among plants families (Thaler & Bostock, 2004; Stout *et al*., 2006). However, since most of this pioneering work was done with dicotyledonous plants, the role that these signalling molecules might play in cereals such as rice has been poorly understood until recently (Schweizer *et al*., 1998; Kogel & Langen, 2005).

Signalling in rice has been found to differ from the model that was developed for dicotyledonous plants. Rice contains relatively high background levels of endogenous SA that do not increase after infection by pathogens (Silverman *et al*., 1995). This result sheds doubt on the possibility that SA is the mobile signal for induced resistance in rice (Yang *et al*., 2004). Even if SA is not the signal in rice, the high endogenous levels of SA appear to function as an antioxidant, protecting the plant against oxidative stress and plant pathogens. SA-deficient transgenic plants had elevated levels of H_2O_2 and superoxide and suffered a higher incidence of lesions under intense sunlight (Yang *et al*., 2004). Furthermore, blast fungus infection led to more pathogenic lesions on SA-deficient transgenic plants than on control plants.

Even if SA does not play a role as a signalling compound for induced defence pathways in this system, rice appears to share other subsequent, 'downstream', steps of the induction pathway with dicotyledonous plants (Chern *et al*., 2005; Kogel & Langen, 2005). It is quite possible that monocots use an additional signalling chemical since the currently known signals cannot account for all of the responses that have been observed (Schweizer *et al*., 1997; Yang *et al*., 2004).

Some of the genes involved in induced resistance against blast fungus have been identified and expression of gene products conferring resistance have been found to be mediated by JA, and not SA (Lee *et al*., 2001). Wounding in rice caused levels of JA to increase immediately in the wounded leaf and to accumulate with a delay of several hours in leaves that were not directly wounded (Schweizer *et al*., 1998; Lee *et al*., 2004). The SA and JA pathways may be antagonistic, and endogenous SA levels decreased during the initial JA burst (Lee *et al*., 2004). The increase in JA caused greater production of gene products normally associated with induced responses to pathogens rather than wounding or insect damage and provided induced resistance against rice blast fungus.

Induced responses in rice appear to vary in response to different pest species. Chewing damage caused by armyworm or cluster caterpillars, *Spodoptera litura* (Fabricus) (Lepidoptera: Noctuidae), caused signal cascades and expression of genes normally associated with induced resistance against herbivores, such as the JA pathway, phenyl propanoid pathway and terpene biosynthesis (Xu *et al*., 2003). This result suggests that the JA signalling pathway in rice is involved with induced resistance against caterpillars. This result contrasts with plant responses to phloem-feeding insects.

In general, phloem-feeding insects appear to be perceived by plants as pathogens and induce either SA or JA/ethylene signalling pathways, resulting in the production of pathogenesis-related proteins (Walling, 2000). Gene expression studies show that *N. lugens* feeding in rice probably induces the SA rather than the JA pathway (Xu *et al*., 2003; Zhang *et al*., 2004). Genes for pathogenesis-related proteins were significantly overexpressed when planthoppers fed on rice (Kanno *et al*., 2005; Wang *et al*., 2005). The redundancy in plant responses may allow cross-protection between planthoppers and fungal pathogens. For example, rice plants previously inoculated with white-backed planthoppers, *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae), had fewer lesions from the rice blast fungus (Kanno *et al*., 2005). The SA pathway also produces other defensive chemicals, such as phenols and flavonoids (Dixon *et al*., 2002); increases in rice phenolics following infection by rice blast pathogens or gall midges may also be controlled by the SA pathway (Bentur & Kalode, 1996; Babu *et al*., 2003a).

Planthopper feeding induces the expression of a variety of other defence genes (Wang *et al*., 2004, 2005; Yuan *et al*., 2004; Zhang *et al*., 2004). For instance, Yuan *et al*. (2004) found that mechanical damage, ethylene, and *N. lugens* feeding induced expression of a novel rice gene, although its role in defence has not yet been established. *Nilaparvata lugens* feeding induced expression of protease-inhibitor (PI) genes such as oryzacystatin (Zhang *et al*., 2004; Wang *et al*., 2005). These are thought to interfere with insect protein digestion in the midgut (Broadway & Duffey, 1986, Jongsman & Bolter, 1997). *Nilaparvata lugens* feeding also induced the expression of β-glucosidase, which is thought to be involved with release of volatile terpenoids (Wang *et al*., 2005). The pathways controlling these other defence genes are unclear, but they could be induced by a common signalling molecule from the SA pathway.

Gene expression studies indicate that induced responses can be both rapid and persistent. Although the precise timing of induced responses has not been studied, some responses can occur within 24 h (Xu *et al*., 2002). Induced resistance can also last for quite a long time. For example, induction by white-backed planthoppers protected the rice plant for more than 15 days against rice blast (Kanno *et al*., 2005).

Strategies for increasing resistance in rice

Insects as elicitors

Induced resistance can be rapid, acting directly upon the insect that causes the initial damage, or delayed, acting upon insects that subsequently attack the plant. Some cultivars of Japonica rice produce watery lesions rapidly at the site of oviposition in response to whitebacked planthopper eggs (Suzuki *et al*., 1996) and to a lesser degree to brown planthopper eggs (Yamasaki *et al*., 2000). These watery lesions contain an ovicidal compound, benzyl benzoate, which causes high rates of egg mortality (up to 80% depending upon cultivar, developmental stage and other factors). No ovicidal substance was detected in undamaged plants or in locations away from oviposition sites on damaged plants (Seino *et al*., 1996). A single plant gene conferring ovicidal activity has recently been identified (Yamasaki *et al*., 2003).

All crops, including rice, serve as hosts for a wide range of herbivores (see above for a discussion of insects on rice).

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Some of these herbivore species and biotypes within species are far more damaging to the crop than are others. Herbivores differ in their abilities to build up large populations. Plants also vary greatly in their tolerance as hosts of different herbivores; some pests cause much more economic loss per capita than others. These generalizations apply well to rice (Way & Heong, 1994; Matteson, 2000). For instance, rice seedlings of a resistant variety Phalguna exhibit a hypersensitive response including localized necrosis immediately surrounding the oviposition sites in reaction to several biotypes of the Asian rice gall midge, *Orseolia oryzae* (Bentur & Kalode, 1996; Sardesai *et al*., 2001). This hypersensitive response caused 100% mortality of first instar maggots within four days. Tillers that were produced subsequently by these induced plants were well protected against avirulent biotypes. In addition, seedlings that had been exposed to an avirulent biotype gained resistance against more damaging biotypes of the rice gall midge; resistance induced by the avirulent midges continued to protect plants for several weeks (Bentur & Kalode, 1996). This suggested that releases of the avirulent biotype could protect plants against the spread of more damaging biotypes. Efforts are underway to map and clone the genes responsible for this delayed induced resistance against gall midges (Sardesai *et al*., 2001; Harris *et al*., 2003).

Rice plants that are attacked early in development can become more resistant to subsequent attacks. For example, young plants that were fed on by early instar caterpillars of *Spodoptera frugiperda* (the fall armyworm of North America) became locally and systemically more resistant to growth by subsequent caterpillars compared to controls (M.J. Stout, unpublished). Similarly, prior feeding by two species of planthoppers reduced the quality of rice plants as food for subsequent planthoppers (Matsumura & Suzuki, 2003).

Rice plants that are attacked by armyworm or cluster caterpillars (*Spodoptera litura*) release blends of volatile compounds that are repellent to brown planthoppers (Xu *et al*., 2002). Adult brown planthopper females were less likely to choose rice plants damaged by caterpillars compared with undamaged plants, mechanically damaged plants or plants infested with brown planthoppers in dual-choice experiments conducted in flight tunnels. This result indicates that induced plant volatiles could be used to make plants less attractive to important pests such as brown planthoppers although caterpillar numbers are difficult to manipulate at agricultural scales and unlikely to be useful as actual inducers. Recent work has attempted to identify the active volatiles in tests combining y-tube olfactometers with chemical techniques to examine the pathways that produced elevated plant emissions (Xu *et al*., 2003; Zhou *et al*., 2003).

Chemicals as elicitors

Inoculating plants with avirulent strains or species of insects to gain protection against damaging ones is conceptually straightforward although this strategy faces several practical problems. It must be possible (and cost effective) to acquire, transport and introduce the avirulent inducer. This often requires considerable labour, expertise to distinguish the virulent and avirulent insects, and trust on the part of the farmers. Some of these problems can be solved by applying chemicals that induce resistance against pest insects. These chemical inducers are not directly toxic or inhibitory to the pest insects but cause the plant to increase its level of resistance. In some cases, the chemical inducers are 'botanicals' or plant extracts. For example, leaf extracts from *Datura metel* (Solanaceae) have been used to induce systemic resistance against several economically important pathogens of rice in India (Kagale *et al*., 2004). Some plant-derived substances are inexpensive and readily available in developing countries although we are not aware of their commercial use to control pathogens or insect pests of rice anywhere. Similarly, treating rice seeds before planting with chemical 'sensitizers' stimulated phytoalexin responses and other defensive responses when the seedlings were challenged subsequently by pathogens (Cartwright *et al*., 1977; Sinha & Hait, 1982; Hait & Sinha, 1987; Munusamy *et al*., 2004). Various fertilizers and growth stimulants have been reported to also increase plant resistance to insects. For example, several zinc or iron based soil additives have the additional effects of reducing insect populations. Rice plants receiving applications of these fertilizers had approximately half the populations of whitebacked planthoppers as untreated controls and produced higher grain yields (Rath & Misra, 1998). Several authors have questioned the potential of strategies relying on chemicals to boost induced responses because the resistance has been relatively short-lived and may not be cost effective in some instances (Deacon, 1988; Hedin, 1990; Isman, 2006).

Some cultural practices change the rice plant so that it becomes more susceptible, rather than more resistant, to pests. For example, several widely used pesticides have been found to increase populations of planthoppers (Wu *et al*., 2001, 2004). The mechanisms responsible varied depending upon the pesticide and the insect although they involved changes in numerous plant traits.

An understanding of the signalling process has gone hand in hand with developing artificial elicitors of resistance that can be used to control levels of plant resistance under agricultural conditions. Several synthetic mimics of SA were developed that caused plants to react much as they would when they were attacked by pathogens (Gorlach *et al*., 1996). One of these, benzothiadiazole, has been marketed commercially (as Bion) and registered for control of many diseases in cereal crops. It protects rice against fungal and bacterial infections more effectively than SA (Schweizer *et al*., 1999; Babu *et al*., 2003b). We are not aware of rice farmers using benzothiadiazole successfully in commercial field situations.

As mentioned above, JA is generally regarded as a key component of the signalling pathway involved with induced plant resistance to insects with chewing mouthparts, such as caterpillars. Synthetic analogues of jasmonates are more potent elicitors of plant responses associated with the JA pathway than are naturally occurring compounds (Schuler *et al*., 2001). Although the signalling process is not well understood in rice, the JA pathway appears to be involved in induced responses caused by wounding or by chewing herbivores (see above). Plants sprayed with JA at 1 mM had approximately half as many larvae of rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), as untreated controls in trials in North America (M.J. Stout, unpublished). Similarly, relative growth rates of *S. frugiperda* caterpillars were reduced by the application of 0.5 mM JA (M.J. Stout, unpublished). No chemical elicitors have been marketed commercially for control of insect pests of rice although this strategy holds considerable promise.

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Genetic techniques to incorporate induced resistance

Classical breeding programmes for plant resistance to diseases and herbivores have been limited by the existing heritable variation present in the species (or closely related species). Genetic engineering offers the exciting possibility of incorporating novel resistance traits from other species, families, and even phyla into rice varieties that show desirable traits. For example, rice varieties in China have been transformed using Agrobacterium to incorporate inducible cowpea trypsin inhibitors. These transformed plants showed enhanced resistance against stem borers (Hu-Qi *et al*., 2005). Transformed plants supported smaller populations of several caterpillars including stem borers and rice leaffolders and reduced levels of damage compared to untransformed controls in field trials (Li-Yue *et al*., 2005). Other resistance traits (e.g. a gene that provides resistance against planthoppers) that are not inducible have also been incorporated into agronomically desirable rice varieties (Nagadhara *et al*., 2004). Other inducible traits that have been characterized genetically, such as genes associated with ovicidal responses to planthopper eggs, may be amenable to genetic engineering in the near future (Yamasaki *et al*., 2003).

In addition, it should be possible to make a trait that is now constitutively expressed inducible by fusing it with an inducible promoter. It would then only be expressed following insect attack or following activation by a chemical elicitor. Such specificity would reduce impacts of genetically modified plants on non-target organisms. Recently, a gene involved in pathogen resistance in rice has been linked successfully to an inducible promoter (Mei *et al*., 2006). Attempts are underway at several laboratories around the world to develop such tools to genetically improve rice by increasing resistance against insects as well as pathogens (Kogel & Langen, 2005).

Induced resistance and integrated pest management

Relationships between insect control and disease control

Resistance to insects is influenced by many factors including the plant's nutritional state, its constitutive and induced traits and its environment. Integrated pest management is an attempt to manipulate the plant and its environment so as to manage losses to insects and pathogens and to maximize economic return to the growers. There has been a growing realization that managing plants for resistance to insect herbivores is both strongly affected by and also strongly influences resistance to pathogens (Karban & Baldwin, 1997; Stout *et al*., 2006). As mentioned above, for many plant species, responses to pathogens are thought to be mediated by the SA pathway, while responses to herbivores are mediated by the JA pathway. However, for rice and perhaps other cereals, the processes controlled by these two pathways are interrelated in complex ways. For example, treatment of rice plants with JA has been found to make them more attractive to some herbivores, such as brown planthoppers, in addition to deterring others (Lou *et al*., 2005). This is consistent with the observation that brown planthopper damage causes responses associated with the SA pathway rather than the JA pathway (Xu *et al*., 2003). Because these two pathways interact, attempts to manage pathogens can have strong effects on insect pests, and vice versa.

In rice, responses against insects and pathogens are clearly not always independent. For example, plants that have hosted white-backed planthoppers are strongly protected against symptoms of rice blast fungus (Kanno & Fujita, 2003; Kanno *et al*., 2005). This negative interaction was found to occur even if the planthopper and the fungus did not overlap precisely in time and space. On a larger scale, in agricultural paddies, the application of insecticides to control white-backed planthopper numbers increased the incidence of rice blast disease (Satoh *et al*., 2005). Levels of plant parasites (both insects and pathogens), as well as tactics used to control them, are likely to have complex and far-reaching affects on plant resistance.

Relationships between herbivores and their predators and parasites

Plant responses to attack by insects may also have effects on other organisms in the agroecosystem, such as the predators and parasites of herbivores. Certainly, insecticides targeted at rice pests also reduce populations of beneficial insects (Way & Heong, 1994; Matteson, 2000). If induced plant responses increase rates of predation or parasitism of herbivores, these changes may provide indirect defences for the plants. For example, rice plants that were infested with *Spodoptera litura* caterpillars or with brown planthoppers emitted volatiles that were repellent, under some circumstances, to other planthoppers that arrived subsequently (Xu *et al*., 2002, although see also Lou *et al*., 2005). Each specific herbivore species caused plants to emit a specific blend of volatiles. Volatiles released when plants were attacked by planthoppers also attracted parasitoid wasps that were specific for planthopper eggs (Lou *et al*., 2002). Similarly, rice plants treated with JA released volatiles that were attractive to parasitoids (Lou *et al*., 2005). Plants near neighbours treated with JA experienced greater rates of parasitism of brown planthopper eggs in the greenhouse and the field. This suggests that chemical elicitors may be useful as inducers of direct defences in rice as well as indirect defences mediated by predators and parasitoids.

Future prospects for induced resistance in rice IPM

Although induced resistance has played relatively little role in managing insect pests of rice, it holds great promise as a management tool for the future. Below, we consider the prospects for employing the three strategies discussed above. This may be an excellent system in which to allow early season pests to induce resistance against later ones. As discussed above, early 'vaccinations' may protect plants against later infestations of the same insect species. Rice varieties have been identified that have high levels of induced resistance against the rice gall midge and against white and brown planthoppers. Since the rice genome is so well characterized, it should be possible in the near future to incorporate induced resistance against these important pests into rice varieties that have other desirable traits.

Early attack by economically unimportant species may also provide resistance against more damaging species of rice insects. For example, leaffolders are common early season feeders although they rarely cause economic losses. Although leaffolders have often been targeted by growers using pesticides, encouraging small, natural

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populations may provide resistance against more damaging insects that attack later in the season. This possibility is currently being investigated by researchers in the Philippines, China and Malaysia. Although previous attempts to use early season insects to vaccinate against later season ones have not been adopted on a large scale, rice offers several advantages that were absent from attempts in other systems. For example, the rice leaffolder is easy to identify in the field, it has a wide natural distribution, and it can be easily introduced. Leaffolders are unlikely to become serious pests although they have the potential to help protect plants against more costly species. As noted above, using vaccinations for pest management is information intensive and labor intensive. Whereas governments and universities in North America are cutting back on field research and extension efforts, considerable infrastructure is in place in many Asian growing regions to provide information and assistance to rice farmers (Matteson, 2000; Huan *et al*., 2005).

Chemical elicitors of induced resistance may also allow rice farmers to manipulate the levels and timing of plant resistance. Several of the economically important rice pests have been found to be affected by host plant resistance that is mediated by plant hormones such as JA and SA. Experiments are currently underway to evaluate vaccinations using these elicitors as means of controlling levels of resistance of rice in production agriculture. Improved basic knowledge of the mechanisms, specificity, timing and natural history of plant hormones and their effects will make this effort more effective. Similarly, as we gain a more complete understanding of additional plant regulators and how they interact, it is likely that we will have more candidates that can be used in agriculture to manipulate plant defences.

Cereal grains were problematic candidates for improvement using biotechnology because transforming them by adding novel genes was not possible for many years. These difficulties have been solved to a large extent, and rice has become a particularly good candidate crop for biotechnological approaches since the genome has been relatively well characterized (Repellin *et al*., 2001). Biotechnological approaches require that traits providing induced resistance be identified, the genes controlling them must be mapped, and techniques for transferring them into desirable varieties be developed. Since biotechnological approaches can be extremely specific, they can theoretically provide greater safety in terms of minimizing environmental problems and undesirable secondary chemicals associated with inducers of more generalized plant responses. Additional control over expression of resistance traits may be possible if genes can be fused to inducible promoters so that the desired products can be switched on and off as needed. It remains unclear whether this potential can be realized and how many years in the future this realization may be.

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References

Babu, R.M., Sajeena, A., Samundeeswari, A.V., Sreedhar, A., Vidhyasekaran, P., Seetharaman, K. & Reddy, M.S. (2003a) Induction of systemic resistance to *Xanthomonas oryzae* pv. *oryzae* by salicylic acid in *Oryza sativa* (L.). *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **110**, 419–431.

Babu, R.M., Sajeena, A., Samundeeswarf, A.V., Sreedhar, A., Vidhyasekeran, P. & Reddy, M.S. (2003b) Induction of bacterial blight (*Xanthomonas oryzae* pv. *oryzae*) resistance in rice by treatment with acibenzolar-S-methyl. *Annals of Applied Biology* **143**, 333–340.

Bandong, J.P. & Litsinger, J.A. (2005) Rice crop stage susceptibility to the rice yellow stemborer *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae). *International Journal of Pest Management* **51**, 37–43.

Barrion, A.T., Litsinger, J.A., Medina, E.B., Aguda, R.M., Bandong, J.P., Pantua P.C. Jr., Viajante, V.D., de la Cruz, C.G. & Vega, C.R. (1991) The rice *Cnaphalocrocis* and *Marasmia* (Lepidoptera: Pyralidae) leaffolder complex in the Philippines: taxonomy, bionomics and control. *Philippine Entomologist* **8**, 987–1074.

Beauverie, J. (1901) Essais d'immunization des vegetaux contre les maladies cryptogamiques. *Comptes Rendus Hebdomadaires des Seances de l'Acadamie des Sciences, Paris* **133**, 107–110.

Bentur, J.S. & Kalode, M.B. (1996) Hypersensitive reaction and induced resistance in rice against the Asian rice gall midge *Orseolia oryzae*. *Entomologia Experimentalis et Applicata* **78**, 77–81.

Broadway, R.M. & Duffey, S.S. (1986) Plant proteinase inhibitors: mechanism of action and effect on the growth and digestive physiology of larval *Heliothis zea* and *Spodoptera exigua*. *Journal of Insect Physiology* **32**, 827–833.

Campbell, R. (1989) The use of microbial inoculants in the biological control of plant diseases. pp. 67–77 *in* Campbell, R. & Macdonald, R.M. (*Eds*) *Microbial inoculation of crop plants*. Oxford, Oxford University Press.

Cartwright, D., Langcake, P., Pryce, R.J., Leworthy, D.P. & Ride, J.P. (1977) Chemical activation of host defence mechanisms as a basis for crop protection. *Nature* **267**, 511–513.

Chatterjee, P.B. (1979) Rice leaf folder attacks in India. *International Rice Research Newsletter* **4** (3), 21.

Chern, M.S., Fitzgerald, H.A., Canlas, P.E., Navarre, D.A. & Ronald, P.C. (2005) Over-expression of a rice NPR1 homologue leads to constitutive activation of defense response and hypersensitivity to light. *Molecular Plant–Microbe Interactions* **18**, 511–520.

Chester, K.S. (1933) The problem of acquired physiological immunity in plants. *Quarterly Review of Biology* **8**, 129–154. 275–324.

Dale, D. (1994) Insect pests of the rice plant – their biology and ecology. pp. 363–485 *in* Heinrichs, E.A. (*Ed*.) *Biology and management of rice insects*. New York, Wiley.

Deacon, J.W. (1988) Biocontrol of soil-borne plant pathogens with introduced inocula. *Philosophical Transactions of the Royal Society of London B* **318**, 249–264.

Dhaliwal, G.S., Shahi, H.N., Gill, P.S. & Maskina, M.S. (1979) Field reaction of rice varieties to leaf folder at various nitrogen levels. *International Rice Research Newsletter* **4**, 7.

Dixon, R.A., Achine, L., Kota, P., Liu, C.J., Reddy, M.S.S. & Wang, L.J. (2002) The phenylpropanoid pathway and plant

https://doi.org/10.1017/S0007485307005056 Published online by Cambridge University Press

defence – a genomics perspective. *Molecular Plant Pathology* **3**, 371–390.

Farmer, E.E., Johnson, R.R. & Ryan, C.A. (1992) Regulation of expression of proteinase inhibitor genes by methyl jasmonate and jasmonic acid. *Plant Physiology* **98**, 995–1002.

Gallagher, K.D., Kenmore, P.E. & Sogawa, K. (1994) Judicial use of insecticides deters planthopper outbreaks and extends the life of resistant varieties in Southeast Asian rice. pp. 599–614 *in* Perfect, T. (*Ed.*) *Planthoppers: their ecology and management*. New York, Chapman & Hall.

Gorlach, J., Volrath, S., Knauf-Bleter, G., Hengy, G., Beckhove, U., Kogel, K.H., Oostendorp, M., Staub, T., Ward, E., Kessmann, H. & Ryals, J. (1996) Benzothiadiazole, a novel class of inducers of systemic acquired resistance, activates gene expression and disease resistance in wheat. *Plant Cell* **8**, 629–643.

Green, T.R. & Ryan, C.A. (1972) Wound-induced proteinase inhibitor in plant leaves: a possible defense mechanism against insects. *Science* **175**, 776–777.

Hait, G.M. & Sinha, A.K. (1987) Biochemical changes associated with induction of resistance in rice seedlings to *Helminthosporium oryzae* by seed treatment with chemicals. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **94**, 360–368.

Harris, M.O., Stuart, J.J., Mohan, M., Nair, S., Lamb, R.J. & Rohfritsch, O. (2003) Grasses and gall midges: plant defense and insect adaptation. *Annual Review of Entomology* **48**, 549–577.

Haukioja, E. & Hakala, T. (1975) Herbivore cycles and periodic outbreaks. Formulation of a general hypothesis. *Report of the Kevo Subarctic Research Station* **12**, 1–9.

Hedin, P.A. (1990) Bioregulator-induced changes in allelochemicals and their effects on plant resistance to pests. *Critical Reviews in Plant Sciences* **9**, 371–379.

Huan, N.H., Thiet, L.V., Chien, H.V. & Heong, K.L. (2005) Farmer's participatory evaluation of reducing pesticides, fertilizers and seed rates in rice farming in the Mekong Delta, Vietnam. *Crop Protection* **24**, 457–464.

Hu-Qi, Y., Li-Yue, R., Zheng-Yu, Hu-Xi, B., Zhang-Xaio, J. & Li-Ben, J. (2005) Insecticidal activity of transgenic rice expressing CpTI or CpTI + Bt against *Chilo suppressalis* Walker. *Journal of Fujian Agriculture and Forestry University, Natural Science Edition* **34**, 185–188.

Isman, M.B. (2006) Botanical insecticides, deterrents, and repellents in modern agriculture and the increasingly regulated world. *Annual Review of Entomology* **51**, 45–66.

Jongsma, M.A., & Bolter, C. (1997) The adaptation of insects to plant protease inhibitors. *Journal of Insect Physiology* **43**, 885–895.

Kagale, S., Marimuthu, T., Thayumanavan, B., Nandakumar, R. & Samiyappan, R. (2004) Antimicrobial activity and induction of systemic resistance in rice by leaf extract of *Datura metel* against *Rhizoctonia solani* and *Xanthomonas oryzae* pv. *oryzae*. *Physiological and Molecular Plant Pathology* **65**, 91–100.

Kanno, H. & Fujita, Y. (2003) Induced systemic resistance to rice blast fungus in rice plants infested by white-backed planthopper. *Entomologia Experimentalis et Applicata* **107**, 155–158.

Kanno, H., Satoh, M., Kimura, T. & Fujita, Y. (2005) Some aspects of induced resistance to rice blast fungus, *Magnaporthe grisea*, in rice plant infested by white-backed planthopper, *Sogatella furcifera*. *Applied Entomology and Zoology* **40**, 91–97.

Karban, R. & Baldwin, I.T. (1997) *Induced responses to herbivory*. 319 pp. Chicago, University of Chicago Press.

Karban, R. & Carey, J.R. (1984) Induced resistance of cotton seedlings to mites. *Science* **225**, 53–54.

Kenmore, P.E., Cariño, F.O., Perez, C.A., Dyck, V.A. & Gutierrez, A.P. (1984) Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stål) within rice fields in the Philippines. *Journal of Plant Protection in the Tropics* **1**, 19–37.

Khan, Z.R., Barrion, A.T., Litsinger, J.A., Castilla, N.P. & Joshi, R.C. (1988) Mini review: a bibliography of rice leaffolders (Lepidoptera: Pyralidae). *Insect Science and Its Application* **9**, 129–174.

Khan, Z.R., Litsinger, J.A., Barrion, A.T., Villaneuva, F.F.D., Fernandez, N.J. & Taylor, B. (1991) *World bibliography of rice stem borers, 1794–1990*. 415 pp. Los Banos, Philippines, International Rice Research Institute.

Kogel, K.H. & Langen, G. (2005) Induced disease resistance and gene expression in cereals. *Cellular Microbiology* **7**, 1555–1564.

Kuc, J. (1982) Induced immunity to plant disease. *BioScience* **32**, 854–860.

Kuc, J. (1995) Induced systemic resistance – an overview. pp. 169–175 *in* Hammerschmidt, R. & Kuc, J. (*Eds*) *Induced resistance to diseases in plants*. Amsterdam, Kluwer.

Lee, A., Cho, K., Jang, S., Rakwal, R., Iwahashi, H., Agrawal, G.K., Shim, J. & Han, O. (2004) Inverse correlation between jasmonic acid and salicylic acid during early wound response in rice. *Biochemical and Biophysical Research Communications* **318**, 734–738.

Lee, M.W., Qi, M. & Yang, Y. (2001) A novel jasmonic acid-inducible rice *myb* gene associates with fungal infection and host cell death. *Molecular Plant-Microbe Interactions* **14**, 527–535.

Li-Yue, R., Hu-Qi, Y., Zheng-Yu, Hu-Xi, B., Zhang-Xiao, J. & Li-Ben, J. (2005) Field evaluation of the resistance of transgenic rice expressing CpTI or CpTI + Bt to lepidopterous pests. *Journal of Fujian Agriculture and Forestry University, Natural Science Edition* **34**, 181–184.

Lou, Y., Cheng, J., Ping, X., Tang, F., Ru, S. & Du, M. (2002) Mechanisms on host discrimination between two hosts *Nilaparvata lugens* and *Sogatella furcifera* by the egg parasitoid *Anagrus nilaparvatae*. *Acta Entomologica Sinica* **45**, 770–776.

Lou, Y., Du, M., Turlings, T.C.J., Cheng, J. & Shan, W. (2005) Exogenous application of jasmonic acid induces volatile emissions in rice and enhances parasitism of *Nilaparvata lugens* eggs by the parasitoid *Anagrus nilaparvatae*. *Journal of Chemical Ecology* **31**, 1985–2002.

Malamy, J., Carr, J.P., Klesig, D.F. & Raskin, I. (1990) Salicylic acid: a likely endogenous signal in the resistance response of tobacco to viral infection. *Science* **250**, 1002–1004.

Matsumura, M. & Suzuki, Y. (2003) Direct and feeding-induced interactions between two rice planthoppers, *Sogatella furcifera* and *Nilaparvata lugens*: effects on dispersal capability and performance. *Ecological Entomology* **28**, 174–182.

Matteson, P.C. (2000) Insect pest management in tropical Asian irrigated rice. *Annual Review of Entomology* **45**, 549–574.

Mei, C., Qi, M., Sheng, G. & Yang, Y. (2006) Inducible overexpression of a rice allene oxide synthase gene increases the endogenous jasmonic acid level, *PR* gene expression and host resistance to fungal infection. *Molecular Plant–Microbe Interactions* **19**, 1127–1137.

https://doi.org/10.1017/S0007485307005056 Published online by Cambridge University Press

Métraux, J.P., Signer, H., Ryals, J., Ward, E., Wyss-Benz, M., Gaudin, J., Raschdorf, K., Schmid, E., Blum, W. & Inverardi, B. (1990) Increase in salicylic acid at the onset of systemic acquired resistance in cucumber. *Science* **250**, 1004–1006.

Miyashita, T. (1985) Estimation on the economic injury level in the rice leafroller *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). I. Relation between yield loss and injury of rice leaves at heading or in the grain filling period. *Japanese Journal of Applied Entomology and Zoology* **29**, 73–76.

Munusamy, M., Selvaraj, P., Murugaiyan, S., Sundaram, S., Chung, H.Y., Yang, J.C., Subbiah, S. & Sa, T.M. (2004) Growth promotion and induction of systemic resistance in rice cultivar Co-47 (*Oryza sativa* L.) by *Methylobacterium* spp. *Botanical Bulletin of Academia Sinica* **45**, 315–324.

Nagadhara, D., Ramesh, S., Pasalu, I.C., Kondala Rao, Y., Sarma, N.P., Reddy, V.D. & Rao, K.V. (2004) Transgenic rice plants expressing the snowdrop lectin gene (gna) exhibit high-level resistance to the whitebacked planthopper (*Sogatella furcifera*). *Theoretical and Applied Genetics* **109**, 1399–1405.

Rath, L.K. & Misra, D.S. (1998) Induced resistance in rice through certain micronutrient fertilizer application to whitebacked planthopper, *Sogatella furcifera* (Horvath). *Journal of Insect Science* **11**, 26–29.

Ray, J. (1901) Les maladies cryptogamiques des vegetaux. *Revue Generale de Botanique* **13**, 145–151.

Repellin, A., Baga, M., Jauhar, P.P., & Chibbar, R.N. (2001) Genetic enrichment of cereal crops via alien gene transfer: new challenges. *Plant Cell, Tissue and Organ Culture* **64**, 159–183.

Ross, A.F. (1961) Systemic acquired resistance induced by localized virus infections in plants. *Virology* **14**, 340–358.

Sardesai, N., Rajyashri, K.R., Behura, S.K., Nair, S. & Mohan, M. (2001) Genetic, physiological and molecular interactions of rice and its major dipteran pest, gall midge. *Plant Cell, Tissue and Organ Culture* **64**, 115–131.

Satoh, M., Nakajima, T. & Kanno, H. (2005) Induced resistance to rice blast disease in rice plants infested with the whitebacked planthopper, *Sogatella furcifera*, in a paddy field. *Japanese Journal of Applied Entomology and Zoology* **49**, 105–111.

Schuler, G., Gorls, H. & Boland, W. (2001) 6-substituted indanoyl isoleucine conjugates mimic the biological activity of coronatine. *European Journal of Organic Chemistry* **2001**, 1663–1668.

Schweizer, P., Buchala, A. & Metraux, J.P. (1997) Gene-expression patterns and levels of jasmonic acid in rice treated with the resistance inducer 2,6–dichloroisonicotinic acid. *Plant Physiology* **115**, 61–70.

Schweizer, P., Buchala, A., Budler, R. & Metraux, J.P. (1998) Induced systemic resistance in wounded rice plants. *Plant Journal* **14**, 475–481.

Schweizer, P., Schlagenhauf, E., Schaffrath, U. & Dudler, R. (1999) Different patterns of host genes are induced in rice by *Pseudomonas syringae*, a biological inducer of resistance, and the chemical inducer benzothiadiazole (BTH). *European Journal of Plant Pathology* **105**, 659–665.

Seino, Y., Suzuki, Y. & Sogawa, K. (1996) An ovicidal substance produced by rice plants in response to oviposition by the whitebacked planthopper, *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae). *Applied Entomology and Zoology* **31**, 467–473.

Shepard, B.M., Barrion, A.T. & Litsinger, J.A. (1995) *Rice-feeding insects of tropical Asia*. Manila, Philippines, International Rice Research Institute.

Silverman, P., Seskar, M., Kanter, D., Schweizer, P., Metraux, J.P. & Raskin, I. (1995) Salicylic acid in rice. Biosynthesis, conjugation, and possible role. *Plant Physiology* **108**, 633–639.

Sinha, A.K. & Hait, G.N. (1982) Host sensitization as a factor in induction of resistance in rice against *Drechslera* by seed treatment with phytoalexin inducers. *Transactions of the British Mycological Society* **79**, 213–219.

Stout, M.J., Thaler, J.S. & Thomma, B.P.H.J. (2006) Plant-mediated interactions between pathogenic microorganisms and herbivorous arthropods. *Annual Review of Entomology* **51**, 663–689.

Suzuki, Y., Sogawa, K. & Seino, Y. (1996) Ovicidal reaction of rice plants against the whitebacked planthopper, *Sogatella furcifera* Horvath (Homoptera: Delphacidae). *Applied Entomology and Zoology* **32**, 530–532.

Thaler, J.S. & Bostock, R.M. (2004) Interactions between abscisic-acid mediated responses and plant resistance to pathogens and insects. *Ecology* **85**, 48–58.

Walling, L.L. (2000) The myriad plant responses to herbivores. *Journal of Plant Growth Regulation* **19**, 195–216.

Wang, X., Ren, X., Zhu, L. & He, G. (2004) *OsBi1*, a rice gene, encodes a novel protein with a CBS-like domain and its expression is induced in responses to herbivore feeding. *Plant Science* **166**, 1581–1588.

Wang, X.L., He, R.F. & He, G.C. (2005) Construction of suppression subtractive hybridization libraries and identification of brown planthopper-induced genes. *Journal of Plant Physiology* **162**, 1254–1262.

Way, M.J. & Heong, K.L. (1994) The role of biodiversity in the dynamics and management of insect pests of tropical irrigated rice – a review. *Bulletin of Entomological Research* **84**, 567–587.

Wu, J., Xu, J., Yuan, S., Liu, J., Jiang, Y. & Xu, J. (2001) Pesticide-induced susceptibility of rice to brown planthopper *Nilaparvata lugens*. *Entomologia Experimentalis et Applicata* **100**, 119–126.

Wu, J., Hui-Min, H., Yang, G., Liu, J., Liu, G. & Wilkins, R.M. (2004) Effective duration of pesticide-induced susceptibility of rice to brown planthopper (*Nilaparvata lugens* Stål, Homoptera: Delphacidae), and physiological and biochemical changes in rice plants following pesticide application. *International Journal of Pest Management* **50**, 55–62.

Xu, T., Zhou, Q., Xia, Q., Zhang, W.Q. & Gu, D.X. (2002) Effects of herbivore-induced rice volatiles on the host selection behavior of brown planthopper, *Nilaparvata lugens*. *Chinese Science Bulletin* **47**, 1355–1360.

Xu, T., Zhou, Q., Chen, W., Zhang, G., He, G., Gu, D. & Zhang, W. (2003) Involvement of jasmonate-signaling pathway in the herbivore-induced rice plant defense. *Chinese Science Bulletin* **48**, 1982–1987.

Yadava, C.P., Santaram, G., Israel, P. & Kalode, M.B. (1972) Life history of rice leaf-roller, *Cnaphalocrocis medinalis* Guenee (Lepidoptera: Pyralidae) and its rection to some rice varieties and grasses. *Indian Journal of Agricultural Science* **42**, 520–523.

Yamasaki, M., Yoshimura, A. & Yasui, H. (2000) Mapping of quantitative trait loci of ovicidal response to brown planthopper (*Nilaparvata lugens* Stål) in rice (*Oryza* sativa L.) *Breeding Science* **50**, 291–296.

https://doi.org/10.1017/S0007485307005056 Published online by Cambridge University Press

Yamasaki, M., Yoshimura, A. & Yasui, H. (2003) Genetic basis of ovicidal response to whitebacked planthopper (*Sogatella furcifera* Horvath) in rice (*Oryza sativa* L.) *Molecular Breeding* **12**, 133–143.

Yang, Y.N., Qi, M. & Mei, C.S. (2004) Endogenous salicylic acid protects rice plants from oxidative damage caused by aging as well as biotic and abiotic stress. *Plant Journal* **40**, 909–919.

Yuan, H.Y., Chen, X.P., Zhu, L. & He, G.C. (2004) Isolation and characterization of a novel rice gene encoding a putative insect-inducible protein homologous to wheat Wir1. *Journal of Plant Physiology* **161**, 79–85.

Zhang, F., Zhu, L. & He, G. (2004) Differential gene expression in response to brown planthopper feeding in rice. *Journal of Plant Physiology* **161**, 53–62.

Zhou, Q., Xu, T., Zhang, G.R., Gu, D.X. & Zhang, W.Q. (2003) Repellent effects of herbivore-induced rice volatiles on the brown planthopper, *Nilaparvata lugens* Stål. *Acta Emotomologica Sinica* **46**, 739–744.

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