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Integrating gene deployment and crop management for improved rice resistance to Asian planthoppers

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ABSTRACT

This review examines the effects of crop management on the efficiency and durability of planthopper resistant rice in Asia. Historical evidence and selection experiments indicate that the proportion of virulent individuals in planthopper populations is normally sufficiently high for populations to overcome major resistance genes within 12–15 generations. Pyramiding resistance may prolong durability, but will depend on avoiding concurrent deployment of monogenic and pyramided lines that share resistance genes, and on the capacity of planthoppers to maintain virulence to ≥2 genes. Combining major genes with quantitative resistance will increase durability. Planthopper population size is likely to be the main contributor to virulence adaptation during the early stages of varietal adoption. High fertilizer inputs increase the availability of soluble proteins, thereby increasing rice susceptibility to planthoppers. Resurgence insecticides can directly increase host plant susceptibility, increase planthopper fecundity, and/or deplete natural enemy abundance, leading to rapid increases in planthopper densities. Nevertheless, comparative experiments indicate that the relative fitness of planthoppers on resistant and susceptible varieties is often maintained across gradients of fertilizer and insecticide applications. However, densities of planthoppers will increase in response to high inputs thereby enhancing the potential for populations to overcome resistance. Avoiding excessive fertilizer applications and resurgence insecticides, rotating rice varieties, increasing rice genetic diversity in the landscape, and maintaining generalist natural enemies will slow planthopper population growth, enhance resistance and has the potential to prolong durability. Because insecticides reduce the profitability of using resistant varieties, host plant resistance must be accompanied by a concomitant decline in insecticide use if it is to achieve its goals as an efficient, economic and environmentally friendly pest management option.

1. Introduction

Host plant resistance has been the main focus of public research into the management of Asian rice planthoppers (Hemiptera: Delphacidae) for the last several decades (Horgan, 2017). The term 'host plant resistance' (HPR) refers to the utilization of rice plants with specific anatomical, physiological or biochemical properties to protect against insect damage. Deploying planthopper-resistant rice is regarded as an amenable management strategy that is compatible with biological control and unaffected by insecticides or other pesticides (Heinrichs, 1986). To date several researchers have identified a range of resistance genes and quantitative trait loci (QTLs)(Zhang, 2007; Fujita et al., 2013; Hu et al., 2016a), examined their modes of action (Fujita et al., 2013) and, using marker-assisted selection (MAS), have introgressed one or more resistance genes into susceptible high-yielding varieties (HYVs) (Hu et al., 2012, 2013; Liu et al., 2016), sometimes in combination with other traits such as disease resistance (Xu, 2013; Ji et al., 2016). However, despite the tremendous advances in scientific knowledge of HPR, the actual impact of resistant rice varieties in reducing planthopper-related damage and yield losses in farmers' fields has been difficult to quantify.

At the initiation of this review, all scientific papers on HPR against the brown planthopper, *Nilaparvata lugens* (Stål) or whitebacked planthopper, *Sogatella furcifera* (Horváth) published since 2000 (100 papers, until 2017) were examined to assess authors' expectations for HPR. Authors claimed HPR to be 'economical', 'efficient' and/or 'environmentally friendly' in 73% of these papers (Fig. 1). However, evidence to support these claims was generally weak; only 34 papers supplied any references to back up claims of success. However, when investigated further, these references also lacked any concrete evidence of HPR having functioned in reducing planthopper damage or preventing outbreaks in farmers' fields. Heinrichs (1986), who offers one of

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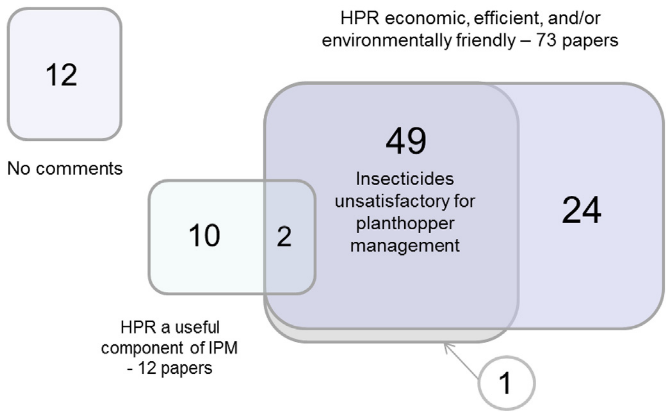

Fig. 1. Venn diagram representing researcher-expressed beliefs of the benefits of planthopper-resistant rice. Numbers are based on comments in 100 peer-reviewed articles published between 2000 and 2017 (retrieved using 'resistance', '*Nilaparvata*' and '*Sogatella*' as search terms in ISI Web of Science and Google Scholar).

very few accounts of the possible success of rice HPR, suggests that by the mid-1980s, over 80% of rice in Asia had included some resistance to the brown planthopper. However, because this referred to resistance mainly derived from the *Bph1* and *bph2* genes that are now ineffective throughout Asia (Myint et al., 2009a; Horgan et al., 2015, 2017a), much of the rice currently grown in the region is likely to be without any major functioning resistance. For example, during an outbreak in Central Java (Indonesia) in 2011–2012, 48 varieties were reported as heavily damaged by the brown planthopper; of these 56% were mentioned in government literature as having some resistance against the planthopper (F. Horgan and A.M. Stuart, unpublished data). The emergence of adapted planthopper populations (often referred to as 'biotypes': but see Claridge and Den Hollander, 1983) remains a major challenge to the effectiveness of resistant rice in Asia. Although resistant varieties with novel genes (e.g., *Bph14* and *Bph15*) have recently been released, particularly in China (Wang et al., 2009; Hu et al., 2012, 2013, 2015), there is still little available information on their deployment or effectiveness in farmers' fields.

Almost 50% of recent planthopper-HPR papers also suggest that the application of insecticides is an unsustainable approach to managing planthopper outbreaks, and/or has associated deleterious effects on human health or the environment (Fig. 1). These papers promote HPR as an alternative to insecticides in Asian rice production. The reduction of insecticide use is an important objective of HPR because planthopper outbreaks have been associated with excessive insecticide applications (Ge et al., 2009; Wang et al., 2010; Azzam et al., 2011; Bottrell and Schoenly, 2012; Horgan and Crisol, 2013; Horgan, 2017). However, it is now apparent that HPR against planthoppers has failed to reduce insecticide use among rice farmers in Asia. Indeed, during the same time that research has intensified into the search for genes and the molecular breeding of resistant rice varieties, trade in insecticides across Asia has dramatically increased (Spangenberg et al., 2015; Horgan et al., 2016a; Horgan, 2017). Furthermore, rice farmers have significantly increased the number of insecticide applications they make each season, with many farmers moving toward prophylactic spray schedules as opposed to using insecticides as a curative measure in integrated management (Robinson et al., 2007; Spangenberg et al., 2015; Horgan, 2017).

The present paper focuses on strategies to enhance the potential benefits of HPR in rice production systems. Improved integrated management strategies are necessary to ensure that resistant varieties become truly 'efficient', 'economical' and 'environmentally friendly' to meet the desired outcomes expressed by the scientists and research institutes that have helped to develop them. Furthermore, to maximize research investments, resistance must be made more durable (i.e., resistant varieties must last through more rice cropping seasons before planthopper populations become predominantly virulent to their resistance genes), particularly since rice resistance genes are likely to be rare in nature (Chang, 1989). This paper therefore examines the role of crop management in determining the efficiency and durability of resistance in Asian rice fields and examines some of the proposed strategies to prolong that durability. Finally, empirical studies into the integrated pest management (IPM) of rice planthoppers often overlook the role of variety-planthopper interactions in determining the outcome of management interventions (Horgan et al., 2016a; Gurr et al., 2016). Furthermore, rice breeders tend to deploy resistance through national research centres, without consideration of the local ecology of planthoppers, or without informed directives for the proper management of resistance (Van Emden, 1991; Wang et al., 2009; Horgan, 2017). This paper therefore examines ways in which HPR might work in synergy with other elements of IPM as a component of sustainable rice farming practices.

2. Review methods

Literature related to HPR against Asian planthoppers in rice was identified by applying relevant search terms (including: '*Oryza*' or 'rice' and '*Nilaparvata*' or '*Sogatella*', based on records from January 1960 to July 2017) using the ISI Web of Knowledge and Google Scholar. Relevant unpublished records and theses were also retrieved from the rice library at the International Rice Research Institute (IRRI). The review was structured to examine issues of varietal deployment and to relate these to the role of population size in determining resistance strength and durability. Aspects of crop management that related directly to planthopper fitness and population size on resistant varieties were then examined. The review did not focus in depth on aspects of rice breeding, which have been thoroughly reviewed in a number of recent publications (Zhang, 2007; Fujita et al., 2013; Hu et al., 2016a), but focused instead on the 'in field' dynamics between resistant rice and planthoppers. The review uses the term 'breakdown' to describe the loss of effective resistance in rice fields, which is generally, but not necessarily, attributed to planthopper adaptation to resistance genes.

3. The nature of resistance

Currently, over 40 genes have been identified with resistance to the brown and whitebacked planthoppers in rice (Zhang, 2007; Fujita et al., 2013; Srinivasan et al., 2016). A key feature of 'resistance' is that it is a relative condition usually weighed against some standard of susceptibility. Furthermore, resistance is not only a feature of the host plant, but a feature of interactions between the plant and the insect. As such, resistance is highly dependent on the nature of the insect and on the co-evolutionary history of the host-herbivore relationship (Simms and Fritz, 1990). Planthoppers are typical r-strategists that reproduce rapidly, have a short generation time, and invest little in defence against natural enemies (Dyck et al., 1979). Because planthoppers often have ≥ 3 generations on a single rice plant, they can become maladapted to their host and exhibit fitness reductions when they must move to a new host phenotype (Claridge and Den Hollander, 1982; Claridge et al., 1982; Horgan and Ferrater, 2017). Resistance, albeit weak resistance, can therefore result from a lack of planthopper experience with the host phenotype (i.e., variations in plant volatiles, physical barriers, or other anatomical and biochemical features) (Claridge et al., 1982). Such variations are mainly governed by quantitative traits, but some may also be related to major genes (i.e., presence/absence of some volatile component or surface feature such as waxes: Woodhead and Padgham, 1988). Presumably, adult planthoppers will face the greatest barriers to host switching on those varieties that are most genetically distant from the varieties on which they developed as nymphs (Claridge and Den Hollander, 1982; Claridge et al., 1982; Horgan and Ferrater, 2017; Horgan et al., 2017a). Several authors have indicated that a