



Unanticipated benefits and potential ecological costs associated with pyramiding leafhopper resistance loci in rice

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ABSTRACT

We tested the hypotheses that increasing the number of anti-herbivore resistance loci in crop plants will increase resistance strength, increase the spectrum of resistance (the number of species affected), and increase resistance stability. We further examined the potential ecological costs of pyramiding resistance under benign environments. In our experiments, we used 14 near-isogenic rice lines with zero (T65: recurrent parent), one, two or three resistance loci introgressed through marker-assisted selection. Lines with two or more loci that were originally bred for resistance to the green rice leafhopper, *Nephotettix cincticeps*, significantly reduced egg-laying by the green leafhopper, *N. virescens*. Declines in egg-number and in nymph weight were correlated with the numbers of resistance loci in the rice lines. To test the spectrum of resistance, we challenged the lines with a range of phloem feeders including the zig-zag leafhopper, *Recilia dorsalis*, brown planthopper, *Nilaparvata lugens*, and whitebacked planthopper, *Sogatella furcifera*. There was an increase in the number of tested species showing significant declines in egg-laying and nymph survival on lines with increasing numbers of loci. In a screen house trial that varied rates of nitrogenous fertilizer, a line with three loci had stable resistance against the green leafhopper and the grain yields of infested plants were maintained or increased (overcompensation). Under benign conditions, plant growth and grain yields declined with increasing numbers of resistance loci. However, under field conditions with natural exposure to herbivores, there were no significant differences in final yields. Our results clearly indicate the benefits, including unanticipated benefits such as providing resistance against multiple herbivore species, of pyramiding anti-herbivore resistance genes/loci in crop plants. We discuss our results as part of a review of existing research on pyramided resistance against leafhoppers and planthoppers in rice. We suggest that potential ecological costs may be overcome by the careful selection of gene combinations for pyramiding, avoidance of high (potentially redundant) loci numbers, and introgression of loci into robust plant types such as hybrid rice varieties.

1. Introduction

Recent advances in marker-assisted selection for food and fibre crops have streamlined breeding programs (Bourke et al., 2018; Garrido-Cardenas et al., 2018) and given new insights into the ecological and evolutionary relations between plants and components of their environment (O'Rourke et al., 2014; Odjo et al., 2017). One area

where knowledge has rapidly accumulated is in the understanding of plant–herbivore interactions, particularly for monophagous and oligophagous phloem-feeding (Zhang et al., 2017) and gall-inducing (Sinha et al., 2017) insects that exhibit highly specific molecular challenge-and-defence interactions with their hosts. Where gaps in knowledge still exist, paradigms concerning anti-herbivore resistance are often borrowed from advances in disease resistance or from recent developments

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in transgenic research (Gould, 2003; Zhao et al., 2005; Horgan, 2018) without adequate empirical research using insect herbivores on conventionally bred varieties. Some paradigms, for example the maintenance of refuge areas to delay virulence adaptation, continue to govern current management practices for resistant crops without consideration of the inherent differences between transgenic resistance and conventional resistance based on ‘native’ genes (i.e., derived from the crop species or its wild relatives) (Horgan, 2018).

A range of phloem-feeding insects, including leafhoppers (e.g., the green rice leafhopper [GRH], *Nephotettix cincticeps*, and green leafhopper [GLH], *N. virescens*) and planthoppers (e.g., the brown planthopper [BPH], *Nilaparvata lugens*, and whitebacked planthopper [WBPH], *Sogatella furcifera*), currently challenge rice production in Asia. These species can cause severe yield reductions to intensified rice agroecosystems, particularly where farmers are encouraged to use high rates of nitrogenous fertilizer and prophylactic insecticide applications (Bottrell and Schoenly, 2012; Crisol et al., 2013). Host plant resistance has been the principal focus of public research into the management of rice leafhoppers and planthoppers for the last several decades and has gained new impetus from recent advances in molecular breeding (Fujita et al., 2013; Hu et al., 2016a). Because the success of host plant resistance is limited by herbivore adaptation to resistant varieties (often referred to as ‘virulence adaptation’), there has been a clear focus on selecting recognized ‘broad spectrum’ genes/loci, or on pyramiding a number of genes/loci into a single genotype to prolong resistance durability (Myint et al., 2012; Wang et al., 2017; Horgan et al., 2018a). A number of research groups have now developed multiple near-isogenic rice lines with a range of different resistance genes either singly introgressed (monogenic) or pyramided (polygenic) into high-yielding varieties, each with > 85% recovery of the recurrent parent genes (Fujita et al., 2010; Hu et al., 2016b; Jena et al., 2017). Polygenic resistance to herbivores is predicted to be stronger (Fujita et al., 2010; Hu et al., 2013; Asano et al., 2015), have a broader spectrum (Hu et al., 2016b; Fan et al., 2017), have greater stability (Ali et al., 2006), and be more durable (Myint et al., 2012; Wang et al., 2017; Horgan et al., 2018a) than monogenic resistance. Ecological theory suggests that strong resistance is also likely to have associated costs as plants must balance growth, reproduction and defence (including maintenance) to achieve optimal life-history strategies in their respective niches (Hermes and Mattson, 1992; Horgan et al., 2009). Research on traditional rice varieties with polygenic herbivore resistance supports many of these ideas (Hirae et al., 2007; Horgan et al., 2015, 2017). However, despite the tremendous investments into pyramiding herbivore resistance genes/loci, surprisingly few researchers have tested these hypotheses using available near-isogenic materials.

In the present study, we use a series of near-isogenic monolocus and pyramided (henceforth PYLs) lines to examine hypotheses concerning the number of herbivore resistance genes and the nature of resulting resistance. We developed clear tests to assess hypotheses concerning the strength, spectrum, stability and costs of resistance. We predicted that lines with higher numbers of genes/loci would have stronger resistance to phloem-feeders, irrespective of the identity of the genes. We predicted that lines with higher numbers of genes/loci would also affect a greater spectrum of phloem feeders due to the increasing probability of introducing non-specific resistance genes to lines through greater numbers of pyramided loci. Broad spectrum resistance is often evaluated in terms of the number of populations of a single species affected by the resistance. In our study, we examine the spectrum of resistance in terms of the number of different herbivore species affected by lines with increasing numbers of genes. Resistance stability can be measured as the consistency of resistance during different stages of plant growth or under different environments. We predicted that lines with increasing numbers of loci would maintain resistance and yields when attacked by leafhoppers under a gradient of fertilizer applications. Finally, we examined the potential costs of resistance for the rice plants. We predicted that under benign conditions (i.e., not challenged by

herbivores), lines with higher numbers of loci would express trade-offs in plant growth and development or in reproductive output (yield). To our knowledge, this is the first study to test these hypotheses in a systematic manner using a collection of near-isogenic rice lines.

2. Materials and methods

2.1. Plant materials

A series of 14 near-isogenic lines (NILs) with Taichung 65 (T65), a *japonica* cultivar, as the genetic background were developed using marker-assisted selection and backcrossing. Four rice lines (IR24, DV85, IRGC104630, and IRGC105715) with recognized resistance to the green rice leafhopper (GRH), *N. cincticeps*, were used as donor parents. These were obtained from the Genetic Resources Center of the International Rice Research Institute (IRRI) in the Philippines. The following resistance loci have been identified and tagged from these donors: *GRH1* (from IR24, an *indica* variety: Yasui and Yoshimura, 1999), *GRH2* and *GRH4* (from DV85, an *indica* variety from Bangladesh: Yazawa et al., 1998), *GRH5* and *qGRH4* (from IRGC104630 [W1962], a wild accession of *Oryza rufipogon* from China: Fujita et al., 2006) and *GRH6* (from IRGC105715, a wild accession of *O. nivara* from Cambodia: Fujita et al., 2004).

Repeated backcrossing (three to six times) with T65 using marker-assisted selection produced *GRH1*-NIL (BC₃), *GRH2*-NIL (BC₆), *GRH4*-NIL (BC₆), *GRH5*-NIL (BC₄), *GRH6*-NIL (BC₃), and *qGRH4*-NIL (BC₄). Eight PYLs, *GRH2/GRH4*-PYL, *GRH2/GRH6*-PYL, *GRH4/GRH6*-PYL, *GRH5/qGRH4*-PYL, *GRH2/GRH5*-PYL, *GRH4/GRH5*-PYL, *GRH5/GRH6*-PYL, and *GRH2/GRH4/GRH6*-PYL were developed by crossing pairs of NILs with the corresponding GRH-resistance genes. The F₁ plants carrying two or three GRH-resistance genes were self-pollinated and individuals with homozygous alleles at the resistance gene loci were selected through the F₂ populations. Seed for the experiments was bulked up in a screen house at IRRI during the dry season when temperatures were coolest.

The NILs and PYLs had previously been evaluated for resistance against GRH in Japan. Nymphal mortality on the lines was generally high (> 74%) at two and eight weeks after sowing in seedling and leaf-blade bioassays, respectively (mortality on T65 ≤ 4%). Only *GRH4*-NIL did not exhibit antibiosis against nymphs in the tests (*GRH1*-NIL, *qGRH4*-NIL and *GRH5/qGRH4*-PYL were not evaluated: Fujita et al., 2010).

2.2. Herbivore species

We used two leafhopper species (GLH and the zig-zag leafhopper (ZLH), *Recilia dorsalis*) and two planthopper species (BPH and WBPH) in our experiments; however, GLH was the model species for most of our experiments because it was most affected by the resistance loci and is closely related to GRH. Colonies of all four species were initiated in 2008 using wild-caught individuals from Laguna Province in the Philippines (14°16'N, 121°21'E). Colonies were initiated with ca. 500 adults placed on TN1 (> 30 DAS) in wire mesh cages of 120 × 60 × 60 cm (H × L × W) under greenhouse conditions (temperatures ranged from 25 to 37 °C, L12:D12 photoperiod). During the first two generations of rearing, the colonies were monitored for possible transmission of rice viruses. The leafhoppers did not transmit viruses.

2.3. Resistance strength

Aspects of resistance strength were assessed in greenhouse bioassays with GLH and BPH on potted plants. Germinated seeds of the 14 lines were each sown to size-0 (5 × 2.5 cm: H × R) pots under acetate cages (45 × 5 cm: H × R) and tended until 20-days after sowing (DAS), after which two gravid females were introduced to the cages. IR24 was

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