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Resistance and tolerance to the brown planthopper, *Nilaparvata lugens* (Stål), in rice infested at different growth stages across a gradient of nitrogen applications

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ABSTRACT

High resource availability can reduce anti-herbivore resistance (a plant's ability to defend against herbivores and reduce damage) in rice, *Oryza sativa* L, but may also increase tolerance (a plant's ability to withstand damage by, for example, compensatory growth). Through a series of greenhouse, screenhouse and field experiments, this study examines fitness (survival and development × reproduction) of the brown planthopper, *Nilaparvata lugens* (Stål), on resistant (IR62) and susceptible (IR22) rice varieties and age-related rice tolerance to planthopper damage under varying resource (nitrogenous fertilizer) availability. Planthoppers reared on IR62 in the greenhouse had lower fitness than planthoppers on IR22. IR62 became increasingly resistant as plants aged. IR22 was generally more tolerant of planthopper damage, and tolerance increased in IR22, but declined in IR62, as the plants aged. Rice plants infested at pre-tillering stages (3–4 leaf stage) in the screenhouse had greater losses to root, shoot and grain yield per unit weight of planthopper than plants infested at tillering stages, particularly in IR22. These trends were mainly due to the impact of planthoppers during pre-tillering stages and the length of exposure to the planthoppers. High nitrogen compromised IR62 resistance, particularly in tillering plants in the greenhouse study; however, high nitrogen did not increase planthopper biomass-density on IR62 in greenhouse or field cages. Tolerance to damage in IR62 at mid-tillering stages declined under increasing levels of nitrogen, but nitrogen increased tolerance during late-tillering stages. Planthopper damage to IR22 in field cages was severe and hopperburn (plant death) occurred in 83% of IR22 plants under high nitrogen (60–150 kg N ha^{-1}). In contrast, despite planthopper infestations, damage to IR62 was low in field-grown plants and productivity (tillers, roots, shoots and grain) increased in IR62 under increasing nitrogen. Our results indicate that, whereas nitrogenous fertilizer increases planthopper fitness on susceptible and resistant varieties, the net effects of high nitrogen on IR62 include decreased planthopper biomass-density (apparent in all experiments) and higher tolerance to damage during later growth stages (observed in the greenhouse, and during one of two seasons in field cages).

1. Introduction

Vigorously growing plants, such as plants growing under nutrient-rich and high-light conditions, are often more attractive to herbivores (plant vigour hypothesis, PVH: Price, 1991). In a meta-analysis by Cornelissen and Fernandes (2008) of 71 published studies, phloem-feeding herbivores (Hemiptera) in particular, were shown to increase in abundance (up to 75%) on more vigorous plants or modules, in effect, decreasing anti-herbivore resistance (the ability to defend against herbivores: Table 1). Since tolerance to herbivory (a plant's ability to withstand herbivore attack by, for example compensatory growth: Table 1) is often higher under high resource/low competition conditions (compensatory continuum hypothesis, CCH: Maschinski and Whitham, 1989), vigorous plants are also expected to better tolerate herbivore damage than less vigorous plants. This has been demonstrated across a range of wild and cultivated plants (Müller-Schärer

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Table 1
Functional categories of plant-herbivore interaction.[a]

Functional category	Definition	Effects on herbivores[b]	Effects on plant[b]	Estimated in this study
Susceptibility	Inability of a plant to deter or defend against damage from herbivores	No negative effects	Normally high damage	Comparison of damage (biomass loss) against resistant variety
Resistance	A plant trait that reduces potential damage from herbivores compared to susceptible plants	Relative decline in fitness through antixenotic or antibiotic effects[c]	Relative decline in damage	Comparison of damage (biomass loss) against susceptible variety
Antixenosis	Plant traits (mechanisms) that deter herbivores from ovipositing or from initiating feeding	Relatively low oviposition and/or feeding preferences	Relative decline in damage	Not estimated here (requires choice bioassays)
Antibiosis	Plant traits (mechanisms) that adversely affect the survival, growth or reproductive output of herbivores	Relative decline in survival, biomass, development time, or fecundity	Relative decline in damage	Comparisons of oviposition, nymph survival, nymph biomass, development times, and feeding efficiency (honeydew) with susceptible variety
Tolerance	A plant's capacity to withstand herbivore damage and continue to grow and/or yield satisfactorily during and after herbivore attack	No negative effects	Maintains relatively high growth rates (biomass) or reproductive output (yield) per unit of herbivore biomass[d]	Estimated as the relative decline in plant fitness per unit weight of planthopper across a gradient of environments

[a] For further details see Strauss and Agrawal (1999) and Smith (2005).
[b] Comparative effects relative to a susceptible variety.
[c] Fitness is a quantitative representation of reproductive success (genetic contribution to future generations through survival and development × reproductive output) in a given environment.
[d] Observed during low levels of intraspecific competition between herbivores.

et al., 2004; Wise and Abrahamson, 2007; Lv et al., 2008; Horgan et al., 2017). As evidence accumulates, a number of exceptions to these general trends have become apparent (Huberty and Denno, 2006; Rubia-Sanchez et al., 2003; Butler et al., 2012; Horgan et al., 2016a), putting into question the predictive value of general hypotheses about plant-herbivore interactions (Wise and Abrahamson, 2005, 2007). Identifying the mechanisms that underlie such exceptions will improve knowledge of the dynamic nature of herbivore-plant interactions and help define practical applications for herbivore management in agricultural systems.

Rice, *Oryza sativa* L, is a useful model for understanding resource effects on herbivore-plant interactions. This is because, as a grass, rice is a typical modular plant that continuously produces tillers during the vegetative growth phase (Counce et al., 2000). Rice is also a well-researched agricultural crop with a diverse assemblage of associated insect herbivores (Heinrichs, 1994a,b; Heinrichs and Barrion, 2004). When grown under high nitrogen conditions, rice is more attractive to a range of herbivores and diseases (Visarto et al., 2001; Jiang and Cheng., 2003; Hu et al., 2016). Rice also compensates well for herbivore damage, often with increased tolerance under higher nitrogen conditions (Rubia-Sanchez et al., 1999; Reay-Jones et al., 2008; Horgan et al., 2016a). However, in a recent study, Horgan et al. (2016a) identified some exceptions to these trends. In particular, although nitrogen increased rice tolerance to the whitebacked planthopper, *Sogatella furcifera* (Horváth), and yellow stem borer, *Scirpophaga incertulas* (Walker), in their experiments, these authors noted the opposite effect in plants infested with the brown planthopper, *Nilaparvata lugens* (Stål). It appeared that the brown planthopper, which is often regarded as the most serious pest of rice in Asia, is able to pre-empt extra available nutrients from the plant phloem before these can be used by the host plant – thereby decreasing plant tolerance under high nitrogen (Horgan et al., 2016a).

For the last several decades, research into host plant resistance has dominated literature on the management of rice planthoppers (Fujita et al., 2013). This research has greatly increased knowledge of planthopper-rice interactions and has identified over 30 potentially useful resistance gene loci as well as several major quantitative trait loci (Fujita et al., 2013). However, it is clear that target planthoppers can rapidly adapt to resistant varieties and genes and that several resistance sources (either donor varieties or genes) are now no longer effective over much of the planthopper range (Tanaka and Matsumura, 2000; Myint et al., 2009; Horgan et al., 2015). Studies have also indicated that host plant resistance is influenced by crop management practices, particularly the use of pesticides (Gallagher et al., 1994) and fertilizers (Salim and Saxena, 1991; Jiang and Cheng., 2003; Horgan et al., 2016b). Few studies have incorporated crop management as a contributing factor in the successful resistance of rice against planthoppers and other insect herbivores in the field (but see Cuong et al., 1997; Visarto et al., 2001; Zhu et al., 2004).

Successful deployment of resistant rice varieties is further complicated by a gap in the current understanding of how planthopper-rice interactions change over the course of plant development (often referred to as ontogenetics). Since plants face distinct challenges as they grow and develop, they are predicted to shift their defence strategies to counter their most probable biotic stresses (Price, 1991; Herms and Mattson, 1992). Resistance to planthoppers in rice may increase or decrease during plant development (Rapusas and Heinrichs, 1982; Baqui and Kershaw, 1993; Vu et al., 2014; Horgan et al., 2016b) presumably depending on underlying resistance mechanisms or resistance genes (Srinivasan et al., 2015, 2016). Therefore, the age at which plants are attacked, how resistance changes over plant development and how farmers manage their crop (vis-à-vis fertilizer and pesticide inputs) represent key determinants of planthopper population growth and damage responses in fields of resistant rice.

In the present study, we examine the integrity of rice resistance under a range of nitrogen levels through a series of greenhouse,