



Limited ecological risk of insect-resistance transgene flow from cultivated rice to its wild ancestor based on life-cycle fitness assessment

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Abstract Ecological impact caused by transgene flow from genetically engineered (GE) crops to their wild relatives is largely determined by the fitness effect brought by a transgene. To estimate such impact is critical for the ecological risk assessment prior to the commercialization of GE crops. We produced F_1 and F_2 hybrid descendants from crosses of two insect-resistant GE rice lines (*Bt*, *Bt/CpTI*) and their non-GE rice parent with a wild rice (*Oryza rufipogon*) population to estimate the transgenic fitness. Insect damages and life-cycle fitness of GE and non-GE crop-wild hybrid descendants as well as their wild parent were examined in a common-garden experiment. No significant differences in insect damages were observed between the wild rice parent and GE hybrid descendants under high-insect pressure. The wild parent showed significantly greater relative survival-regeneration ratios than its GE and non-GE hybrid descendants under both high- and low-insect pressure. However, more seeds were produced in GE hybrid descendants than their non-GE counterparts under high-insect pressure. Given that the introduction of *Bt* and *Bt/CpTI* transgenes did not provide greater insect resistance to crop-wild hybrid descendants than their wild parent, we predict that transgene flow from GE insect-resistant rice to wild rice populations may not cause considerable ecological risks.

Keywords Environmental impact · Fecundity and survival · Genetically modified organisms · Lepidopteran · *Oryza sativa* · Wild relative

1 Introduction

The wide application of transgenic biotechnology in agriculture has contributed tremendously to the global crop production and food security [1]. To date, more than twenty genetically engineered (GE) crop species have been commercially cultivated, which covers more than 180 million hectares of agricultural lands globally [1]. However, the commercial cultivation of GE plants has stimulated worldwide concerns over the biosafety issues [2–4]. The unwanted ecological consequences caused by transgene flow from GE crops into their wild and weedy relatives are among the most debated biosafety issues [5, 6]. It is widely anticipated that the introgression of transgenes into crops' wild and weedy relatives may change their survival and fecundity, resulting in more invasive weeds or reduced genetic diversity of wild relatives [6–10]. This is more likely to happen when transgenes confer novel traits with strong natural selective advantages, such as those resistant to biotic and abiotic stresses [2, 11–13]. Therefore, the appropriate biosafety assessment of potential ecological risks caused by transgene flow and introgression becomes essential prior to the commercial cultivation of GE crops [3, 4, 10, 14].

To understand transgene-associated fitness change in wild relative populations is the key component for assessing potential ecological risks caused by transgene flow, provided that the frequency of crop-wild gene flow for a particular pair of species (a pollen donor and

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recipient) is determined. Hypothetically, the fitness change caused by a transgene may considerably affect the demographic pattern and evolutionary destiny of wild populations [2, 6, 13–15], resulting unwanted ecological consequences. Two aspects are critical for such fitness estimate: survival and fecundity in the context of population demographics [16]. It is particularly important to estimate the survival for a perennial species that reproduces or propagates both sexually and asexually. Although the trade-offs of survival and fecundity is highly variable between species with different life-history strategies, ecological studies suggest that fitness of perennial species depends more heavily on survival than fecundity [17]. This emphasizes the importance of proper estimates of survival and fecundity for fitness effects in the context of life history and population dynamics. Furthermore, the estimate of fitness should also consider the types of transgenes (e.g., insect-resistance) and the ambient environment to which the transgenic plants expose [10, 18, 19].

The perennial common wild rice (*Oryza rufipogon* Griff., referred to as wild rice hereafter) is the direct ancestor of Asian cultivated rice (*Oryza sativa* L.)—an important world's cereal crop [9, 20]. As a perennial grass species, wild rice can reproduce sexually through seed dissemination, as well as asexually through ratooning [20]. Wild rice occurs over the tropics and subtropics of monsoon Asia [20], in which China represents its northernmost distribution [21]. This wild species is also found in America, most likely introduced along with Asian cultivated rice through seed mixture [22]. It is widely recognized that wild rice harbors important germplasm, including the well-known male sterility gene (*ms*), for the genetic improvement of cultivated rice [23–25]. Wild rice is endangered in China and many Asian countries, because of dramatic changes in agriculture land uses, rapid urbanization, and other human disturbances [25–27]. The design of effective conservation strategies for this wild species is critical [20]. However, the potential introgression of transgenes into wild rice populations and the subsequent consequences have posed a new problem to the conservation of wild rice, given that the likelihood of commercial cultivation of GE rice is very high in the future [10, 25, 28].

Previous studies indicated moderate to high frequencies of gene flow from cultivated rice to *O. rufipogon* populations, based on data from population genetic analyses, gene flow field experiments, and simulation of pollen-mediated gene flow modeling [29–32]. In addition, Xia et al. [33] reported normal expression of the insect-resistant transgene (*Bt*, *CryIAc*) in F_1 and F_2 hybrid descendants derived from crosses between a GE rice line and a *O. rufipogon* population from China. Altogether, these results suggest the great potential of transgene flow to wild rice and its associated environmental impact on wild rice populations. Song

et al. [34] estimated the fitness of crop–wild F_1 hybrids (without the involvement of any transgene) in a common-garden field experiment, where the crop–wild F_1 hybrids did not show a consistent trend of fitness changes compared to their wild (*O. rufipogon*) and cultivated rice parents. Although further fitness studies of crop–wild rice hybrid descendants with insect-resistance transgenes (*Bt* and *CpTI*, cowpea trypsin inhibitor) did not show considerable effects of the transgenes on seed germination and dormancy [35], and on litterbag decomposition of hybrid residues [36]. Nevertheless, little is known about the life-cycle fitness change associated with insect-resistance transgenes in wild rice hybrid populations.

We produced transgene-present and transgene-absent F_1 and F_2 hybrid lineages derived from crosses of two insect-resistant GE rice lines (*Bt* and *Bt/CpTI*) and their non-GE parental rice variety (Minghui-86) with a wild rice accession from China. The available plant materials of different generations allow us to estimate the life-cycle fitness effect of the insect-resistance transgenes on wild rice. This study attempts to address the following questions. (1) Can insect-resistance transgenes (*Bt* and *Bt/CpTI*) considerably increase the resistance of crop–wild hybrid descendants to target insects compared to their wild parent? (2) Do crop–wild hybrid descendants carrying insect-resistance transgenes survive better than their wild parent? (3) Can insect-resistance transgenes considerably increase the fecundity of transgenic crop–wild hybrid descendants compared to its non-GE counterparts, under low- and high-insect pressure? The answers to these questions will help us to assess the potential ecological risks caused by the introgression of insect-resistance transgenes from GE rice into populations of its wild relatives.

2 Materials and methods

2.1 Production of crop–wild hybrid lineages

To simulate transgene flow from GE rice to wild rice, crop–wild hybrid lineages (F_1 and F_2) were produced by artificial crosses. Two insect-resistant GE rice lines: B2B containing a *Bt* transgene (*cryIAb*); and the marker free Kefeng-8 containing two tightly linked *Bt/CpTI* transgenes [*Bt* (*cryIAc*) and *CpTI* (cowpea trypsin inhibitor, *sek*)] in a double insertion, were used as the pollen donors. One accession of perennial common wild rice (*O. rufipogon*, coded as W) collected from Suixi County in Guangdong Province, China, was used as the pollen recipient (maternal parent). In the B2B line, the *cryIAb* transgene was driven by an ubiquitin promoter (from maize) and the selectable marker gene (*hyg*, for hygromycin resistance) was driven by a CaMV35s promoter. In the Kefeng-8 line,

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