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Battling against Brown Planthopper in Rice: Genomic Selection in Backcross Breeding to Produce Resistant Cultivars - A Review

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Abstract

Brown Planthopper (BPH), *Nilaparvata lugens* Stål, imposes a significant threat to the rice cultivation in Sri Lanka, generating 5–10% of annual yield losses. Rice farmers mainly adopt chemical methods to control the BPH attacks. The intensive use of insecticides is a crucial trigger for the development of resistance and hence continuous BPH outbreaks. Thus, the chemical methods of control do not provide a permanent solution to the BPH. The most recommended strategy of resolving the BPH crisis in rice is the development of resistant cultivars. Most of the Sri Lankan rice germplasm has already been screened for BPH resistance; however, reliable molecular breeding strategies must be implemented to achieve this target. Development of BPH resistant cultivars relies on utilizing appropriate genomic selection protocols in breeding schemes such as marker-assisted backcrossing. Therefore, a literature survey was carried out to evaluate BPH control methods and to emphasize the employment of backcross breeding with the genomic selection approach as a precise tool to develop BPH resistant rice varieties. The genetic basis of BPH resistance has been unravelled for many rice cultivars however, further screening is required to identify locally available resistant sources. The polymorphic markers for the foreground and background selection must be developed for the introgression of the BPH resistant genes and recovery of the recurrent parent genome. The validation of the markers developed in the international breeding and genetics programmes for the local germplasm is also an essential step prior to the genomic selection of BPH resistant rice varieties.

Keywords: Backcross breeding, BPH, BPH resistant rice, foreground and background selection, *Nilaparvata lugens*

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1. Introduction

Brown Planthopper (BPH), (*Nilaparvata lugens* Stål) is one of the most destructive pests in rice farming (Visarto et al. 2001; Matsumura and Morimura 2010). Prolong and persistent outbreaks of BPH resulting devastating effects have been encountered by rice-growing nations worldwide including Sri Lanka. BPH also renders damage to its host by acting as a carrier for two viruses, Ragged Stunt Virus and Grassy Stunt Virus (Cabauatan et al. 2009; Noda et al. 1991). Since the initial outbreaks, enormous attempts have been made to eradicate the pest; however, a long-term solution is still not available (Tanaka et al. 2000; Senthil-Nathan et al. 2009). BPH has continually evolved resistance against both biological and chemical controlling strategies (Nickel 1964). At present, BPH is immune to insecticides, including neonicotinoids, the most employed BPH monitoring method (Liu and Han 2006; Wang et al. 2008). However, the chemical treatments are applied in many instances, regardless of safety protocols imposing harmful impacts on both farmers and the public.

Consequently, farmers experience secondary outbreaks and resurgences, mainly because of this continuous application of insecticides without concerning the long-term effects rather than

short term solutions (Lim and Heong 1984; Wu et al. 2004). Most of the techniques employed during insecticide-induced destruction of pests have caused lethal effects on non-target and beneficial organisms further disrupting the ecological balance (Tanaka et al. 2000). Under the given circumstances, BPH resistant rice varieties produced through breeding are recognized as the most reliable solution to tackle the problem (Pathak and Khush 1979; Horgan 2009). Breeding for resistance is currently a more popular approach in comparison to the genetically modified pest-resistant crops, which have immense negative perception among the public (Moose and Mumm 2008; Herring 2008; Palmgren et al. 2015). The Sri Lankan rice germplasm has been screened for resistance towards BPH on several occasions and rice varietal improvement has also shown tremendous success throughout the past years. An array of rice varieties (Bw453, At306, Bg250, At307, Bg454, 62_355, At402, Bg403, At362, Bw367, Ld371, Bg310, and Ld253) reported to be resistant to diverse BPH types have also been developed by the Rice Research and Development Institute (RRDI), Bathalagoda (RRDI 2018).

Nevertheless, Marker-Assisted Backcross Breeding (MABB) has not been widely employed in achieving resistance against diverse BPH biotypes up to date. Given the higher adaptability of BPH, it can continue

developing resistance even against the newly improved varieties emphasizing the need for persistent varietal improvement. Therefore, we reviewed the genetics of BPH tolerance in rice and the application of backcross breeding to produce BPH tolerant varieties.

2. Rice varietal resistance for BPH

The rice varietal resistance has been identified as one of the best economical ways of controlling BPH outbreaks (Pathak 1970; Pathak 1977). Accordingly, the varietal resistance studies on BPH have commenced in 1969 in various countries such as India (Kalode and Krishna 1979), Japan (Kaneda and Kisimoto 1979), and Solomon Islands (Stapley et al. 1979).

Table 1. Biotypes of BPH and the genes of resistance.

Biotype	Distribution	Resistant gene	Dominance /Recessiveness
1	South East and East Asia	None	-
2	South East and East Asia	<i>Bph1</i>	Dominant
3	Sri Lanka	<i>Bph2</i>	Recessive
4	Indian Subcontinent	<i>Bph3</i>	Dominant

Source: Khush and Brar (1991).

Since then, many entries of the world rice germplasm have been screened for BPH resistance (Pathak and Khush 1979).

Damage incurred by hopper burn and BPH's population can be used as basic criteria to evaluate the host resistance (Stapley et al. 1979). The degree of rice varietal resistance towards BPH shows a significant variation

(Sangha et al. 2013). Dependence of varietal resistance on the site of cultivation and the type of resistant rice cultivar have also been studied. Both field and greenhouse trials have been done to determine the levels of resistance (Pathak and Khush 1979) and the resistant genes have been designated based on BPH biotypes (Kabis and Khush 1988) (Table1). Thus, varietal resistance further facilitates the studies on biotypes of BPH. All rice varieties do not have identical resistance to different BPH biotypes, and the rapid evolution of biotypes hinders the consistency of varietal resistance (Pathak and Khush 1979; Saxena and Barrion 1985).

BPH resistant mechanisms in host plant

The resistance of rice varieties against BPH comprises three main mechanisms: antibiosis, tolerance, and antixenosis. These resistance modes are displayed by any host plant, including rice, to deter herbivory (Panda and Heinrichs 1983; Kennedy et al.

1987; Alam and Cohen 1998a; Qiu et al. 2013).

Antibiosis reveals the reaction of the insect towards the plant (Heinrichs 1986). The metabolism of pest is highly disturbed due to antibiosis (Tingey 1981). Hence, antibiosis resistance is conferred against the biology of the insect (Heinrichs 1986). The major impacts of antibiosis are weakened persistence of insects and lowered rate of reproduction and growth followed by host tissue (Panda and Heinrichs 1983; Kennedy et al. 1987; Qiu et al. 2013).

In contrast, tolerance refers to the response of the plant to the insect (Heinrichs 1986). Tolerance minimizes the intensity of insect damage before reaching the economic threat levels (Kennedy et al. 1987). Loss of the host plant's weight, damage caused, and reduction in the yield are considered key indicators of tolerance (Panda and Heinrichs 1983). Tolerance enables producing a crop of high quality and yield despite insect infestation (Panda and Heinrichs 1983; Kennedy et al. 1987; Qiu et al. 2013).

Non-preference is generally termed as antixenosis (Kogan and Ortman 1978). Non-preference includes the characters responsible for oviposition and feeding-related to the pest (Heinrichs 1986); thus, reduces the establishment of the pathogen or oviposition on the host (Panda and Heinrichs 1983; Kennedy et al. 1987; Qiu et

al. 2013). Durable resistance can be achieved through tolerance compared to other modalities as it would not cause selection among insects, which prevents the development of new biotypes. Thus, unlike the other two modes, insects' feeding behaviour or health is not affected by tolerance (Panda and Heinrichs 1983; Wu et al. 2014).

3. Genetics of BPH resistance

Many rice cultivars express genes conferring either tolerance or antibiosis, while others have both mechanisms (Panda and Heinrichs 1983). *Bph6* and *Bph12* of *Nipponbare* (Qiu et al. 2012) and *Balamawee* (He et al. 2013) have strong antibiosis and antixenotic effects. *PtB33* has a high level of antixenosis (Thamarai and Soundararajan 2017), while *Bph14* shows antibiosis. *DV85* (Du et al. 2009; Qiu et al. 2013), *Bph28(t)* (Wu et al. 2014) of *Kaharamana* and, *Pokkali* display tolerance (He et al. 2013).

Pyramiding the Quantitative Trait Loci (QTLs) with major resistant genes has indicated enhanced resistance in host species. The QTLs associated with antixenosis and antibiosis are not widely known yet. However, a novel QTL associated with antixenosis, *Q-Bph8* has been discovered in rice chromosome 8. Pyramiding of several other BPH resistant

genes has shown enhanced antixenotic effects (Qiu et al. 2013). There is a greater necessity of investigating the antibiosis and tolerance genes related to BPH resistance, which has not been undertaken in greater depth to date (Qiu et al. 2011).

The breeding strategies are intensely focused on producing varieties resistant to BPH using tolerance alone or in combination with vertical resistant mechanisms, antixenosis, and antibiosis (Panda and Heinrichs 1983).

Resistant sources

Development of horizontal resistance, gene pyramiding, multiline varieties, and donor gene identification have allowed the successful accomplishment of the varietal resistance (Saxena and Barrion 1985). Certain BPH resistant genes have been discovered using the microarray analysis (Wang et al. 2012).

The wild rice varieties such as *Oryza officinalis*, *O. minuta*, and *O. rufipogon* Griff have been identified as critical reserves for BPH resistant genes (Renganayaki et al. 2002; Rahman et al. 2009; Li et al. 2010). *O. rufipogon* has been genetically analysed for its resistant genes *Bph20 (t)* and *Bph21 (t)* (Rahman et al. 2009; Huang et al. 2013). Wild species of *O. sativa* is an abundant source of resistant genes that must be

readily exploited to screen the genetics of BPH resistance (Jena and Kim 2010).

Apart from wild rice varieties, *indica* native varieties account for more excellent resistance in comparison to *japonica* varieties. Fine mapping of these resistant genes from wild rice/*indica* accessions allows ultimate cloning and breeding schemes. Specific BPH resistant genes have now been fine-mapped (Chen et al. 2006), and map-based cloning of *Bph13 (t)* has been successfully carried out (Renganayaki et al. 2002). Dominant or recessive natures of these genes have been identified (Sidhu and Khush 1978). Diverse resistant mechanisms have been analysed using a protein-based technique to unravel the genes underlying the BPH resistance (Wei et al. 2009).

Proteins synthesized in response to BPH attack allow gene cloning and a broader understanding of varietal resistance (Chen et al. 2002). Protein-based approaches are considered more realistic ways of identification of BPH resistant genes through expression analysis of several defence-related proteins (Sangha et al. 2013). Differential expression levels of Expression Sequence Tags (ESTs) have been exploited in mapping BPH resistant genes (Ren et al. 2004).

The varietal resistance mainly deals with the feeding behaviour of the pest (Cheng et al. 2013). Genes expressed distinctively during BPH feeding have been identified through Representational Difference Analysis (RDA), which examines the unique expression of *Bph* genes (Park et al. 2007). Specific and rare genes activated during the feeding of BPH have also been investigated using the Suppression Subtractive Hybridization (SSH) (Wang et al. 2005). Further, explorations on the BPH salivary gland related genes have been done using the SSH and Mirror Orientation Selection (MOS) in understanding the expression of defence proteins associated with BPH feeding (Wang et al. 2015).

A comprehensive idea of interactions between BPH and rice plants must be acquired to improve durably resistant varieties. Thereby, a model has been proposed to explain BPH's molecular-level interactions with rice plants in terms of immunity (Cheng et al. 2013). In the model, a greater varietal resistance has been conferred by combining significant resistance genes with minor resistant genes compared to the sole use of significant genes. The resistance of certain varieties with inherent genes has been evaluated, and the resistance level is further widened by the incorporation of several resistant genes (Saxena and Barrion 1985). Resistant varieties were then screened for pathogen-

induced genes such as wound-induced genes and genes involved in the biosynthesis of antioxidants and lignin (Jannoey et al. 2017). The extent of BPH resistance under nutrient enrichment has also been studied by administering micronutrients such as silicon, which showed enhanced resistance levels (He et al. 2015).

Genetics of BPH resistance in rice

Studies on the genetic basis of resistance were commenced in the early 1960s, along with the research on breeding for resistant cultivars (Kawaguchi et al. 2001). These studies have been recognized as the paths to the most effective solutions for the escalating rates of BPH outbreaks. Most of the resistance sources are initially found in substandard agronomic backgrounds with insignificant morphological characteristics (Khush 1977).

Diverse programmes have been launched to identify the genes conferring genetics of resistance, their means of inheritance, and the allelic relationships (Khush 1979). Bulk Segregant Analysis (BSA) and linkage analysis have enabled the positioning of the resistance genes to their respective chromosomes (Kawaguchi et al. 2001). Trisomic analysis and techniques such as Fluorescent *In-Situ* Hybridization (FISH) were readily employed (Jairin et al. 2007). New genes conferring BPH resistance have

been identified, and these discoveries are beneficial in the development of BPH resistant cultivars (Khush et al. 1985).

Several studies have been performed to determine the genetics of resistance for specific BPH biotypes. These studies have enabled the detection of BPH resistant genes (Table 1) that can be successfully employed in developing broad-spectrum resistance, achieved by integrating several resistant genes (gene pyramiding) into a single susceptible cultivar (Khush 1977; Khush et al. 1985).

Resistant genes

Up to date, 21 resistant genes and several QTLs distributed among eight chromosomes have been identified (Alam and Cohen 1998a; Jairin et al. 2007; Jena and Kim 2010). Out of 21 *Bph* genes, 13 dominant genes, and eight recessive genes have been distinguished (Jena and Kim 2010). Specific BPH resistant genes have shown a switch in its dominance or recessiveness depending on the genetic background (Jairin et al. 2010). The most widely used genes in breeding programmes are *Bph1*, *Bph2*, *Bph3* and, *Bph4* (Voramisara and Sa-nguansaj 1994).

Bph1 and *Bph2* have been identified linked to each other. while *Bph3* and *Bph4* are known to be independently segregating

(Khush 1977). Certain resistant varieties are also known to carry more than one resistant genes; *PtB33*, for example, carries both *Bph2* and *Bph3* (Jairin et al. 2007). Specific dominant genes, such as *Bph4*, have been discovered to behave in a recessive manner following the genetic background (Jairin et al. 2010). Eighteen of the genes are distributed in six of the 12 chromosomes of rice, most of them forming distinct clusters (Jena and Kim 2010; Liu et al. 2015). Six genes stemmed from wild *Oryza* species encompass either duplicated locations in their respective chromosomes or inaccuracies in their nomenclature (Jena and Kim 2010; Hu et al. 2016). *Bph14* and *Bph18* have been cloned as well (Jena et al. 2006; Du et al. 2009; Jena and Kim 2010).

The BPH-resistant genes investigated are from different genetic bases, including landraces and *Oryza's* wild relatives (Ikeda et al. 1994; Yang et al. 2002; Jena and Kim 2010). Most of the BPH resistant varieties possess low agronomic traits such as greater plant height, drooping leaves, and fragile stems and have lower yields.

Thus, the resistant genes must be transferred successfully to the improved and high yielding varieties (Khush 1977). Once the resistance genes are identified, marker-assisted gene pyramiding can be performed (Sun et al. 2005). Many such

genes have been incorporated into mega or more popular rice varieties (Khush et al. 2001) leading to the production of multiline varieties with prolonged overall resistance. Some markers are tightly linked to resistant genes, which provides avenues for MAB strategies to develop BPH resistance in susceptible cultivars (Jairin et al. 2007). Gene pyramiding can thus be expanded to efficient use of tightly linked Simple Sequence Repeat (SSR) markers (Jena and Mackill 2008).

Linkage and allelic relationships must be thoroughly investigated in the successful development of resistant cultivars of rice (Jena and Kim 2010). The latest research studies on BPH genetics and other important details are listed in Table 2.

4. Breeding for BPH Resistance

Breeding programmes against BPH are conducted worldwide to release resistant varieties. Breeding for BPH resistance was initiated in 1967 in conjunction with screening for resistant cultivars (Heinrichs 1986). These efforts have been immensely supported by the whole genome sequence of rice made accessible by the Rice Genome Sequencing Project (Fujisawa et al. 2005). However, breeding for resistance is hampered by the constant evolution of biotypes, absence of effective screening procedures, issues related to the selection of

donors, improper trait combinations within donors, and low consumer preference for the newly bred pest-resistant varieties. Besides, breeding strategies depend on the attributes of the area of cultivation (Heinrichs 1986). Thus, mutual efforts of breeders and genomic scientists are indispensable for further developments of the specific discipline. Most breeding plans exploit the greater diversity of wild rice varieties since they can thrive in many habitats and are not under frequent human selection. Analysis of several crucial genes of many wild rice accessions has also been facilitated by the *Oryza* Map Alignment Project (OMAP) (Ammiraju et al. 2006).

Major steps in breeding for resistance involve manipulating genes responsible and their successful incorporation into susceptible cultivars *via* MAS or gene pyramiding (Brar et al. 2009). Introgression lines (ILs) also play a prominent role in backcross breeding in providing breeding materials for developing genetically stable mega varieties and gene pyramiding (Ali et al. 2006). The breeding programmes are further accelerated by the QTLs that govern significant traits. Also, the pyramiding of QTLs can be performed to produce BPH resistant varieties (Ammiraju et al. 2006). Current biotech tools have permitted breeders to locate valuable commercial varieties, landraces, or wild relatives (Negrao et al. 2008). 'Smart breeding' that

employs natural variations of genes inbreeding (McCouch 2004) and 'Breeding by Design' (Peleman and van der Voort 2003) that exploits the allelic variations to design better-quality genotypes are famous as the modern trends in breeding for resistance.

Backcross breeding

Backcross breeding is a standard approach of plant breeding (Allard 1960) that could be readily employed to introgress BPH

Table 2. The advances in the field of BPH research

Major Research Outcome	Reference/s
Screening of rice varieties for resistance revealing novel BPH resistant genes	Athwal et al. (1971); Khush (1979); Kim and Sohn (2005)
Identification of locations of <i>Bph</i> genes in rice Chromosome (<i>Bph9</i>) and the intricately linked molecular markers	Chang et al. (2006)
Mapping of <i>Bph</i> genes (<i>Bph2</i>) and marker-assisted breeding to breed BPH resistant varieties	Li et al. (2006)
Exploitation of phenotype-based approaches for screening	Jairin et al. (2010)
Investigation of traditional rice varieties such as <i>Salkathi</i> for novel QTLs of BPH resistance	Brar et al. (2009); Mohanty et al. (2017)
Marker analysis done mostly using SSR markers to explore resistant genes	Kumari et al. (2010)
Marker assisted selection (MAS) of BPH resistant cultivar	Suh et al. (2011)
Mapped out of location of <i>Bph</i> genes in the rice chromosomes with exception of <i>Bph5</i> and <i>Bph8</i>	Hou et al. (2011); Yang et al. (2012); Cheng et al. (2013); Hu et al. (2016); Jing et al. (2017)
Introgression of <i>Bph</i> genes into the susceptible rice cultivars	Wan et al. (2014); Jena et al. (2017)
Simultaneous research attempts on BPH using sophisticated technologies such as Next Gen Sequencing	Wan et al. (2014)
Map based cloning of <i>Bph</i> genes (<i>Bph29</i> , <i>Bph18</i> and <i>Bph26</i>) followed by successful characterization	Tamura et al. (2014); Wang et al. (2015); Ji et al. (2016)
Employment of breeding strategies that make use of allelic diversity of <i>Bph</i> gene clusters	Zhao et al. (2016)
QTL analysis to identify and map the resistant breaking genes of BPH that are active against the anti-feeding mechanism of rice resistant gene	Kobayashi et al. (2014)
Mapping and MAS of <i>Bph</i> genes (<i>Bph2</i>) to produce BPH resistant varieties	Kaur et al. (2015); Suh et al. (2015)
Fine mapping and pyramiding of genes such as <i>Qbph3</i> and <i>Qbph4</i>	Hu et al. (2015)
Allelic diversity studies of resistant genes (<i>Bph18</i>)	Ramkumar et al. (2016)
Successful adoption of MABB to develop NILs using the resistant cultivars	Xiao et al. (2016)
Detection of major <i>Bph</i> resistant genes (31 up to date) in both indica and wild rice varieties	Jing et al. (2017)
The associations between BPH and its host plant, rice have been experimented broadly as a typical simulation in deciphering host plant interactions	Jing et al. (2017)
Fine mapping of genes including <i>Bph31</i> and pyramiding of other genes such as <i>Bph3</i> and <i>Bph27</i>	Prahalada et al. (2017)
Fine mapping of certain broad-spectrum resistant genes, their introgression into a mega variety and subsequent analysis of gene expression	Prahalada et al. (2017)
Cloning of four <i>Bph</i> resistant genes (<i>Bph14</i> , <i>Bph26</i> , <i>Bph18</i> and <i>Bph9</i>)	Liu et al. (2015); Jing et al. (2017)

resistant genes from landraces into elite cultivars. Backcross breeding involves incorporating foreign germplasm from a closely related cultivar, with undesirable traits into a crop cultivar of economic and/or agronomic importance (Brown et al. 1989). Backcross breeding is beneficial in breeding programmes in which the donor parent possesses a greater number of undesirable traits (Hagiwara et al. 2001). Recurrent backcrossing is considered as the traditional aspect of this technique (Hasan et al. 2015).

Gene integration using this strategy is a comparatively slow procedure (Stam 1981). This method especially poses a problem in the recovery of recessive alleles, which is tedious (Brown et al. 1989). The linkage drag hinders the successful recovery of the desired allele during the backcross breeding. Thus, markers that assist in the foreground and background selection are readily employed in the modern recurrent backcrossing schemes to reduce the linkage drag (Frisch et al. 1999). Thereby, it renders the conventional backcross procedure more laborious (Wissuwa et al. 2002). Consequently, overall efficiency must be increased by employing markers in the selection of backcrossed progeny. This procedure is termed as Marker Assisted Backcross Breeding (MABB) (Frisch et al. 1999).

MABB exploits markers' potential to identify resistant genes that account for favourable traits such as durable resistance to abiotic and biotic stresses (Hasan et al. 2015).

Backcross breeding can be done in combination with conventional selection methods to produce rice cultivars resistant to abiotic stresses such as drought (Lafitte et al. 2006). The procedure has been successfully carried out in developing host plant resistance in wheat against commonly found rust diseases using a single backcross breeding approach (Singh et al. 2005). It has even been carried out for higher plants, which include the revival of American Chestnut Tree, eliminated by blight (Hebard 2006). MABB has also been successfully carried out for specific barley cultivars resistant to the yellow dwarf virus (Tester and Langridge 2010) and to increase food quality parameters in soybeans (Maranna et al. 2016) and to improve the cooking quality of rice (Kwon et al. 2011). Nevertheless, backcrossing cannot be applied effectively for many other crops due to the absence of DNA marker systems, causing them to lag forward genetic approaches. Backcrossing cannot perform for vegetatively propagated crops and species with long regeneration times and high heterozygosity (Bradford et al. 2005). However, given the wealth of genomic information available for rice, MABB can be readily employed to produce BPH resistant rice varieties (Fig. 1).

Foreground selection

Foreground selection is defined as selecting individuals that carry the genes of the donor parent (for example, BPH resistant gene) with the assistance of the markers to guarantee the presence of genes without being lost during the backcross (Fig. 1). The presence of the desired donor genes in the recombinant genome is confirmed by linked markers (Jun-Yan et al. 2006). QTL segments of the crossed populations are analysed for the donor like alleles (Lecomte et al. 2004). The potential use of markers for background and foreground selection in backcross breeding programs has been well studied (Hospital and Charcosset 1997). Tightly linked or flanked markers enable efficient foreground selection (Jun-Yan et al. 2006). Flanking markers facilitate the reduction of linkage drag while linked markers validated across different parental combinations allow excellent recovery of recurrent parent traits (Gopalakrishnan et al. 2008).

A minimum of three markers must be used to achieve successful foreground selection (Hospital and Charcosset 1997). Foreground selection through phenotypically active functional markers is more feasible than that of phenotypically neutral random DNA markers. Single nucleotide polymorphism (SNP), SSR, Cleaved Amplified Polymorphism (CAP), Single Feature Polymorphism (SFP), Restriction-site

Associated DNA (RAD) and, Diversity Array Technology (DArT) are random genetic markers currently available for foreground selection (Wenzl et al. 2004; Hazen et al. 2005; Gupta et al. 2010). Nevertheless, functional markers are comparatively more effective (Bagge and Lübberstedt 2008). Foreground selection is categorized as direct selection and indirect selection. Indirect selection uses a single linked marker or two flanking markers during selection (Jun-Yan et al. 2006). Foreground selection using markers is an alternative to the direct phenotypic evaluation, which is time-consuming, inflated, and unfeasible (Hospital and Charcosset 1997).

However, foreground selection can be executed simultaneously with the phenotypic selection, an inexpensive strategy that allows the rapid identification of introgressed lines (Suh et al. 2013). Initial foreground selection and subsequent thinning of the number of individuals used for the foreground selection are less costly, mainly when several QTLs are analyzed (Hospital and Charcosset 1997). Foreground selection followed by background selection has been successfully carried out for the development of NILs of disease-resistant soybeans (Kim et al. 2008).

Background selection

Background selection is defined as selecting the genetic background of the individuals

who receive the desired gene (for example, BPH resistant gene) from a donor parent (Fig. 1). It is supported by the evidence from molecular or phenotypic markers, which enhance the rate of retrieval of its genetic background (Jun-Yan et al. 2006). Thereby, it ensures the recovery of the recombinants of a progeny that possess the recurrent parent genome (Gopalakrishnan et al. 2008). Plants that display the nearest genetic background to that of the recipient parent are thus designated (Lecomte et al. 2004). Background selection allows retrieving the genome outside the QTL regions of interest (Hospital and Charcosset 1997).

The methodology can be categorized into three major approaches; random selection, genomic similarity selection, and marker index selection (Jun-Yan et al. 2006). The efficacy of background selection and the subsequent genome recovery is further improved using markers. Hence, the possible use of markers for background selection in backcross breeding programs has been thoroughly investigated (Hospital and Charcosset 1997). The DNA markers used are polymorphic between two donors and recurrent parents (Neeraja et al. 2007). Efficient background selection can be carried out using mapped molecular markers, either flanked or tightly linked to the desired gene (Jun-Yan et al. 2006). Amplified Fragment Length Polymorphism (AFLP), DArT, and SSR markers have been

frequently used in background selection (Thabuis et al. 2004; Gupta et al. 2010). Nevertheless, specific PCR based markers are inefficient in background selection, as they require many marker data points to recover the desirable quality traits in recombinants. Recovery of the whole genetic background requires genomic similarity selection or marker-index selection (Jun-Yan et al. 2006).

This approach involves the distribution of markers on the entire genome, which is less feasible and costly. Thus, consideration of only the economically valuable traits for selection has been identified as a less expensive tactic. Background selection is carried out for both carrier and non-carrier chromosomes, for only a limited number of individuals resulting from initial foreground selection (Hospital and Charcosset 1997). Multi-step background selection with two or more selection steps is identified more effective (Gupta et al. 2010).

The background genome recovery percentage can be calculated after the background selection (Suh et al. 2013). Background selection can be very efficiently employed in back crossbreeding programs (Hospital and Charcosset 1997). It can be carried out in a backcross breeding program where several QTLs are analysed for pyramiding (Suh et al. 2013).

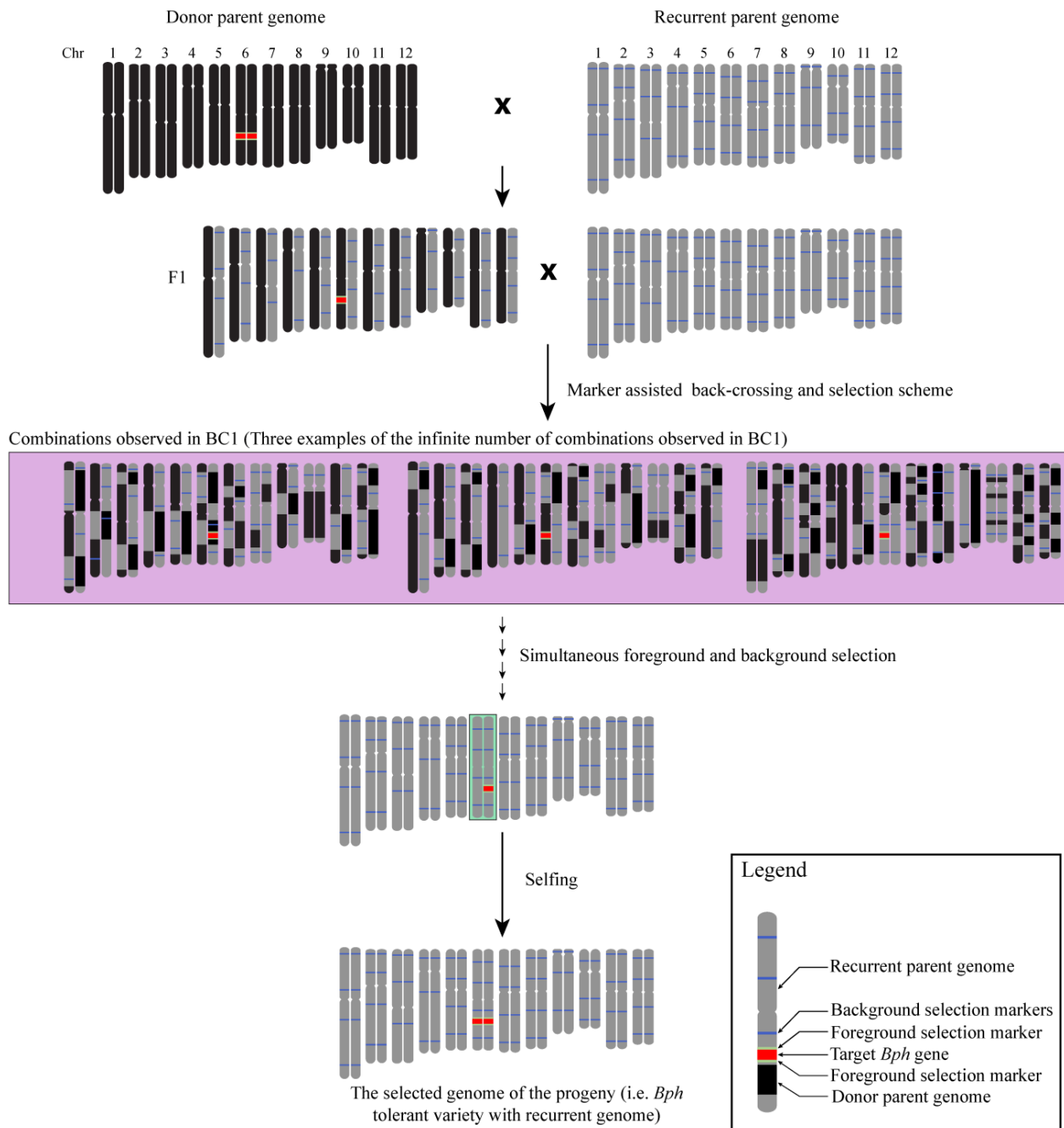


Figure 1. A diagram on the foreground and background selection scheme for developing a BPH resistant cultivar through recurrent backcrossing. The donor parent genome (black) residing the gene of interest (red) from a local landrace resistant to BPH is crossed with the recurrent parent genome (grey) from an improved mega variety which is sensitive to BPH attack. Foreground selection is carried out via two foreground markers (light green) flanking the gene of interest. Simultaneous background selection is carried out by employment of a large number of background markers chosen to cover the whole length of each of the twelve rice chromosomes. The confirmation of hybridity is carried out with the use of the background and foreground markers. Subsequently, a marker-assisted selection scheme with repeated backcrossing is implemented across several generations for the selection of the target donor gene via foreground selection and selection of the recurrent parent genome via background selection. The progeny plants with the successful introgression of the donor gene and the highest recovery of the recurrent parent genome are selected and selfed. The independent segregation of the selfed progeny results in homozygous progeny plants with BPH resistance.

5. Conclusions

Despite the attempts to improve the agronomic quality of rice, MABB has not been widely employed for the development of BPH resistant varieties. This review of the research studies on the varietal improvement for BPH resistance conveys the need for rigorous search of polymorphic markers for the foreground and background selection, which allows successful introgression of the BPH resistant genes and recovery of the recurrent parent genome resulting in commercial cultivars that are resistant to BPH attacks. A number of markers, especially employable in background selection schemes, must be widened in making the procedure more effective. The review further concludes that the other means of control of BPH, especially the chemical means, are not favourable in terms of rice cultivation and farmers' livelihood. However, it is further emphasized that the simultaneous deployment of biological and cultural methods or the integrated management strategies and the varietal improvement will generate more fruitful outcomes. In order to achieve the above goals, the farming communities must be made aware, and Breeders' Guides can be prepared in popularizing the MABB programs as a key mode of breeding for BPH resistance.

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