Intercropping of rice varieties increases the efficiency of blast control through reduced disease occurrence and variability

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Abstract
Creating a crop-heterogeneous system by intraspecific mixtures of different rice varieties can substantially reduce blast diseases. Such variety mixtures provide an ecological approach for effective disease control, maintaining high yields with the minimum fungicide applications. Whether such an approach is universally applicable for random rice variety combinations and what is the variation pattern of the diseases under intercropping still remains unclear. We conducted two-year large-scale field experiments involving 47 rice varieties/lines and 98 variety-combinations to compare the occurrence of rice blast in monoculture and intercropping plots at multiple sites. In the experiments, the plant height of the selected traditional varieties was about 30 cm taller, and their life cycle was 10 days longer, than that of the improved rice varieties. The monoculture included either traditional or modern rice varieties grown in separate plots. The intercropping included both traditional and modern rice varieties planted together in the same plots. Results from the field experiments under natural disease conditions demonstrated significant reduction for rice blast disease in intercropping plots, compared with that in monoculture plots. For traditional varieties, the average blast incidence reduced from ~26% in monoculture to ~10% in intercropping, and the disease severity reduced from ~17 in monoculture to ~5 in intercropping. For modern varieties, the average blast incidence reduced from ~19% in monoculture to ~10% in intercropping, and the severity from ~10 in monoculture to ~4 in intercropping. Traditional rice varieties (~72%) had a much greater increase in the efficiency of disease control than modern varieties (~60%). In addition, substantially lower values of variance in the blast incidence and severity was detected among the variety combinations in intercropping plots than in monoculture plots. Based on these results, we conclude that the intercropping or mixture of rice varieties greatly reduces the occurrence and variation of rice blast disease in particular variety combinations, which makes the intercropping system more stable and consistent for disease suppression on a large scale of rice cultivation.

Keywords: Oryza sativa, cropping system, disease suppression, disease variation, mixed-planting, pure-planting, crop heterogeneity

1. Introduction
Crop disease control is one of the major agricultural activities to maintain high crop yields (Dordas 2008). There are many
methods for crop disease control, including the application of chemical, biological, physical, and cultural approaches (Palti 1981). One of the effective and environmental friendly ways to control diseases is to apply ecological approaches in modern agricultural systems (Risch et al. 1983; Altieri 1999; Tilman et al. 2001), in which crop heterogeneity is created to provide substantial disease suppression (Garrett & Mundt 2000; Zhu et al. 2000; Leung et al. 2003). An excellent example is the successful control of rice blast disease (Magnaporthe grisea) demonstrated by the large-scale field experiment with mixed-planting of traditional and modern rice varieties (Zhu et al. 2000). This example substantiated that “intraspecific crop diversification provides an ecological approach to disease control that can be highly effective over a large area and contribute to the sustainability of crop production” (Zhu et al. 2000).

As an important world’s cereal crop, rice (Oryza sativa) provides staple food for nearly one half of the global population (Lu and Snow 2015). In China, rice also serves as one of the top food crops, which is consumed across the entire country, in addition to its important cultural values such as liquor production (Luo et al. 2008) and religious folk services (Zeng et al. 2012). Therefore, the high yielding and sustainable production of rice is critical for the food security in this country. However, the sustainable rice production is threatened by various fungus diseases, particularly by the rice blast disease, which “spreads through multiple cycles of asexual conidiophores production during the cropping season, causing necrotic spots on leaves and necrosis of panicles” (Zhu et al. 2000). Rice blast is the major disease of the rice crop in many rice planting regions (Dean et al. 2005). Statistical data suggest that 10–20% of rice yield losses are caused by the severe attacks of rice blast disease in China (Sun et al. 1998; Liu et al. 2004). The commonly used methods to control rice blast disease are chemical controls (Sun et al. 1998; Liu et al. 2004; Wen et al. 2013), which causes considerable pollution in the rice ecosystems and increases the costs for rice production (Yang et al. 2012). However, Zhu et al. (2000, 2003a) achieved about 94% less blast disease and 89% greater grain yield for disease-susceptible traditional rice varieties only by growing these varieties in mixtures with disease-resistant modern rice varieties. The approach of Zhu et al. (2000, 2003a) using the ecological method of intraspecific diversity may provide an effectual alternative to control this disease in rice, in addition to its values for in situ conservation of rice genetic resources (Zhu et al. 2003b).

Undoubtedly, the above studies have set an excellent example for the ecological control of the rice blast disease using the genetic diversity of rice varieties, but only two traditional rice varieties (Huangkenuo and Zinuo) and two modern hybrid rice varieties (Shanyou 63 and Shanyou 22) with four or six variety combinations were used in the field experiments to determine the efficacy of rice blast control in the intercropping and monoculture systems (Zhu et al. 2000, 2003a). However, the question arises as to whether the same level of efficacy for reduced disease can be remained if a greater number of rice varieties and combinations is included in more extensive rice planting regions. This is because many rice varieties are currently grown in Yunnan and the neighboring provinces in China. Can all these rice varieties be utilized in the intercropping system for rice blast control? In other word, do randomly selected combinations of traditional and modern rice varieties in intercropping or mixed-planting have the universal effects on rice blast reduction? In addition to the generally reduced rice blast severity and occurrence in the intercropping system, are there any other reasons responsible for the control of rice blast in the intercropping system?

These questions should be addressed if a more universal application of this intercropping technique is adopted effectively for reducing rice blast in rice ecosystems. Apparently, these questions can be answered by including a greater number of rice varieties with more variety combinations at multiple field experimental sites. To meet this purpose, we conducted extensive field experiments in which the biodiversity cultivation (intercropping) of rice varieties was deployed in 2001–2002 to investigate the efficiency of disease control. The field experiments involved 76 rice varieties/lines that formed 98 variety combinations, and were located in eight districts in Yunnan Province. The objectives of this study were to determine (1) whether the efficient reduction of rice blast disease is a general pattern when a large set of rice varieties with diverse origins in random combinations were cultivated in the intercropping system; (2) what is the variation pattern of blast occurrence among the variety combinations under intercropping, compared to that under monoculture. The generated knowledge will be useful to facilitate our understanding of the dynamics of the blast disease in different rice eco-systems, and eventually to guide the design of biodiversity cultivation of rice varieties for the efficient control of the rice blast disease in the intercropping system.

2. Results

2.1. Efficiency of rice blast control in different combinations of rice varieties

In general, the occurrence of rice blast disease was significantly reduced in the intercropping (mixed-planting) plots both for the traditional and modern improved rice varieties, compared with the occurrence of rice blast in the monoculture (pure-planting) plots (Table 1, Figs. 1 and 2).
Results indicated the efficiency of rice-blast control for the traditional rice varieties (up to 71.8% of blast reduction) and the improved rice varieties (up to 62.8%). However, considerable variation in blast occurrence was detected among different rice varieties (in monoculture) and variety combinations (in intercropping) at different experimental sites, as well as between the two experimental years. Such variation was possibly due to the differences in genetic background of rice varieties used in the experiments and the environmental conditions at various experimental sites. Apparently, intercropping had substantial effects on rice blast control, as estimated by the incidence and severity index of the rice disease, based on the analysis of variance for a total of 98 rice varietal combinations in the two successive experimental years.

For traditional rice varieties, the average incidence of rice blast was reduced from 27.6 and 24.7%, respectively for the two-year experiments in monoculture plots, to 17.8 and 16.7% in the intercropping plots with modern varieties. Similarly, the average severity index of rice blast was also reduced from 10.4 and 10.7%, respectively for the two-year experiments in the monoculture plots, to 5.4 and 4.8% in the intercropping plots. For modern rice varieties, the average incidence of rice blast was reduced from 18.5 and 19.6%, respectively for the two-year experiments in the monoculture plots, to 10.2 and 10.3% in the intercropping plots. Likewise, the average severity index of rice blast was also reduced from 7.4 and 8.4%, respectively for the two-year experiments in the monoculture plots, to 4.1 and 4.3% in the intercropping plots (Fig. 1). The median values of rice blast incidence and severity showed the similar pattern in the monoculture and intercropping plots (Table 1, Fig. 2).

There was a clear trend that the rice blast control was much more efficient for the traditional rice varieties than for the modern rice varieties when these varieties were grown in the intercropping plots. For the traditional varieties, the average values of blast control efficiency were 71.8% (ranging from 30.2–96.6%) and 71.5% (33.2–99%) in the intercropping plots in the two-year experiments. However for the modern varieties, these values were 62.8% (ranging from 5.8–90.5%) and 58.2% (25.3–91.5%) in the intercropping plots. The generally increased efficiency of rice blast control both for traditional and modern rice varieties in the intercropping system suggested its universal application for rice blast reduction.

Noticeably, some traditional rice varieties used in this study showed substantial variation in the efficiency of rice blast control when intercropped with different modern improved rice varieties. For example, when a widely used traditional rice variety Huangkenuo was used in the combination with a modern variety Hexi 24, the recorded efficiency of blast control was as high as 96.6% in the intercropping plots. However, when Huangkenuo was used in the combination with another modern variety Dianxi 4, the observed efficiency of blast control was only about 30%. This result suggested that the genetic background of the paired rice varieties

<table>
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<th>Variety and cultivation mode¹)</th>
<th>Average (SE)</th>
<th>Median</th>
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<th>Maximum value</th>
<th>Variance</th>
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<tr>
<td>Incidence (%)</td>
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<tr>
<td>Traditional M</td>
<td>27.56 (2.287)***</td>
<td>24.45</td>
<td>5.0</td>
<td>100.0</td>
<td>261.41</td>
<td>95.00</td>
</tr>
<tr>
<td>Traditional I</td>
<td>10.36 (1.766)</td>
<td>8.00</td>
<td>1.7</td>
<td>89.3</td>
<td>156.01</td>
<td>87.60</td>
</tr>
<tr>
<td>Modern M</td>
<td>18.51 (1.994)***</td>
<td>16.32</td>
<td>1.9</td>
<td>81.2</td>
<td>198.73</td>
<td>79.30</td>
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<tr>
<td>Modern I</td>
<td>7.39 (1.216)</td>
<td>4.50</td>
<td>0.4</td>
<td>51.6</td>
<td>73.90</td>
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<td>2.0</td>
<td>64.5</td>
<td>177.23</td>
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<td>39.6</td>
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<td>1.2</td>
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<td>143.81</td>
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<tr>
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<td>67.0</td>
<td>188.46</td>
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<tr>
<td>Traditional M</td>
<td>16.65 (1.695)***</td>
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<td>2.2</td>
<td>45.0</td>
<td>137.83</td>
<td>42.84</td>
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<td>0.1</td>
<td>22.6</td>
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<td>42.0</td>
<td>69.89</td>
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<tr>
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<td>2.90</td>
<td>0.2</td>
<td>22.0</td>
<td>20.61</td>
<td>21.82</td>
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¹) M, monoculture; I, intercropping. **, P<0.01; ***, P<0.001.
Fig. 1  Significant differences in the average values of rice-blast incidence (A and B) and severity index (C and D) between monoculture and intercropping rice plots scored based on 98 rice varietal combinations in the two experimental years. T, traditional varieties; M, modern improved (including pure-line and hybrid) varieties. Bar indicates standard error (SE). The same as below. **, P<0.01; ***, P<0.001.

Fig. 2 Comparison of variation in rice-blast incidence (A and B) and severity index (C and D) between monoculture (white box plots) and intercropping (dark-gray box plots) rice plots scored based on 98 rice varietal combinations in the two experimental years. In the box plots, the center black lines indicate the median values; the boxes indicate interquartile ranges (at 25 and 75%); the whiskers (below or above the boxes) indicate values beyond the interquartile ranges (<25% or >75%), with the minimum and maximum observed values at the two ends.
may have an important role in the efficiency of reducing the occurrence of rice blast, although environmental conditions may also be the reason for such variation.

2.2. Variation of rice blast between the monoculture and intercropping plots

Results from the further analysis of the 98 rice variety combinations demonstrated substantially reduced variance for rice blast incidence and severity in the intercropping plots, compared with the variance detected from the rice varieties grown in the monoculture plots (Fig. 2). For the traditional rice varieties, the interquartile ranges (at 25 and 75%) of the rice blast incidence reduced considerably from 16.9–35% and 15.3–32.4% in the two-year monoculture plots, to 5.7–12.3% and 5–13.3%, respectively, in the two-year intercropping plots (Fig. 2). Similarly, the interquartile ranges of the severity index reduced from 7.9–26.9 and 7.35–22.7 in the two-year monoculture plots, to 1.6–8 and 1.4–7, respectively, in the two-year intercropping plots (Fig. 2). For the modern rice varieties, the interquartile ranges of the blast incidence reduced considerably from 10.3–22.7% and 10.4–24.3% in the two-year monoculture plots, to 2.5–9.4% and 2.2–12.6%, respectively, in the two-year intercropping plots (Fig. 2). Likewise, the interquartile ranges of severity index reduced markedly from 4.8–13 and 5–13.9, to 1.4–5.1 and 1.8–5.2, respectively, in the two-year intercropping plots (Fig. 2).

For both traditional and modern rice varieties, the variation in the blast incidence and severity index for the 98 variety-combinations was substantially reduced in the intercropping plots in comparison with that in the monoculture plots (Fig. 2). The variances and differences between the maximum and minimum values of the blast incidence and severity index were also reduced substantially in the intercropping plots (Table 1). These results of reduced variances in the incidence and severity index of rice blast diseases suggested greater stability in the intercropping plots than in the monoculture plots, which reflected efficient blast control for both the traditional and modern rice varieties.

3. Discussion

3.1. Mixtures of rice varieties reduces rice blast disease in the intercropping systems

Our results of the biodiversity cultivation or intercropping system indicated significant reduction of rice blast diseases in the rice experimental fields with mixtures of traditional and modern varieties, compared to the blast diseases in monoculture. The observation is based on the field experiments with a large number of rice varieties (with diverse origins) and variety combinations. Consequently, the selected traditional and modern rice varieties grown in the intercropping system presented much lower rice blast occurrence than that grown in the corresponding monoculture system, as estimated by the disease incidence and severity of the rice blast. Although considerable variation was observed among different rice combinations grown at the multiple sites, our findings are consistent with the previous studies reported by Zhu et al. (2000, 2003a) in which a much fewer number of rice varieties and combinations was included in their field experiments. Our field experiments demonstrated the substantial reduction of rice blast disease for both traditional and improved modern rice varieties in the intercropping plots at different experimental sites, compared to that in the monoculture plots. These results were based on a total of 47 rice varieties with 98 variety combinations. The findings suggest the potential of universal application of the biodiversity cultivation or intraspecific intercropping system for rice blast control in different rice ecosystems.

Noticeably, field experiments demonstrated a considerable variation in disease reduction among different variety combinations in the intercropping system. In other words, some combinations of rice varieties, such as Huangkenuo 1/Shanyou 63, showed much greater efficacy to reduce blast disease than other combinations such as Huangkenuo 3/Dianxi 4. This finding indicates that not all rice varieties in a random combination will provide substantial suppression to rice blast disease when they are grown in the intercropping system. This phenomenon was also reported in previous studies of rice varieties grown in intercropping (Sun et al. 2002; Lang et al. 2015), where the resistance gene analogue (RGA) and insertion/deletion (InDel) molecular data from included rice variety-pairs (or combinations) showed a negative correlation between their genetic relatedness and the occurrence of rice blast diseases. Although many studies have shown the efficiency of varietal intercropping for the reduction of rice blast diseases and increase in rice yield (Zhu et al. 2000, 2003a; Leung et al. 2003; Li et al. 2009), the underlying mechanisms for this phenomenon are still unclear. The hypothesis of genetic differentiation/distance between the traditional and modern varieties grown in mixtures is proposed to be one of the reasons for the reduction of rice blast diseases in the biodiversity cultivation system (Zhu et al. 2000, 2003a; Lang et al. 2005). Further studies should be conducted to explore the influence of genetic background of rice variety-pairs on blast disease reduction when the two varieties are cultivated in mixtures. This will not only reveal the underlying mechanisms for the benefits of biodiversity cultivation of rice varieties, but also provide a practical guide for selecting proper rice variety pairs for the biodiversity cultivation.
3.2. Intercropping of rice varieties narrows down the variation for blast in rice fields

Based on our two-year experimental data from the multiple field sites, rice varieties grown in the intercropping system not only demonstrated significantly reduced incidence and severity of the rice blast disease, but also substantially reduced variation for the incidence and severity, compared to those grown in the monoculture system. This finding is particularly important, although it has not been frequently reported. That is, the reduced variation of blast occurrence in the intercropping system indicates that the mixed cultivation of different rice varieties in the same field with a particular planting mode can greatly restrain the extremity or high-level blast disease in the system, in addition to the general decrease in the rice blast diseases. In other words, the intercropping of different rice varieties with divergent genetic background in the same field will create a particular environment in which the occurrence of the extremely high level of rice blast disease is suppressed to a moderate level. Such effects created by a moderate level of blast diseases in rice fields probably make the intercropping system more stable or consistent, which ensures the stable rice production. Therefore, the generally reduced level of rice blast diseases coupled with the limited variation of rice blast diseases in the intercropping system with different rice varieties have played important roles in the effective control of rice blast diseases in the rice fields.

To create a stable and consistent cultivation environment with a low level and moderate variation of crop disease is critical for the sustainable production of crops, including rice, cultivated at a large scale. Such an environment can be established by crop heterogeneity in a given field with different varieties or even different crop species (Tilman et al. 2006; Li et al. 2009). Our findings from this study support the theoretic concept (Browning and Frey 1969; Wolfe 1985) and practices (Zhu et al. 2000, 2003a, b) of using genetic diversity to control crop diseases. However, it seems that the efficiency of disease control by the mixtures of rice varieties did not follow a random pattern. In other words, only a certain rice variety in a particular combination can achieve substantial reduction of rice blast disease. The genetic background of rice variety combinations may play an important role in disease control and should be studied in details. The theoretical and empirical studies have indicated an evident correlation between genetic diversity and stability in an ecosystem (Murdoch 1975; Tilman & Downing 1994; Jones et al. 2004; Hughes et al. 2008). Our recent studies also showed a correlation between the genetic divergence of rice varieties grown in mixtures and rice blast (Lang et al. 2015), suggesting the non-random choices of rice variety combinations in mixed-planting or mixtures for the control of the rice blast disease. With the improved understanding of the relationships between genetic diversity and disease occurrence in rice, as well as in other crops, the intercropping system will provide a more effective method of disease control in current rice ecosystems where a few uniform modern rice varieties grown on a large scale have led to the vulnerability of the agro-ecosystems for rice production. It is therefore possible to retain the sustainable rice production in a better designed intercropping system with effective disease control.

4. Conclusion

It is proven that rice cultivation with genetic heterogeneity in the same field achieved by intercropping or mixed-planting of different varieties with genetic diversity is an effective approach to control rice blast diseases (Zhu et al. 2000, 2003a). However, it was unclear as to whether the randomly selected rice varieties in casual combinations can provide an effective approach for the control of the rice blast disease at a large scale. Our multi-location and two-year field experiments including a set of 76 rice varieties/lines with 96 varietal combinations showed significant reduction of rice-blast disease in the intercropping plots, compared with that in the monoculture plots. However, only some rice combinations grown in mixture showed more effective control of the rice blast than other combinations, indicating the non-random features of variety combinations for efficient rice blast control. The substantially reduced variation in the incidence and severity of the rice blast among variety combinations suggests the suppression of the extremities of rice blast in the rice fields with variety mixtures, which provides a more stable and consistent system for rice blast control. In summary, the significantly reduced rice blast disease coupled with the narrowed variation has resulted in less blast occurrence in intercropping fields where diverse rice varieties are grown in mixtures. Therefore, properly combined traditional and modern rice varieties with differential disease resistant abilities (Zhu et al. 2000, 2003a) and genetic diversity (Lang et al. 2015) grown in intercropping will facilitate the effective control of rice blast diseases in a large scale of rice ecosystems.

5. Materials and methods

5.1. Rice varieties and their combinations used in the field experiment

A total of 76 rice varieties, including 36 traditional and 40 modern varieties with the diverse genetic background, were used for the field experiments (Appendix A). These varieties are commonly cultivated in the experimental regions of
Yunnan Province, China. All traditional varieties collected from local farmers in Yunnan Province were low to medium yielded and commonly susceptible to rice blast disease. The modern varieties were medium to high yielded and usually resistant to rice blast disease. The traditional and modern varieties were selected either to grow in the monoculture (pure-planting) system or to form rice pairs or combinations for cultivating in the intercropping (mixed-planting) system, following the description by Zhu et al. (2000, 2003a). For selecting rice combinations, the plant height of the traditional varieties was about 30 cm taller than that of improved varieties. The life cycle of traditional rice varieties was 10 d longer than that of modern rice varieties. Eventually, a total of 98 rice combinations (50 combinations in 2001; 48 in 2012) were selected and included in the field experiment (Appendix B).

### 5.2. Field experimental design

The field experiments were conducted during 2001–2002 at multiple sites in eight districts of Yunnan Province, including Zhaotong, Wenshan, Lijiang, Puer, Lincang, Xishuangbanna, Chuxiong, and Baoshan districts. At each experimental site, three field plots were included each planted with either a traditional or modern rice variety in monoculture of, or a combination of traditional and modern rice varieties in intercropping. The size of each plot was ~0.07 ha. Consequently, a total of 62.7 ha of the experimental field were planted with different rice varieties or combinations of rice varieties in this study. The field design of monoculture and intercropping plots followed the description of Zhu et al. (2000, 2003a). For the monoculture plots, different rice varieties were transplanted at the same time; whereas for the intercropping plots, the improved rice varieties were transplanted 1–3 d earlier than the traditional varieties. The experimental fields were managed following the local rice management style (Zhu et al. 2003a). No chemical fungicides were applied to experimental plots to allow the rice blast to occur naturally.

### 5.3. Rice blast score and data analysis for disease evaluation

A total of 50 plants distributed in five areas of a plot were sampled for rice blast disease evaluation (Zhu et al. 2003). Three indices, i.e., rice blast incidence, rice blast severity, and the efficiency of rice blast control were scored at the panicle maturing stage. Rice blast incidence index (%) was scored as the number of rice panicles having the blast disease against the total number of investigated rice panicles. Rice blast severity index (%) was scored as the number of rice panicles having the blast disease with different catego-

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