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POLYVARIETAL PLANTING AND RICE BLAST CONTROL IN PHILIPPINE UPLANDS

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ABSTRACT: *I employed what could be called genotype by environment biogeography in a case study of an upland ricefield in the Philippines in order to better explain why outbreaks of rice blast disease are more prevalent in fields composed of a single rice variety than in ricefields composed of mixtures of multiple varieties. According to genotype by environment biogeography, distributions of organisms and interactions of biota across space are causally connected to genotype by environment (GxE) and, more specifically, signal transduction pathway by environment (STPxE) interactions. I observed that planting mixtures of multiple rice genotypes results in a form of rice blast control called intrafield gene deployment in which polyvarietal planting increases the potential number of different G/STPxE interactions and hence the potential number of different expressions of blast resistance by each rice plant, which thus reduces the efficiency of blast dispersal within a ricefield across space and over time.*

INTRODUCTION: RICE BLAST DISEASE AND VARIETAL MIXTURES

Rice blast disease is the principal disease of rice and has long been a significant constraint to global rice production (Bastiaans et al., 1994; Wolfe, 2000). Rice plants at all developmental stages can be infected with the disease, and those plants that were infected as seedlings or during tillering are usually all killed (Ou, 1985). Blast outbreaks can reduce rice yields by approximately 50% during epidemics and as much as 90% in extreme cases (Bastiaans et al., 1994; Ishiguro and Hashimoto, 1991; Ou, 1985). One of the most widely distributed of plant diseases, blast is present in nearly every rice environment and rice production region throughout the world (Long, 1999; Ou, 1985).

It has long been known that the occurrence and severity of blast in ricefields composed of varietal mixtures are lesser than in fields composed of a single rice variety (Bonman et al., 1986; Mundt, 1994; Zhu et al., 2000). Planting mixtures of multiple rice varieties, i.e., genotypes, within a field has resulted in effective blast control in traditional rice agriculture for centuries (Wolfe, 2000). Current explanations for this phenomenon are based upon the idea that each rice variety, or genotype, has a different genetic resistance to blast, and thus some varieties within the field may be more genetically resistant to blast than the other varieties. There currently exists, however, an incomplete understanding of why blast is better controlled in varietal mixtures than monocultures, especially with respect to how microenvironmental conditions may effect this phenomenon (Falvo, 2000a; Garrett and Mundt, 1999). Because of this incomplete understanding, methods of effective blast control through planting varietal mixtures are currently lacking (Teng, 1994). In what follows, I will employ what could be called *genotype by environment biogeography* in a case study of an upland ricefield in the Philippines in order to illustrate how polyvarietal planting may achieve a form of effective rice blast control called *intrafield gene deployment* (cf. Falvo, 2000a).

GENOTYPE BY ENVIRONMENT BIOGEOGRAPHY

Biogeography is the study of biota within a spatial and temporal context (Cox and Moore, 1993). According to current approaches to biogeography, biogeographical phenomena are causally connected to physiology-environment interactions (cf. Cox and Moore, 1993; Veblen, 1989). According to genotype by environment biogeography, distributions of organisms and interactions of biota across space are also causally connected to genotype by environment (GxE) interactions and, more specifically, *signal transduction pathway by environment (STPxE) interactions* (Falvo, 2000a). The term GxE interactions refers to the fact that the phenotypic expressions of a particular genotype can differ depending on the environment in which the genotype is located (Romagosa and Fox, 1993; Wade et al., 1996). A genotype's signal transduction pathways are strongly influenced by environmental conditions (cf. Wang et al., 1999), and can therefore differ depending on the environmental conditions of a genotype's location on a landscape (Falvo, 2000a). Signal transduction pathways refer to intracellular signaling cascades that involve multiple genes and link recognition of and response to an environmental stimulus (cf. Falvo et al., 2000; Keen, 1997). Since environmental conditions can vary across space and over time, the same would apply to G/STPxE interactions (Falvo, 2000a).

Current evidence supports the idea that rice-blast interactions operate in part according to the concept of gene-for-gene relationships (Dioh et al., 2000; Leung et al., 1988; Silué et al., 1992; Zeigler et al., 1994). Proposed by Flor (1971), this concept states that every pathogen resistance gene in a plant has a matching avirulence gene in the plant's pathogen. In order to successfully infect a plant, a pathogen must lack all avirulence genes that match the plant's pathogen resistance genes. Conversely, a plant must possess pathogen resistance genes that correspond to all of a pathogen's avirulence genes in order to prevent infection.

GENOTYPE BY ENVIRONMENT BIOGEOGRAPHY OF RICE-BLAST INTERACTIONS

Expressions of varietal resistance and susceptibility, however, vary depending on GxE interactions across space and over time, and are not strictly based upon specific interactions between particular blast pathotypes and host or non-host rice genotypes. Such variations in varietal resistance and susceptibility cannot be explained by gene-for-gene relationships in plant-pathogen interactions alone, but must include an understanding of molecular genetic relationships in such interactions. According to a molecular genetic understanding of plant-pathogen interactions, expressions of resistance or susceptibility by plants results from signal transduction pathways that occur from a plant's recognition of a pathogen to the plant's defense response (Beynon, 1997; Dean et al., 1994; Staskawicz et al., 1995).

Genetic relationships in rice-blast interactions could thus be better conceptualized as an example of biochemical lock-and-key instead of gene-for-gene relationships (Falvo, 2000a). As described by Robinson (1996), such a conceptualization involves the existence of a biochemical lock in a plant that matches a biochemical key in the plant's pathogen that is capable of defeating the plant's resistance. In rice-blast interactions, a successful biochemical key would translate to a particular blast pathogen's ability to successfully evade the initiation of a successful signal transduction pathway by a potential host plant based upon the pathogen's pathotype and the rice plant's genotype in addition to G/STPxE interactions. Conversely, an unsuccessful biochemical lock would represent a particular blast pathogen's inability to successfully evade the initiation of a successful signal transduction pathway by a potential host plant based upon the pathogen's pathotype and the rice plant's genotype as well as G/STPxE interactions.

When lock-and-key relationships in rice-blast interactions are examined across space, a particular blast pathogen would have the greatest potential for efficient dispersal within a field composed of rice plants belonging to the same variety, or potential biochemical lock. If within this context G/STPxE interactions are not significantly variable across space, a blast pathogen could possess a key capable of defeating the resistance of any rice plant within the field. As a result, the pathogen could disperse from an infected plant to any nearby host. A particular blast pathogen would have the least potential for efficient dispersal within a field composed of mixtures of different rice plant belonging to different varieties, or potential biochemical locks. Within this context, a blast pathogen could possess the biochemical key to defeat the resistance of only those rice plants with the matching lock. Consequently, the pathogen could only disperse from an infected plant to a nearby host with a matching lock. The likelihood of nearby hosts with matching locks would decrease as the varietal diversity of a mixture increases. If within this context G/STPxE interactions are significantly variable across space, then the number of potential hosts for a particular blast pathogen would further increase.

Polyvarietal planting may achieve a form of blast control called intrafield gene deployment in which planting mixtures of multiple rice varieties, or genotypes, increases the potential number of different G/STPxE interactions across space (Falvo, 2000a). This in turn increases the potential number of different expressions of blast resistance and susceptibility by each rice plant. Since each blast pathotype can only infect rice plants of a particular resistance and susceptibility, mixtures of different expressions of blast resistance and susceptibility through G/STPxE interactions reduces the number of potential hosts for a particular blast pathotype to infect, and thus reduces the efficiency of blast dispersal within a ricefield. An individual plant which would have been a potential host for a certain blast pathotype under the environmental conditions at one moment in time, however, may be an incompatible host for the same pathotype if environmental conditions were to significantly fluctuate, since G/STPxE interactions are not necessarily the same for an individual plant at any two given moments in time. Intrafield gene deployment may therefore reflect a mechanism of reducing the efficiency of pathogen spread in host plant mixtures that could be described as a *probability effect* (Falvo, 2000a).

ENVIRONMENTAL FEEDBACK AND FARMERS' POLYVARIETAL PLANTING BEHAVIORS

These rice-blast interactions across space would provide rice farmers with positive or negative environmental feedback concerning their planting behaviors over time. Since efficient blast dispersal could decrease as varietal diversity increases, polyvarietal planting may result in increased harvests. Conversely, planting fewer varieties could result in more efficient blast dispersal and increased harvest loss. Similarly, experimenting with varietal mixtures and introducing new varieties to the mixture over time may reduce the natural selection of new blast pathotypes by introducing new genotypes with novel blast resistance genes (Crill et al., 1982; Thurston, 1994). Although different rice varieties possess different expressions of blast resistance, the blast pathogen can adapt to create new pathotypes (Valent and Chumley, 1994) that are capable of overcoming certain G/STPxE expressions of resistance over time. Such adaptation occurs in fields continuously planted with the same varieties and varietal mixtures, or sets of potential biochemical locks. Introducing novel varieties to mixtures can prevent the creation of new blast pathotypes by creating a new mixture of potentially different biochemical locks across space and over time. Such polyvarietal planting behaviors could therefore be explained in part by an environmental feedback mechanism of trial-and-error in which rice farmers experiment with varietal mixtures that best reduce blast dispersal and selection, and thus produce the greatest harvests (Falvo, 2000a).

A CASE STUDY FROM THE PHILIPPINES

I observed intrafield gene deployment and environmental feedback in farmers' polyvarietal planting behaviors in a case study of a 0.25-hectare upland ricefield near Tanauan, Batangas, Philippines. An upland ricefield is non-irrigated and characteristically possesses a great diversity of microenvironmental conditions across space (IRRI, 1997). Such a field could be conceptualized as an environmental patch composed of multiple microenvironmental patches within (cf. Kotliar and Wiens, 1990). Farmers perceived the upland ricefield in this case study as having two microenvironmental patches of primary distinction. While a 0.19-hectare area of the field typically experienced moist soil conditions, a 0.06-hectare patch near the center of the field frequently had drier soil conditions. The farmers could distinguish between these two microenvironmental patches since the soils within the drier patch were often lighter in surface color than the soils of the typically moist patch. I employed Munsell® (1994) Soil Color Charts to determine that the patch perceived by the farmers as the drier area had soil surface colors of 10YR 3/2 and lesser in color value, while the frequently moist patch had colors of 10YR 3/2 and greater in color value.

Farmers planted the field with three different rice varieties that they called, *gabi*, *wagwag*, and *C-4*. While what the farmers described as relatively equal numbers of *gabi* and *wagwag* and fewer numbers of *C-4* were randomly distributed as a mixture in the drier patch, relatively equal numbers of *gabi*, *wagwag*, and *C-4* were randomly distributed as a mixture in the moist patch. Farmers related that *gabi* could yield the least grain, while *wagwag* could produce more than *gabi*, and *C-4* could yield the most. The farmers also described how during blast outbreaks that *gabi* was resistant to infection, *wagwag* appeared somewhat resistant, and *C-4* was slightly susceptible (Figure 1).

Like many rice and other grain diseases, blast infections appear to begin and spread from a point source, i.e., an initially infected plant within a field (Kim, 1987). I observed an outbreak of blast in this case study that had started in the drier patch. The blast outbreak was diffuse and did not advance far from its point source or past the perimeter of the drier patch. It is well known that rice plants are more susceptible to blast infection when soil conditions are drier and the plants are experiencing water stress (Ou, 1985; Bonman et al., 1988; Teng et al., 1991) (Figure 2).

I employed the IRRI (1996) Standard Evaluation System for Rice to evaluate and code the blast lesions on the leaves of the infected *gabi*, *wagwag*, and *C-4*, i.e., the phenotypic expressions of the biochemical locks of the three rice genotypes interacting with the drier soil moisture conditions (Table 1). I observed that all *gabi* displayed a code 1 or very strong resistance to the blast pathogen, all *wagwag* expressed a code 3 or moderate blast resistance, and all *C-4* had a code 5 or slight resistance to the blast. Hence, three different biochemical locks resulted from the GxE and STPxE interactions that occurred between the three rice genotypes and the dry soil moisture conditions within which they were located.

Consequently, the blast outbreak in this case study was controlled through intrafield gene deployment, since more than one potential biochemical lock was present during blast dispersal. Farmers related that through experimentation over time they determined that planting different varietal mixtures of *gabi*, *wagwag*, and *C-4* between the drier and moist patches best reduced blast outbreaks in the two different areas and produced the greatest yields. This suggests a trial-and-error mechanism of environmental feedback (cf. Falvo, 2000b) between rice blast control through intrafield gene deployment across space and the farmers' planting behaviors over time.

CONCLUSIONS AND IMPLICATIONS

In this paper, I employed genotype by environment biogeography to provide a more complete understanding of why outbreaks of rice blast disease are more prevalent in fields composed of a single rice variety than in ricefields composed of mixtures of multiple varieties. Findings from the case study in the Philippines suggest that the most effective form of blast control associated with planting varietal mixtures may result from farmers planting different varietal mixtures in consideration of the different microenvironmental patches that exist within a field. This study also suggests that farmers may be able to use color plates, such as those in the Munsell® (1994) Soil Color Charts, in order to determine different microenvironmental patches within a ricefield that could influence a particular rice genotype's expression of blast resistance and susceptibility. With such information, farmers could then strategically plant mixtures of rice genotypes whose expressions of blast resistance and susceptibility under the conditions of a particular

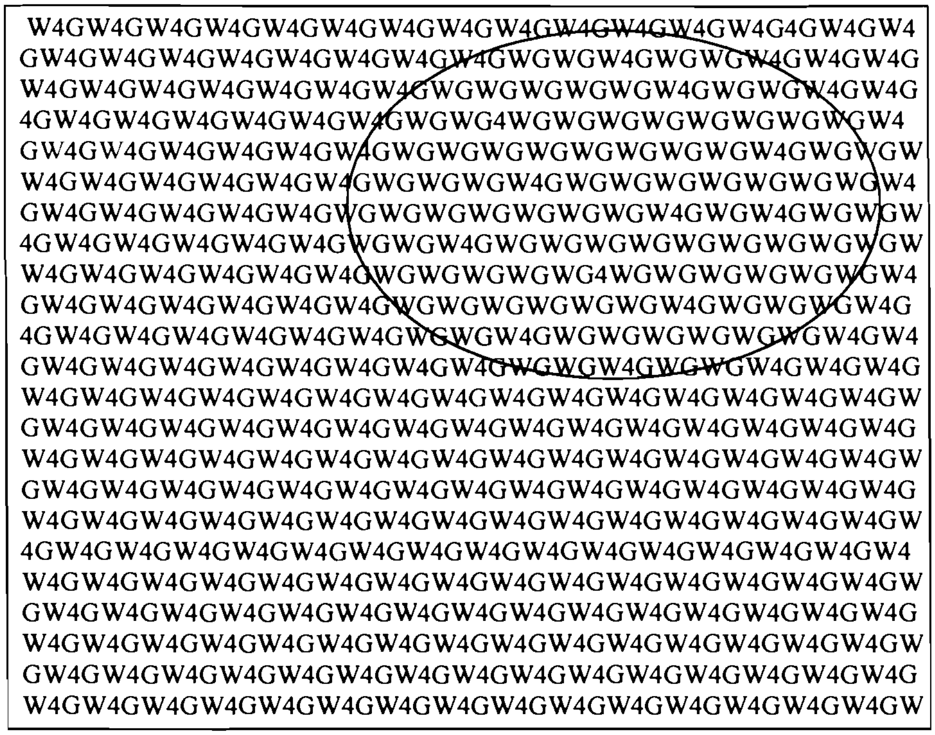

Figure 1: Conceptual diagram of the two varietal mixtures and microenvironmental patches. Area within rectangle = the ricefield; G = *gabi*; W= *wagwag*; 4 = *C-4*; area outside circle = moist soil conditions; area inside circle = drier soil conditions.

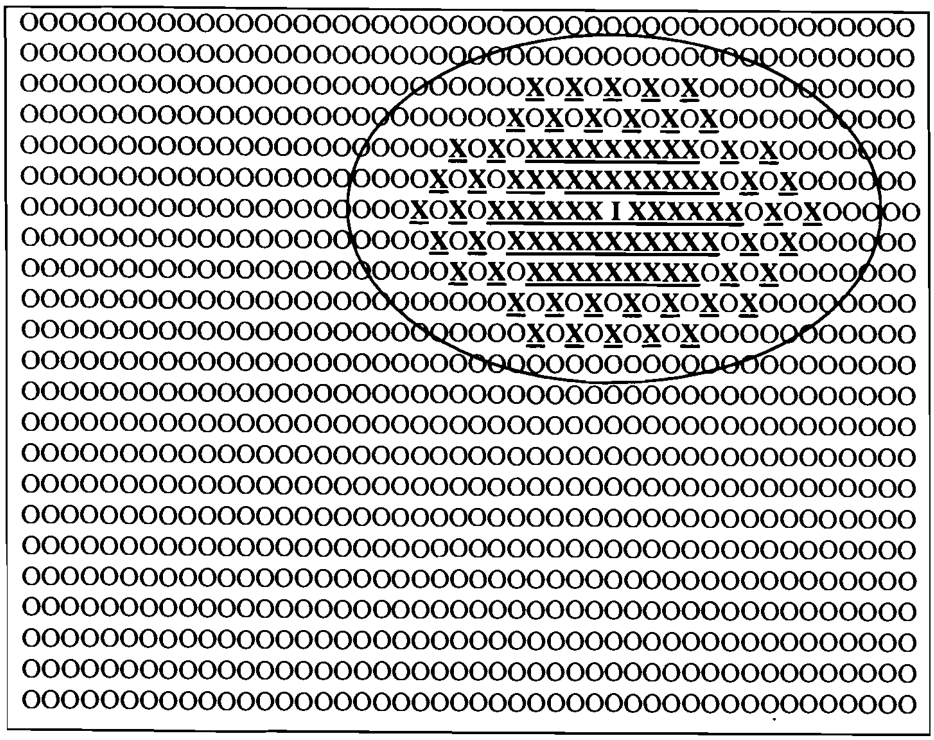

Figure 2: Conceptual diagram of blast outbreak in the case study. **I** = initially infected plant; **X** = infected rice plants; O = noninfected rice plants.

Table 1: Numbers of Infected and Noninfected Plants Within the Drier Patch by Variety

	Gabi	*Wagwag*	*C-4*
Number Infected	267	263	66
Number Noninfected	138	131	34

patch could effectively control blast dispersal. Such planting strategies based upon intrafield gene deployment may also result in effective forms of control for other rice pests, and for pests of other crops. Studies have indicated that the genetic resistance and susceptibility of rice and other plants to other diseases and herbivores are strongly influenced by environmental conditions (Newton, 1997; Salim et al., 1990). The findings of this study also suggest that some farmers may manage and promote the genetic diversity of their rice crop through a trial-and-error environmental feedback mechanism between disease control and their planting behaviors. Such findings may enable us to design and implement better strategies of *on-farm* rice genetic conservation (cf. Bellon et al., 1997; Morin, 1998). The concepts that I addressed in this paper could also apply to and provide us with deeper or novel levels of understanding regarding other biogeographical phenomena and human-environment interactions.

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