Rice Blast Control and Polyvarietal Planting in the Philippines: A Study in Genotype by Environment Biogeography

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Abstract

Current approaches to biogeography are based on organismic biology. Certain biogeographical phenomena, however, cannot be fully understood using organismic approaches to biogeography. I employed an approach based on molecular biology and biochemistry that I call *genotype by environment biogeography* in order to provide a more complete understanding of why the dispersal of rice blast disease is less efficient in fields planted with mixtures of rice varieties. In a case study of an upland ricefield in the Philippines, I found that planting varietal mixtures results in a form of effective blast control that I call *intrafield gene deployment.* I suggest that intrafield gene deployment be used to design more effective methods of blast control in intensive rice agriculture.

Keywords: rice blast control, polyvarietal planting, biogeography, Philippine agriculture, rice agriculture

In a case study of an upland ricefield in the Philippines, I observed that farmers planting mixtures of three rice varieties resulted in an effective form of controlling blast dispersal that can be called intrafield gene deployment. According to this form of blast control, planting a varietal mixture reduces the efficiency of blast dispersal by decreasing the probability of rice plants that are potential hosts within a field. Whether or not a rice plant is a potential host is determined by the variety of the plant and also by how the environmental conditions of the plant's location affect the plant's biochemical ability to prevent a blast infection. In this case study, host potential was influenced by the variety of the rice plant and by how the plant's biochemical ability to prevent blast infection was affected by the soil moisture conditions of the plant's location within the field.

Rice blast disease is caused by the fungal pathogen, *Magnaporthe grisea anamorph Pyricularia grisea Cav.* (Rossman, Howard, & Valent, 1990; Webster & Gunnell, 1992), and has long been the primary constraint to stable rice production throughout the world (Ou, 1985; Pinnschmidt, Teng, & Yong, 1994). Although it is well known that blast dispersal is less efficient within fields planted with a mixture of multiple rice varieties than within fields planted with a single rice variety, understanding of this phenomenon remains incomplete (Mundt, 1994; Wolfe, 2000; Zhu et al., 2000). Because of this incomplete understanding, methods of effective blast control through planting varietal mixtures are currently lacking (Wolfe, 2000). In what follows, I will employ an approach to biogeography that can 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 blast control that can be described as intrafield gene deployment (Falvo, 2001). This form of blast control could provide rice farmers with greater harvests, more income, and an alternative to the more expensive method of chemical control. Biogeography is the study of organisms within a spatial and temporal context (Cox & Moore, 1999). According to current approaches to biogeography, biogeographical phenomena result from effects that the environment produces on the physical functioning of organisms (Simberloff, 1983; Rosen, 1988; Veblen, 1989; Cox & Moore, 1999; May, 1994; Kupfer, 1995; Hengeveld, 1994; Brown & Lomolino, 2000). More specifically, biogeographical phenomena are causally connected to morphology-environment interactions, and are consequently influenced at a morphology-environment interface. While biogeographical phenomena that are largely influenced at the morphology-environment interface can be fully understood using organismic approaches to biogeography, other biogeographical phenomena that are largely influenced at the biochemistry-environment interface simply cannot.

I have thus suggested a new approach to biogeography that is based upon concepts from biochemistry in order to provide a more complete understanding of biogeographical phenomena. This approach can be referred to as genotype by environment biogeography (Falvo, 2001). According to genotype by environment biogeography, biogeographical phenomena result from effects that the environment produces on the physical functioning of organisms in addition to the effects that the environment produces on the molecular genetic and biochemical functioning of organisms. More specifically, biogeographical phenomena are causally connected to genotype by environment *(GxE)* interactions and signal transduction pathway by environment *(STPxE)* interactions at a biochemistry-environment interface, as well as by interactions between the environment and the physical functioning of the organism (Falvo, 2001). The term *GxE interactions* refers to the fact that an organism's phenotype can vary depending on the environment in which the genotype is located (e.g., Romagosa & Fox, 1993; Wade et al., 1995; Wade, McLaren, Samson, Regmi, & Sarkarung, 1996). Similarly, *STPxE interactions* refer to the fact that the functioning of an organism's signal transduction pathways can also vary depending on how they are affected by the environmental conditions in which the genotype is located in space (Falvo, 2001). Signal transduction pathways are intracellular signaling cascades that link recognition of and response to an environmental stimulus (Keen, 1997; Falvo et al., 2000). Such pathways involve multiple genes and proteins (Beynon, 1997). The functioning of an organism's signal transduction pathways are also strongly influenced by environmental conditions other than the specific environmental stimuli that they detect and respond to (cf. Wang et al., 1999). Since environmental conditions can vary across space and over time, so can *G/STPxE* interactions and the biogeographical phenomena that are primarily influenced by such interactions.

Genotype by environment biogeography of rice-blast interactions

In order to employ genotype by environment biogeography so as to provide a more complete understanding of why the spread of blast is less severe within varietal mixtures than rice monocultures, it is first necessary to examine what is currently known about rice-blast interactions. Current evidence suggests that rice-blast interactions operate in part according to the concept of gene-for-gene relationships (Leung, Borromeo, Bernardo, & Notteghem, 1988; Silué, Notteghem, & Tharreau, 1992; Valent & Chumley, 1994; Dioh, Tharreau, Notteghem, Orbach, & Lebrun, 2000). According to this concept, every pathogen resistance gene in a plant has a matching avirulence gene in the plant's pathogen (Flor, 1971). A pathogen resistance gene is a gene of a particular plant that prevents that plant's infection by a certain pathogen (Holub, 1997). An avirulence gene is a gene of a certain pathogen that prevents it from infecting a particular plant (Hulbert, Pryor, Hu, Richter, & Drake, 1997). Hence, a particular pathogen must lack all avirulence genes that match a certain plant's pathogen resistance genes in order to successfully infect that particular plant (Beynon, 1997). Conversely, a particular plant must possess pathogen resistance genes that correspond to all of a particular pathogen's avirulence genes to prevent infection by that pathogen (Schulze-Lefert, Christoph, & Freialdenhoven, 1997).

Expressions of varietal resistance and susceptibility, however, vary depending on *GxE* interactions across space and over time, and are not strictly based upon interactions between particular blast pathotypes and rice genotypes (Falvo, 2001). Thus, 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 the molecular genetics relationships in such interactions and the influence of environmental factors on such relationships. According to a molecular genetic understanding of plant-pathogen interactions, a plant's expression of resistance or susceptibility results from signal transduction pathways that occur from the plant's recognition of a pathogen to the plant's defense response (Dean, Lee, Mithcell, & Whitehead, 1994; Staskawicz, Ausubel, Baker, Ellis, & Jones 1995; Hammond-Kosack & Jones, 1995; Baker, Zambryski, Staskawicz, & Dinesh-Kumar, 1997; Briggs & Kemble, 1997). Since a particular genotype's signal transduction pathways can be affected by different environmental conditions across space and over time (cf. Wang et al., 1999), so can its resulting expression of resistance and susceptibility.

Hence, interactions between particular blast pathotypes and rice genotypes may be based in part upon *G/STPxE* interactions in addition to gene-for-gene relationships. Genetic relationships in rice-blast interactions could therefore be better conceptualized as an example of biochemical lock-and-key instead of gene-for-gene relationships (cf. Falvo, 2001). The molecular genetic concept of biochemical lock-and-key relationships involves the existence of a biochemical lock in a plant that matches a biochemical key in the plant's pathogen that is capable of unlocking the plant's resistance (Robinson, 1996). In rice-blast interactions, a successful biochemical key would represent 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 as well as *G/STPxE* interactions. Conversely, an unsuccessful biochemical lock would be a certain 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 biochemical 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 of the same variety, or the same potential biochemical lock (cf. Falvo, 2001). If within this context *G/STPxE* interactions are not significantly variable across space, a blast pathogen could have the key that is capable of unlocking the resistance of any rice plant within the field. Consequently, the pathogen could disperse from one 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 plants of different varieties, or different potential biochemical locks. Within this context, a blast pathogen could have the biochemical key that can unlock the resistance of only those rice plants that have the matching lock. Consequently, the pathogen could only disperse from one infected plant to only a nearby host that has a matching lock. The likelihood of nearby hosts with matching locks would decrease as the number of different varieties planted as a mixture increases. If within this context *G/STPxE* interactions are significantly variable across space, then the number of incompatible biochemical locks for a particular blast pathogen would further increase.

Polyvarietal planting may achieve an effective form of blast control that I call intrafield gene deployment in which planting mixtures of multiple rice varieties, or genotypes, increases the potential number of different *G/STPxE* interactions across space (cf. Falvo, 2001). This in turn increases the potential number of different expressions of blast resistance and susceptibility by each rice genotype. 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 reduce 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 that 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 reduce pathogen spread in varietal mixtures through what I call a probability effect, in which planting multiple genotypes within a field decreases the probability of a nearby host across space and over time (Falvo, 2001).

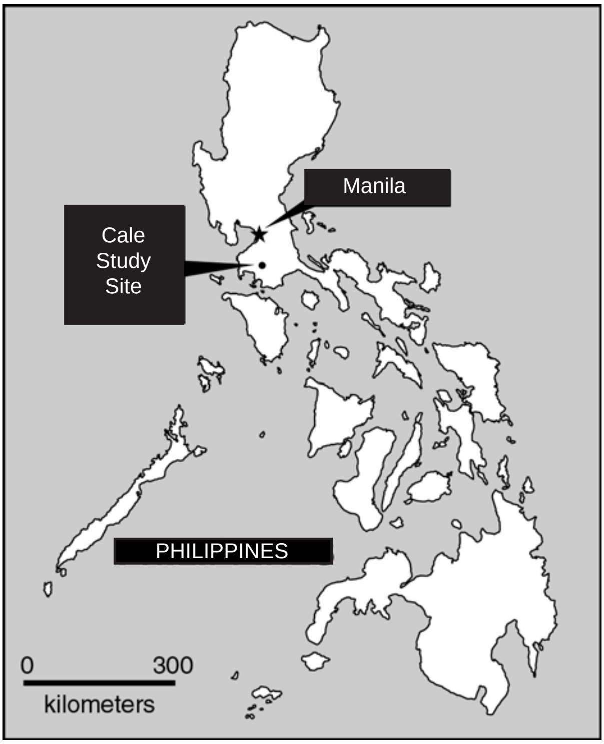
Environmental feedback and farmers' polyvarietal planting practices

These rice-blast interactions across space would provide rice farmers with positive or negative environmental feedback concerning their planting practices over time. Since efficient blast dispersal could decrease as the number of varieties in the field increases, polyvarietal planting may result in increased harvests. Conversely, planting a single or fewer varieties could result in more efficient blast dispersal and increased harvest loss. Additionally, 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, Ham, & Beachell, 1982; Thurston, 1994). Although different rice varieties possess different expressions of blast resistance, the blast pathogen can adapt to create new pathotypes that are capable of overcoming certain expressions of resistance over time (Ahn, 1982; Valent & Chumley, 1994; Zeigler, Tohme, Nelson, Levy, Correa-Victoria, 1994). Such adaptation occurs in fields continuously planted with the same varieties and varietal mixtures, i.e., sets of potential biochemical locks. Introducing novel varieties to mixtures may 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 whereby rice farmers experiment with varietal mixtures that best reduce blast dispersal and selection, and thus produce the greatest yields.

A case study from the Philippines

Falvo (2001) observed intrafield gene deployment and environmental feedback in farmers' polyvarietal planting practices in a case study of a 0.25-hectare upland ricefield in Cale, Tanauan, Batangas, Philippines. An upland ricefield is non-irrigated and has a diversity of microenvironmental conditions across space (IRRI, 1997). Thus an upland ricefield could be conceptualized as an environmental patch that is composed of multiple microenvironmental patches within (cf. Kotliar & Wiens, 1990). Farmers perceived the upland rice field in this study as having two distinct areas, or microenvironmental patches. While approximately 0.19 hectares of the field typically experienced moist soil conditions, a 0.06-hectare patch near the center of the field typically experienced drier soil conditions. Farmers could distinguish between these two patches since the soils of the drier patch were often lighter in surface color than the soils of the frequently 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 greater in Munsell color value, while what they described as the frequently moist area had soil colors of 10YR 3/2 and lesser in Munsell color value (cf. Falvo, 2001). I determined that soil surface colors of 10YR 3/2 and lesser in Munsell color value were indeed indicative of increasing soil moisture since the color of the soil after saturation darkened to 10YR 2/1. Similarly, the soil colors of 10YR 3/2 and greater in Munsell color value were indicative of drier soil moisture conditions since the color of the soil after being sun-dried lightened to 10YR 4/3.

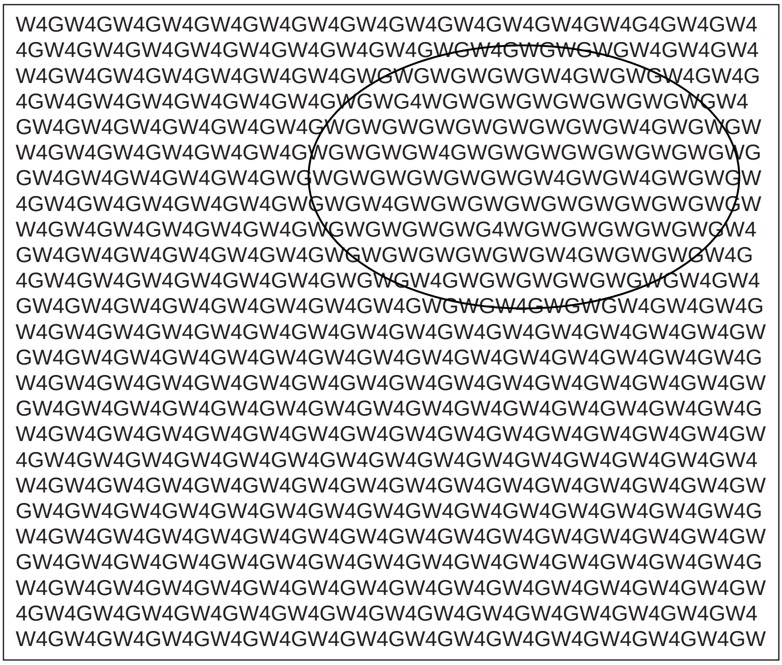
Figure 1. Location of the study site in Cale, Tanauan, Batangas, Philippines



Farmers planted the field with three different rice varieties that they referred to as, *gabi*, *wagwag*, and C-4 (cf. Falvo, 2001). Farmers repored 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. While 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.

Like outbreaks of many other plant diseases, outbreaks of blast begin and spread from an initially infected plant within the ricefield (Kim, 1987; 1994).

Figure 2. Conceptual diagram of the two varietal mixtures and soil moisture conditions



Area within the rectangle = the ricefield
G = gabi; W= wagwag; 4 = C-4
area outside the circle = moist soil conditions and varietal mixture A
area inside the circle = drier soil moisture conditions and varietal mixture B

I observed an outbreak of blast that began within varietal mixture *B*, or the microenvironmental patch with drier soil conditions (cf. Falvo, 2001). The blast outbreak became spatially diffused as it progressed near the boundary between the two mixtures, and it did not advance past the perimeter of varietal mixture *B*. I employed the IRRI (1996b) *Standard Evaluation System for Rice* to evaluate and code the blast lesions on the leaves of the infected *gabi*, *wagwag*, and C-4. The blast lesions represent the phenotypic expressions of the biochemical locks of the three rice genotypes interacting with the environmental conditions of their location. In this case study, *gabi* displayed a code 1 or very strong resistance to the blast, *wagwag* expressed a code 3 or moderate blast resistance, and C-4 had a code 5 or slight susceptibility to blast. Hence, three different biochemical locks resulted from the *G/STPxE* interactions that occurred between the three rice genotypes and the environmental conditions within which they were located, in this case drier soil moisture conditions. It could also be said that additional biochemical locks resulted from the *G/STPxE* interactions between the three rice genotypes and the environmental conditions near the boundary of the two mixtures, since only plants of the three varieties whose leaves were starting to fold due to water stress within mixture *B* became infected. Those plants that did not show signs of water stress near the boundary between the two mixtures did not become infected, and were thus expressing new and incompatible biochemical locks for the blast.

Thus, the spread of the blast outbreak in this case study was controlled through intrafield gene deployment, since more than one potential biochemical lock was present across space at the time of blast dispersal. Furthermore, 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 the spread of blast outbreaks in the two different areas and resulted in the greatest yields. This suggests a trial-and-error mechanism of environmental feedback (cf. Falvo, 2000) between rice blast control involving 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 blast dispersal is less efficient within ricefields composed of multiple varieties. Findings from the case study suggest that the most effective form of blast control associated with polyvarietal planting may result from farmers planting different varietal mixtures within different microenvironmental patches that exist within a field. Furthermore, 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 under the conditions of a particular patch could effectively control blast dispersal. Color charts are already successfully employed by rice farmers to determine a plant's nitrogen rate by observing leaf applications accordingly (IRRI, 1996a).

Polyvarietal planting strategies based upon intrafield gene deployment may also result in effective forms of control of other rice diseases, and of insect rice pests. Studies have indicated that the genetic resistance and susceptibility of rice plants to other diseases and insect herbivores are significantly influenced by environmental conditions (Ou, 1985; Salim, Saxena, & Akbar, 1990; Panda & Khush, 1995). Polyvarietal planting strategies based upon intrafield gene

Figure 3. Conceptual diagram of blast dispersal in the case study

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I = initially infected plant
X = infected rice plants
O = noninfected rice plants
= direction of blast dispersal

deployment may also result in effective forms of control for diseases of other grain crops besides rice, and for their specific insect pests (McDonald, Allard, & Webster, 1988; Akanda & Mundt, 1996; Newton, Ellis, Hackett, & Guy, 1997). The genetic resistance and susceptibility of grain crops other than rice, such as wheat, are strongly influenced by environmental conditions as well.

The findings of this study also suggest that some farmers may manage and promote diversity in their rice crops in part through a trial-and-error mechanism of environmental feedback between blast control and their polyvarietal planting practices. Therefore, such findings may enable us to design and implement better strategies for the on-farm conservation of rice varietal diversity (cf. Altieri & Merrick, 1987; Brush, 1991; Bellon, Pham, & Jackson, 1997; Brush & Meng, 1998; Jarvis & Hodgkin, 1999). On-farm conservation of rice varietal diversity continues natural selection among the varieties, and is thus crucial for rice genetic conservation (cf. Vaughan & Chang, 1992).

Lastly, the concepts that I have 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. For example, I observed in upland rice fields in the Philippines that the damage produced from the rice brown planthopper (BPH) was patchy and spatially associated with areas of different soil moisture conditions. Farmers were aware of these spatial associations and would experiment with planting different varieties in areas with certain soil moisture conditions to see which varieties could best resist BPH attack when planted in those areas. These observations suggest that rice-BPH interactions may also be causally connected to *G/STPxE* interactions, and that a trial-and-error mechanism of environmental feedback may be operating between rice-BPH interactions and the farmers' planting practices.

These observations are similar to the ones presented in this paper concerning rice blast control and environmental feedback in farmers' polyvarietal planting practices, and may provide deeper levels of understanding of rice-BPH interactions.

References

Altieri, M. A., & Merrick, L. C. (1987). In situ conservation of crop genetic resources through maintenance of traditional farming systems. *Economic Botany 41*, 86-96.

Ahn, S. W. (1982). The slow blasting resistance to rice blast. In *Proceedings of the symposium on rice resistance to blast* (pp. 343-370). Montpellier, France: IRAT/GERDAT.

Akanda, S. I., & Mundt, C. C. (1996). Effects of two-component wheat cultivar mixtures on stripe rust severity. *Phytopathology*, *86*, 347-353.

Baker, B., Zambryski, P., Staskawicz, B. J., & Dinesh-Kumar, S. P. (1997). Signaling in plant-microbe interactions. *Science*, *276*, 726-733.

Bellon, M. R., Pham, J. L., & Jackson, M. T. (1997). Genetic conservation: A role for rice farmers. In N. Maxted, B. V. Ford-Llyod, & J. G. Hawkes (Eds.), *Plant genetic conservation: The in situ approach* (pp. 263-289). London, UK: Chapman & Hall.

Beynon, J. L. (1997). Molecular genetics of disease resistance: An end to the "gene-for-gene" concept? In I. R. Crute, E. B. Holub, & J. J. Burdon (Eds.), *The gene-for-gene relationship in plant-parasite interactions* (pp. 359-377). Wallingford, UK: CAB International.

Briggs, S. P., & Kemble, R. J. (1997). Genetic disease control in plants—Where now? In I. R. Crute, E. B. Holub, & J. J. Burdon (Eds.), *The gene-for-gene relationship in plant-parasite interactions* (pp. 329-346). Wallingford, UK: CAB International.

Brown, J. H., & Lomolino, M. V. (2000). Concluding remarks: Historical perspectives and the future of island biogeography theory. *Global Ecology & Biogeography, 9*, 87-92.

Brush, S. B. (1991). A farmer-based approach to conserving crop germplasm. *Economic Botany, 45*, 153-165.

Brush, S. B., & Meng, E. (1998). Farmers' valuation and conservation of crop genetic resources. *Genetic Resources and Crop Evaluation, 45*, 139-150.

Cox, C. B., & Moore, P. D. (1999). *Biogeography: An ecological and evolutionary approach* (6th ed.). Cambridge: Blackwell Science.

Crill, P., Ham, Y. S., & Beachell, H. M. (1982). The rice blast disease in Korea and its control with race prediction and gene rotation. In *Evolution of the gene rotation concept for rice blast control* (pp. 123-130). Los Baños, Philippines: International Rice Research Institute.

Dean, R. A., Lee, Y. H., Mithcell, T. K., & Whitehead, D. S. (1994). Signalling systems and gene expression regulating appressorium formation in *Magnaporthe grisea*. In R. S. Zeigler, S. A. Leong, & P. S. Teng (Eds.), *Rice blast disease* (pp. 23-34). Los Baños, Philippines: International Rice Research Institute; Wallingford, UK: CAB International.

Dioh, W., Tharreau, D., Notteghem, J. L., Orbach, M., & Lebrun, M. H. (2000). Mapping avirulence genes in the rice blast fungus, *Magnaporthe grisea*, with RFLP and RAPD markers. *Molecular Plant-Microbe Interactions, 13* (2), 217-227.

Falvo, D. J. (2000). On modeling Balinese water temple networks as complex adaptive systems. *Human Ecology, 28* (4), 641-650.

Falvo, D. J. (2001). Polyvarietal planting and rice blast control in Philippine uplands. *Middle States Geographer*, *33*, 54-62.

Falvo, J. V., Uglialoro, A. M., Brinkman, B. M. N., Merika, M., Parekh, B. S., Tsai, E. Y., King, H. C., Morielli, A. D., Peralta, E. G., Maniatis, T., Thanos, D., & Goldfield, A. E. (2000). Stimulus-specific assembly of enhancer complexes on the tumor necrosis factor alpha gene promoter. *Molecular and Cellular Biology, 20*, 2239-2247.

Flor, H. H. (1971). Current status of gene-for-gene concept. *Annual Review of Phytopathology, 9*, 275-296.

Hammond-Kosack, K. E., & Jones, J. D. G. (1995). Plant disease resistance genes, unraveling how they work. *Canadian Journal of Botany, 73*, 495-505.

Hengeveld, R. (1994). Biogeographical ecology. *Journal of Biogeography, 21*, 341-351.

Holub, E. B. (1997). Organization of resistance genes in arabidopsis. In I. R. Crute, E. B. Holub, & J. J. Burdon (Eds.), *The gene-for-gene relationship in plant-parasite interactions* (pp. 5-26). Wallingford, UK: CAB International.

Hulbert, S., Pryor, T., Hu, G., Richter, T., & Drake, J. (1997). Genetic fine structure of resistance loci. In I. R. Crute, E. B. Holub, & J. J. Burdon, (Eds.), *The gene-for-gene relationship in plant-parasite interactions* (pp. 27-43). Wallingford, UK: CAB International.

International Rice Research Institute (IRRI). (1997). *Rice almanac*. Los Baños, Philippines: International Rice Research Institute.

_____. (1996a). *Listening to the farmers*. Los Baños, Philippines: International Rice Research Institute.

_____. (1996b). *Standard evaluation system for rice* (4th ed.). Los Baños, Philippines: International Network for Genetic Evaluation of Rice, Genetic Resources Center, & International Rice Research Institute.

Jarvis, D., & Hodgkin, T. (1999). Farmer decision-making and genetic diversity: Linking multidisciplinary research to implementation on-farm. In S. B. Brush (Ed.), *Genes in the field: On-farm conservation of crop diversity* (261-278). Boca, Raton, Florida, USA: Lewis Publishers.

Keen, N. T. (1997). Elicitor generation and receipt: The mail gets through, but how? In I. R. Crute, E. B. Holub, & J. J. Burdon (Eds.), *The gene-for-gene relationship in plant-parasite interactions* (pp. 379-388). Wallingford, UK: CAB International.

Kim, C. K. (1987). Disease dispersal gradients of rice blast from point source. *Korean Journal of Plant Protection, 3*, 131-136.

Kotliar, N. B., & Wiens, J. A. (1990). Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos, 59*, 253-260.

Kupfer, J. A. (1995). Landscape ecology and biogeography. *Progress in Physical Geography, 19* (1), 18-34.

Lai, X. H., Marchetti, M. A., & Petersen, H. D. (1999). Comparative slow-blasting in rice grown under upland and flooded blast nursery culture. *Plant Disease, 83* (7), 681-684.

Leung, H., Borromeo, E. S., Bernardo, M. A., & Notteghem, J. L. (1988). Genetic analysis of virulence in the rice blast fungus *Magnaporthe grisea*. *Phytopathology, 78*, 1227-1233.

May, R. M. (1994). The effects of spatial scale on ecological answers. In P. J. Edwards, R. M. May, & N. R. Webb, (Eds.), *Large-scale ecology and conservation biology* (pp. 1-17). Oxford, UK: Blackwell Scientific Publications.

McDonald, B. A., Allard, R. W., & Webster, R. K. (1988). Responses of two-, three-, and four-component barley mixtures to a variable pathogen population. *Crop Science, 28*, 447-452.

Mundt, C. C. (1994). Use of host genetic diversity to control cereal diseases: implications for rice blast. In R. S. Zeigler, S. A. Leong, & P. S. Teng (Eds.), *Rice blast disease* (pp. 293-308). Los Baños, Philippines: International Research Institute; Wallingford, UK: CAB International.

Munsell®. (1994). *Munsell® soil color charts* (1994 ed.). New Winsor, New York, USA: Munsell® Color, Macbeth Division of Kollmorgen Instruments Corporation.

Newton, A. C., Ellis, R. P., Hackett, C. A., & Guy, D. C. (1997). The effect of component number on Rhynchosporium secalis infection and yield in mixtures of winter barley cultivars. *Plant Pathology, 45*, 930-938.

Ou, S. H. (1985). *Rice diseases* (2nd ed.). Kew, UK: Commonwealth Mycological Institute.

Panda, N., & Khush, G. S. (1995). *Host plant resistance to insects*. Los Baños, Philippines: International Rice Research Institute; Wallingford, UK: CAB International.

Pinnschmidt, H. O., Teng, P. S., & Yong, L. (1994). Methodology for quantifying rice yield effects of blast. In R. S. Zeigler, S. A. Leong, & P. S. Teng (Eds.), *Rice blast disease* (pp. 381-408). Los Baños, Philippines: International Rice Research Institute; Wallingford, UK: CAB International.

Robinson, R. A. (1996). *Return to resistance: Breeding crops to reduce pesticide dependence*. Davis, California, USA: AgAcess.

Romagosa, I., & Fox, P. N. (1993). Genotype *x* environment interaction and adaptation. In M. D. Hayward, N. O. Bosemark, & I. Romagosa (Eds.), *Plant breeding: Principles and prospects,* 1st ed. (pp. 373-390). London, UK: Chapman and Hall.

Rosen, B. R. (1988). Biogeographic patterns: A perceptual overview. In A. A. Myers & P. S. Giller (Eds.), *Analytical biogeography* (pp. 23-55). London, UK: Chapman & Hall.

Rossman, A. Y., Howard, R. J., & Valent, B. (1990). *Pyricularia grisea*, the correct name for the rice blast disease fungus. *Mycologia, 82*, 509-512.

Salim, M., Saxena, R. C., & Akbar, M. (1990). Salinity stress and varietal resistance in rice: Effects on whitebacked planthopper. *Crop Science, 30*, 654-659.

Schulze-Lefert, P., Christoph, P. H., & Freialdenhoven, A. (1997). Mutation analysis for the dissection of resistance. In I. R. Crute, E. B. Holub, & J. J. Burdon (Eds.), *The gene-for-gene relationship in plant-parasite interactions* (pp. 45-63). Wallingford, UK: CAB International.

Silué, D., Notteghem, J. L., & Tharreau, D. (1992). Evidence for a gene-for-gene relationship in sativa-*Magnaporthe grisea* pathosystem. *Phytopathology, 82* (5), 577-580.

Simberloff, D. S. (1983). Biogeography: The unification and maturation of a theory. In A. H. Bush & G. A. Clark (Eds.), *Perspectives in ornithology* (pp. 411-455). London, UK: Cambridge University Press.

Spence, N. J. (1997). The molecular genetics of plant-virus interactions. In I. R. Crute, E. B. Holub, & J. J. Burdon (Eds.), *The gene-for-gene relationship in plant-parasite interactions* (pp. 347-357). Wallingford: UK: CAB International.

Staskawicz, B. J., Ausubel, F. M., Baker, B. J., Ellis, J. G., & Jones, J. D. G. (1995). Molecular genetics of plant resistance. *Science, 268*, 661-667.

Thurston, H. D. (1994). Assessing indigenous and traditional knowledge in farming systems. In R. S. Zeigler, S. A. Leong, & P, S. Teng (Eds.), *Rice blast disease* (pp. 541-558). Los Baños, Philippines: International Rice Research Institute; Wallingford, UK: CAB International.

Valent, B., & Chumley, F. G. (1994). Avirulence genes and mechanisms of genetic instability in the rice blast fungus. In R. S. Zeigler, S. A. Leong, & P. S. Teng (Eds.), *Rice blast disease* (pp. 111-134). Los Baños, Philippines: International Rice Research Institute; Wallingford, UK: CAB International.

Vaughan, D. A., & Chang, T. T. (1992). In situ conservation of rice genetic resources. *Economic Botany, 46* (4), 368-383.

Veblen, T. T. (1989). Biogeography. In G. L. Gaile & C. J. Willmott (Eds.), *Geography in America* (pp. 28-46). Ohio, USA: Merrill.

Wade, L. J., McLaren, C. J., Samson, B. K., Regmi, K. R., & Sarkarung, S. (1996). The importance of environmental characterization for understanding genotype by environment interactions. In M. Cooper, & G. L. Hammer (Eds.), *Plant adaptation and crop improvement* (pp. 549-562). Wallingford, UK: CAB International; Los Baños, Philippines: International Rice Research Institute; Andra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics.

Wade, L. J., Sarkarung, S., McLaren, C. G., Guhey, A., Quader, B., Boonwite, C., Amarante, S. T., Sarawgi, A. K., Haque, A., Harnpichitvitaya, D., Pamplona, A., & Bhamri, M. C. (1995). Genotype x environment interaction and selection methods for identifying improved rainfed lowland genotypes. *Fragile lives in fragile ecosystems* (pp. 885-900). Los Baños, Philippines: International Rice Research Institute.

Wang, Z. X., Yano, M., Yamanouchi, U., Iwamoto, M., Monna, L., Hayasaka, H., Katayose, Y., & Sasaki, T. (1999). The Pib gene for blast resistance belongs to the nucleotide binding and leucine-rich repeat class of plant disease resistance genes. *The Plant Journal, 19* (1), 55-64.

Webster, R. K., & Gunnell, P. S. (1992). *Compendium of rice diseases*. St. Paul, MN, USA: APS Press.

Wolfe, M. S. (2000). Crop strength through diversity. *Nature, 406*, 681-682.

Zeigler, R. S., Tohme, J., Nelson, R., Levy, M., & Correa-Victoria, F. J. (1994). Lineage exclusion: A proposal for linking blast population analysis to resistance breeding. In R. S. Zeigler, S. A. Leong, & P. S. Teng (Eds.), *Rice blast disease* (267-292). Los Baños, Philippines: International Rice Research Institute; Wallingford, UK: CAB International.

Zhu, Y., Chen, H., Fan, J., Wang, Y., Li, Y., Chen, J., Fan, J. X., Yang, S., Hu, L., Leung, H., Mew, T. W., Teng, P. S., Wang, Z., & Mundt, C. C. (2000). Genetic diversity and disease control in rice. *Nature, 406*, 718-722.

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