cursorial birds, when they were already adept cursors with a posterior centre of mass.

The second proposal, that some theropods were derived from currently unknown, flighted ancestors, has been suggested[19]. As noted above, *Caudipteryx*'s locomotory adaptations are consistent with it having been derived from flighted ancestors. However, there is no substantive evidence to support flighted ancestors for any other theropods. Nevertheless, this possibility cannot be dismissed. In the light of problems associated with theories (1) and (2), perhaps the third, that *Caudipteryx* was a secondarily flightless, post-*Archaeopteryx*, cursorial bird, deserves closer scrutiny than it has received so far. We find it a striking coincidence that the only unambiguously feathered theropod was also the only known theropod likely to have utilized locomotory mechanisms identical to those of cursorial birds. □

Methods

Hindlimb and trunk length data

We recorded data on hindlimb element (femur, tibia or tibiotarsus, metatarsal III or tarsometatarsus) and trunk lengths in mature, extant and extinct cursorial (or at least ground-living) birds (from eight orders and 24 genera, including tinamou, cassowary, ostrich, galliforms, roadrunners, bustards, moa and elephantbird) and 38 genera of theropod and ornithopod dinosaurs (see Supplementary Information). Data were collected from avian and dinosaur specimens in museum collections or obtained from published data and/or scale reconstructions. Individuals were included only if the hindlimb skeleton was adequately known and the trunk was sufficiently known that the describers were able confidently to reconstruct the specimen.

The morphometric data collected from each individual included maximum femoral length, maximum tibia (or tibiotarsus) length (excluding the cnemial crest) maximum metatarsus (or tarsometatarsus) length and trunk length. We defined trunk length as the distance between the first dorsal vertebrae and/or head of the first dorsal rib to the posterior rim of the acetabulum.

Juvenile birds have, for a given trunk length, longer hindlimbs than their adult counterparts[20]; the same has been hypothesized for tyrannosaurids[21] and allosaurids[22]. Similarly, *Bambiraptor feinbergi*, a juvenile dromaeosaurid theropod, has a hindlimb/trunk length ratio of 2.0 (ref. 23) that is comparable to that seen in cursorial birds, but we exclude it from our analyses because of its obviously early stage of development. Additionally, *Sinornithoides youngi* was excluded from this study. The specimen also exhibits a bird-like hindlimb/trunk length ratio, is very small and possessed a cartilaginous sternum[24]. These observations indicate that this specimen, originally described as 'nearing maturity', may have been more immature than its describers supposed. To avoid confounding ontogenetic variables, the largest individual for each genus (for which we had data) was used in the analysis and data from known immature extant individuals were omitted as were extinct specimens whose maturity has in doubt.

The developmental maturity of *Caudipteryx* (NGMC 97–4–A and NGMC 97–9–A) is indicated by the well ossified sterna, sternal ribs, wrist bones and ankle bones[14]. Similar ossification is present in two more recently discovered, equivalently sized specimens, *Caudipteryx dongi* (IVPP V 12344)[25] and *Caudipteryx* (uncatalogued IVPP specimen) (Z. Zhou, personal communication), but the former specimen also possesses ossified uncinate processes. As these skeletal elements ossify late in development, there is little doubt that these individuals were mature.

Centre of mass calculations

Lateral and dorsal profiles of *Deinonychus* were compiled from reconstructions in ref. 19. Lateral and dorsal profiles of *Caudipteryx* were reconstructed from NGMC 97–4–A and NGMC 97–9–A. The axial body profiles were mathematically combined to create a solid three-dimensional model from which body volume and the location of centre of mass were calculated (see ref. 18 for details). The lung was conservatively assumed to have been spherical with a volume equal to 10% of body volume and positioned at the anterior portion of the trunk. The density of the lung ($0.4\,kg\,m^{-1}$) was estimated using the ratio of mass-specific lung volume to mass-specific lung parenchyma volume in a large Nile crocodile[26].

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Genetic diversity and disease control in rice

Youyong Zhu*, Hairu Chen*, Jinghua Fan*, Yunyue Wang*, Yan Li*, Jianbing Chen*, JinXiang Fan†, Shisheng Yang ‡, Lingping Hu§, Hei Leung‖, Tom W. Mew‖, Paul S. Teng‖, Zonghua Wang‖ & Christopher C. Mundt‖¶

* *The Phytopathology Laboratory of Yunnan Province, Yunnan Agricultural University, Kunming, Yunnan 650201, China*
† *Honghe Prefecture Plant Protection Station of Yunnan Province, Kaiyuan 661400, China*
‡ *Jianshui County Plant Protection Station of Yunnan Province, Jianshui 654300, China*
§ *Shiping County Plant Protection Station of Yunnan Province, Shiping 662200, China*
‖ *Division of Entomology and Plant Pathology, International Rice Research Institute, MCPO Box 3127, 1271 Makati City, The Philippines*
¶ *Department of Botany and Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, Oregon 97331-2902, USA*

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Crop heterogeneity is a possible solution to the vulnerability of monocultured crops to disease[1–3]. Both theory[4] and observation[2,3] indicate that genetic heterogeneity provides greater disease suppression when used over large areas, though experimental data are lacking. Here we report a unique cooperation among farmers,

researchers and extension personnel in Yunnan Province, China—genetically diversified rice crops were planted in all the rice fields in five townships in 1998 and ten townships in 1999. Control plots of monocultured crops allowed us to calculate the effect of diversity on the severity of rice blast, the major disease of rice[5]. Disease-susceptible rice varieties planted in mixtures with resistant varieties had 89% greater yield and blast was 94% less severe than when they were grown in monoculture. The experiment was so successful that fungicidal sprays were no longer applied by the end of the two-year programme. Our results support the view 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.

Many ecological processes are strongly influenced by spatial scale[6–9], causing a major dilemma for experimental biologists, as large-scale field experiments are often prohibitively expensive. For example, there have been increasing calls for ecological approaches to counter the negative environmental impacts of modern agricultural systems[10,11]. One such approach, the use of within-field crop genetic diversity, has been shown to reduce disease severity in experimental plots and has been used commercially in some

cases[1–4]. However, experimental procedure and the nature of pathogen dispersal can cause substantial underestimation of the impact of increased diversity on disease in small-scale experimental plots[2–4]. On the other hand, observations at larger spatial scale are few[4], and do not allow for unambiguous determination of causal relationships between diversity and disease occurrence.

Our experimental system was blast disease in rice (*Oryzae sativa*). Rice is the staple crop for about half of the population of the world[12]. The fungus that causes blast disease, *Magnaporthe grisea*, spreads through multiple cycles of asexual conidiospore production during the cropping season, causing necrotic spots on leaves and necrosis of panicles. *M. grisea* interacts on a gene-for-gene basis[13,14] with its host and has a very varied pathogenesis[15]. It exists as a mixture of pathogenic races, that is, genetic variants that attack host genotypes with different resistance genes. Thus, host resistance genes often remain effective for only a few years in agricultural production before succumbing to new pathogenic races[16,17].

Our experimental site (Yunnan Province, China) favours the development of rice blast epidemics because of its cool, wet climate. Farmers commonly make multiple foliar fungicide applications to control blast. Glutinous or 'sticky' rice varieties are used for confections and other speciality dishes and have higher market value than other rice types, but have lower yields and are highly susceptible to blast. Non-glutinous, hybrid rice varieties are less susceptible to rice blast and are attacked by a different spectrum of *M. grisea* races. Before 1998, 98% of rice fields in the study area were sown with monocultures of the hybrid rice varieties Shanyuo22 and Shanyuo63. The desirable glutinous varieties were planted in small amounts because of their low yields and vulnerability to blast in this environment. We conducted large-scale tests, made possible through the cooperation of thousands of rice farmers, to determine how the occurrence of rice blast is affected by within-field varietal diversification using mixtures of commonly grown glutinous and hybrid rice varieties. Our approach was based on an observed farmer practice of dispersing single rows of glutinous rice between groups of four rows of hybrid rice at a rate sufficient to meet local demand for glutinous rice (Fig. 1).

In the first year of the experiment, four different mixtures of varieties (Fig. 2) were planted in a 812-ha area consisting of all rice fields in five townships of Shiping County, Yunnan Province. Because of the excellent blast control provided by the variety mixtures, only one foliar fungicide spray was applied. Mixtures were compared to monoculture control plots at 15 survey sites. Unlike standard experiment station fields, control plots of monocultures were small relative to the total area of mixtures planted by farmers in the surrounding area, reducing the potential impact of spore dispersal from the more heavily infected monocultures to the mixture plots[2–4]. The study was expanded to 3,342 ha of rice fields in 1999. This area consisted of all rice fields in 10 townships that spanned Jianshui and Shiping Counties, with five participating townships and 15 survey sites per county. Procedures were the same as in 1998, except that no foliar fungicide applications were made. In addition, some farmers chose to plant mixtures in a ratio of 1 glutinous: 6 hybrid rows, rather than 1:4.

Diversification had a substantial impact on rice blast severity (Fig. 2). In 1998, panicle blast severity on the glutinous varieties averaged 20% in monocultures, but was reduced to 1% when dispersed within the mixed populations (Fig. 2a). Panicle blast severity on the hybrid varieties averaged 1.2% in monoculture and was reduced to varying degrees in mixed plots, though only the larger differences were statistically significant (Fig. 2b). Results from 1998 were very similar to the 1998 season for panicle blast severity on the susceptible varieties (Fig. 2a), showing that the effect of diversification was very robust among mixtures and between seasons and counties. In contrast, effects of crop diversification on blast severity of the hybrid varieties were larger in 1999 than in 1998. Panicle blast severity on these varieties averaged 2.3% in
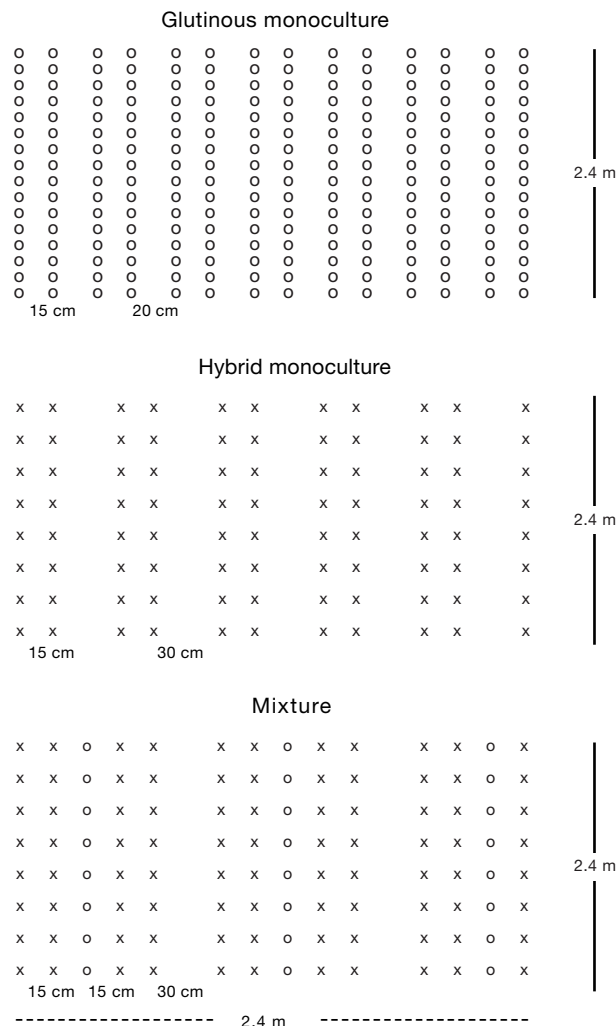

Figure 1 Planting arrangements in rice variety mixture and monoculture survey plots in 1999 and patterned after those used by farmers in Yunnan Province. Each symbol represents a hill of susceptible (O) or resistant (X) rice. Distances between hills within rows were 15 cm for glutinous monocultures, 30 cm for hybrid monocultures and 30 cm for mixtures. Spacings and arrangements were the same in 1998, except that the distance between rows of glutinous rice in monoculture was 13 cm.

monoculture and was reduced to 1.0% in mixed populations (Fig. 2b), despite the fact that hybrids were planted at the same density in both mixture and monoculture survey plots.

Several mechanisms may reduce disease severity in genetically diverse plant populations[2,4,18]. Increased distance between plant

genotypes, which dilutes inoculum of a given pathogenic race as it is dispersed between compatible host varieties, has been considered the most important mechanism contributing to disease reduction in variety mixtures[2]. Such dilution effects almost certainly had a role in reducing blast disease on the susceptible, glutinous varieties
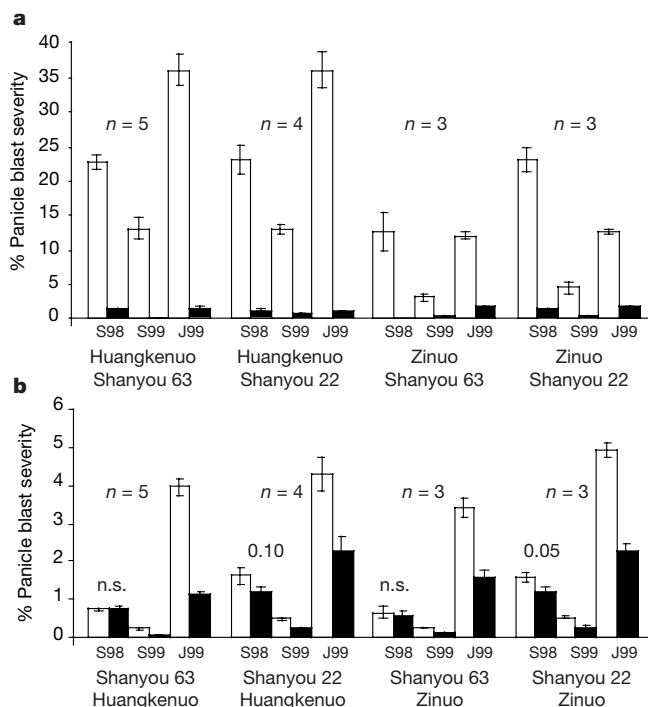

Figure 2 Panicle blast severity (mean percentage of panicle branches that were necrotic due to infection by *Magnaporthe grisea*) of rice varieties planted in monocultures and mixtures. **a**, The susceptible, glutinous varieties Huangkenuo and Zinuo. **b**, The resistant, hybrid varieties Shanyou22 and Shanyou63. S98, Shiping County, 1998; S99, Shiping County, 1999; J99, Jianshui County, 1999; open bar, blast severity for a variety grown in monoculture control plots; black bar, blast severity of the same variety when grown in mixed culture plots in the same fields. Error bars are one s.e.m.; *n*, number of plot means that contribute to individual bars for each of the four combinations of susceptible and resistant variety. All differences between pairs of monoculture and mixture bars are significant at $P < 0.01$ based on a one-tailed *t*-test, unless indicated by 0.05 (significant at $P < 0.05$), 0.10 (significant at $P < 0.10$) or n.s. (not significant at $P = 0.10$).

Table 1 Grain yields and monetary value for rice varieties

Variety or mixture	Hills m$^{-2*,\dagger}$	Grain yield ± s.e.m. (Mg per ha)			Crop value (US$ per ha)		
		Shiping/98	Shiping/99	Jianshui/99	Shiping/98	Shiping/99	Jianshui/99
Huangkenuo	38.1	3.69 ± 0.02	4.07 ± 0.07	5.12 ± 0.05	1291	1424	1794
Shanyuo63	14.8	8.14 ± 0.07	8.41 ± 0.12	9.71 ± 0.07	1709	1765	2039
Mixture	18.5	8.72 ± 0.05	9.53 ± 0.11	10.53 ± 0.12	1912	2166	2341
Huangkenuo	*3.7*	*0.59* (**173**)	*1.19* (**300**)	*0.92* (**186**)	*205*	*415*	*323*
Shanyuo63	*14.8*	*8.13* (**100**)	*8.34* (**99**)	*9.61* (**99**)	*1707*	*1751*	*2018*
Huangkenuo	38.1	3.79 ± 0.03	4.15 ± 0.07	5.08 ± 0.10	1328	1452	1778
Shanyuo22	14.8	7.97 ± 0.11	8.12 ± 0.06	9.08 ± 0.20	1673	1705	1907
Mixture	18.5	8.40 ± 0.12	8.77 ± 0.09	10.00 ± 0.16	1838	1941	2231
Huangkenuo	*3.7*	*0.53* (**151**)	*0.71* (**177**)	*0.94* (**191**)	*184*	*249*	*330*
Shanyuo22	*14.8*	*7.88* (**99**)	*8.06* (**99**)	*9.05* (**100**)	*1654*	*1692*	*1901*
Zinuo	38.1	3.62 ± 0.04	3.97 ± 0.02	4.90 ± 0.09	1268	1390	1716
Shanyuo63	14.8	8.28 ± 0.13	8.40 ± 0.08	9.63 ± 0.17	1739	1765	2022
Mixture	18.5	8.90 ± 0.22	9.23 ± 0.03	10.46 ± 0.18	1937	2056	2315
Zinuo	*3.7*	*0.48* (**146**)	*0.84* (**217**)	*0.84* (**177**)	*170*	*294*	*296*
Shanyuo63	*14.8*	*8.42* (**102**)	*8.39* (**100**)	*9.62* (**100**)	*1767*	*1762*	*2020*
Zinuo	38.1	3.49 ± 0.02	3.82 ± 0.03	4.89 ± 0.11	1220	1337	1711
Shanyuo22	14.8	7.84 ± 0.06	8.14 ± 0.03	9.14 ± 0.05	1646	1710	1919
Mixture	18.5	8.27 ± 0.05	8.86 ± 0.07	9.99 ± 0.03	1807	1965	2227
Zinuo	*3.7*	*0.51* (**160**)	*0.75* (**203**)	*0.92* (**193**)	*178*	*264*	*321*
Shanyuo22	*14.8*	*7.76* (**99**)	*8.10* (**99**)	*9.08* (**99**)	*1629*	*1701*	*1906*

The rice varieties were grown as monocultures or mixed in Shiping and Jianshui counties in 1998 and 1999. Crop values based on market prices of 0.21 US$ per kg for hybrid varieties and 0.35 US$ per kg for glutinous varieties. Italicized values of hills m^{-2}, grain yield, and crop value are for the individual varieties within mixtures. Bold values in parentheses are per-hill yields of varieties in mixture expressed as a percentage of per-hill yield of the same variety in monoculture.
* See also Fig. 1.
† In 1998, density of glutinous varieties in monoculture was 40.4 hill m^{-2}.

in this study. In addition, canopy microclimate data collected at one survey site in 1999 indicate that height differences between the taller glutinous and shorter hybrid varieties resulted in temperature, humidity and light conditions that were less conducive for blast on glutinous varieties in the mixtures than in the monocultures. Disease reductions on hybrid varieties in the mixtures are more difficult to explain. Dilution and microenvironmental modifications are unlikely mechanisms, as the hybrids were planted at the same density in mixtures and monocultures (Fig. 1). The taller glutinous varieties may physically have blocked spore dispersal and/ or altered wind patterns compared with the hybrid monocultures. In addition, induced resistance may have some contribution to disease suppression in the hybrids. Induced resistance occurs when inoculation with avirulent pathogen race(s) induces a plant defence response that is effective against pathogen races that would normally be virulent on that host genotype. This has made significant contributions to disease reductions in variety mixtures of other small grain crops[19,20].

In 1999, we determined the genetic composition of the pathogen populations derived from inter-planting and monoculture fields using polymerase chain reaction (PCR) fingerprinting[21] of pathogen isolates. Preliminary results indicate that fields with mixtures supported diverse pathogen populations with no single dominant strain. In contrast, pathogen populations from monoculture fields were dominated by one or a few strains. The more diverse pathogen population from the mixed stands may have contributed to greater induced resistance from incompatible interactions. In the longer term, this increased pathogen diversity may also slow adaptation of the pathogen to resistance genes functioning within a given mixture. Clarifying the mechanisms by which host diversity influenced disease in our study will be helpful in extending these results to other agro-ecosystems. These mechanistic studies are currently underway.

Grain production per hill of glutinous varieties in mixtures averaged 89% greater than that in monoculture (Table 1). As a result, glutinous rice in mixtures produced 18.2% of monoculture yield, on average, though it was planted at rates of only 9.2 and 9.7% that of monoculture in 1998 and 1999, respectively (see also Fig. 1). Reduced disease severity certainly had a role in this yield response, though other factors (for example, improved light interception) may also have had an influence. Despite the increased overall plant density in mixtures (see Fig. 1, bottom), grain yields per hectare of the hybrids in mixture were nearly equal to the corresponding monocultures. Thus, mixed populations produced more total grain per hectare than their corresponding monocultures in all cases (Table 1). Land equivalent ratios[22], which estimate the ecological efficiency of mixed populations, indicate that an average of 1.18 ha of monoculture crop land would need to be planted to provide the same amounts of hybrid and glutinous rice as were produced in 1 ha of a mixture (Table 2). After accounting for the differing market values of the two rice types, the gross value per hectare of the mixtures was 14% greater than hybrid monocultures and 40% greater than glutinous monocultures (Table 1).

Though disease reductions are theoretically maximized in random mixtures of plants[23], row mixtures provided the most practical approach in our specific application. As rice is hand-harvested in Yunnan Province, farmers can easily separate the hybrid and glutinous grains, which are used for different purposes. However, many other approaches can be used to attain within-field genetic diversity of crops[3,24]. For example, wheat (*Triticum aestivum*) mixtures are grown in the Pacific Northwest of the USA under highly mechanized conditions[4]. In this case, varieties are chosen to be similar in height, maturity and market quality, planted as random mixtures, and harvested and marketed as bulk populations[3].

Commercial-scale use of crop diversity has provided observational support for the disease-suppressive effects of crop diversity in a limited number of cases[4,25,26], most notably the control of barley (*Hordeum vulgare*) powdery mildew (caused by *Erysiphe graminis*) in the former East Germany[26]. However, the varietal diversification program in Yunnan Province provided an unusual opportunity to determine causal relationships between crop diversity and disease, as replicated monoculture controls were available for comparison within a substantial expanse of mixed culture. The impact of crop diversification on blast severity in this study was greater than that reported from small-scale experimental plots with this disease[3], although we do not have proof that this difference is due only to the spatial scale. By the second year of the project, no foliar fungicides were needed for blast control in the diversified area, though this may not be possible in all seasons. The Yunnan diversification program has resulted in great interest by farmers, and the practice has expanded to more than 40,000 ha in 2000.

The 'Green Revolution' has provided remarkable increases in crop productivity over the past four decades[27]. However, this agricultural transformation has also resulted in problems, including loss of crop genetic diversity[11]. The current world population of over six billion does not allow us to return to agricultural production practices of the past. Rather, we need to maintain the benefits of modern agriculture while addressing its drawbacks. In this regard, it is significant that the diversification program described here is being conducted in a cropping system with grain yields approaching 10 Mg ha^{-1}, among the highest in the world. The value of diversity for disease control is well established experimentally and diversity is increasingly being used against wind-dispersed pathogens of small grain cereals[4]. Recent experimental results indicate other applications of diversity, for example, against soil-borne pathogens and for tree crops[4]. The effect of varietal diversification will vary among diseases and agro-ecosystems[4]. Further, one can not expect all variety mixtures to provide functional diversity to a given plant pathogen population[24,28], nor can one predict the time for which they may remain effective. Indeed, we have identified variety combinations that provide little or no blast control in Yunnan Province. Nonetheless, our results demonstrate that a simple, ecological approach to disease control can be used effectively at large spatial scale to attain environmentally sound disease control. □

Methods

Study sites

In 1998, townships participating in the diversification experiment were Baxing, Baoxiu, Songchun, Maohe and Xincheng of Shiping County. These townships are contiguous, and all rice fields in the five townships were involved in the diversification program. In 1999, the study area consisted of all rice fields in ten contiguous townships: Chenguang, Dongba, Mianding, Nanzhuang and Xizhuang in Jianshui County; and Baxing, Baoxiu, Songchun, Maohe and Yafanzi in Shiping County.

Disease assessments

To monitor disease, survey plots were established at 15 sites per county, three in each of the five townships participating in the diversification program (15 sites in 1998, 30 sites in 1999). Seedlings were transplanted into the field in April or May in hills of 4–5 plants for glutinous varieties and 1 plant per hill for the hybrid varieties, which produce a greater number of tillers per plant. All plots were managed by farmers and treated in the same manner as the surrounding mixed variety plantings, including fungicide application. In each of the survey sites, a field was divided into three plots. One plot was planted with the mixture grown most commonly by local farmers, and the remaining two plots were monocultures of the glutinous and hybrid variety included in that mixture. For mixtures, the same row spacing of hybrid rice was used as in monoculture, but one row of glutinous rice was added between each group of four rows of hybrid rice, in an 'addition' approach (Fig. 1). Each of the four mixtures was evaluated for disease severity in 3–5 of the 15 survey

Table 2 Land equivalent ratios for rice yield produced in variety mixtures

Mixture	County and year		
	Shiping 1998	Shiping 1999	Jianshui 1999
Huangkenuo/Shanyuo63	1.16	1.28	1.17
Huangkenuo/Shanyuo22	1.13	1.16	1.18
Zinuo/Shanyuo63	1.15	1.21	1.17
Zinuo/Shayuo22	1.14	1.19	1.18

Land equivalent = (yield ha^{-1} of variety A in mixture/yield ha^{-1} of variety A in monoculture) + (yield ha^{-1} of variety B in mixture/yield ha^{-1} of variety B in monoculture).

sites in each county, depending on the popularity of a given mixture with farmers. Plots ranged from 100 to 450 m² each, depending on field size.

Survey plots were assessed in late August for the severity of blast symptoms, expressed as the percentage of panicle branches that were necrotic due to the effects of *M. grisea*. Disease was assessed at five sampling points in each plot, distributed in a uniform pattern. Twenty hills resulting from the transplanting process were evaluated at each sampling point, with each hill containing about 10 panicles per hill, to give a total of approximately 1,000 panicles evaluated per plot. Each sampled panicle was visually examined by experienced personnel to estimate the percentage of branches that were necrotic due to infection by *M. grisea*. Each panicle was given a rating[29] from 0 to 5, where 0 is no disease; 1 is less than 5% of panicle branches necrotic; 2 is 5–30% necrotic; 3 is 30–50% necrotic; 4 is greater than 50% necrotic; and 5 is 100% necrotic. Disease severity was summarized within each plot as $\{[(n_1 \times 1) + (n_2 \times 2) + (n_3 \times 3) + (n_4 \times 4) + (n_5 \times 5)]/\Sigma n_0 \ldots n_5\} \times 100$, where $n_0 \ldots n_5$ is the number of culms in each of the respective disease categories. Thus, a disease severity of 0% would indicate no disease and 100% would indicate that 100% of panicle branches were necrotic.

Yield evaluation

Plots were hand-harvested, threshed and weighed to determine grain yield. Individual varieties were evaluated separately in mixtures. Land equivalent ratios[22] were calculated as (yield ha⁻¹ of variety A in mixture/yield ha⁻¹of variety A in monoculture) + (yield ha⁻¹ of variety B in mixture/yield ha⁻¹ of variety B in monoculture).

Statistical analyses

Each survey plot was considered to be an experimental unit, and analyses were based on mean disease severities and grain yield for each plot. Statistical analyses were conducted separately by year and county owing to differences in disease level. One-tailed *t*-tests were used to determine if blast severity for each of the two varieties in each of the four mixtures differed significantly from its corresponding monoculture control.

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Fear memories require protein synthesis in the amygdala for reconsolidation after retrieval

Karim Nader, Glenn E. Schafe & Joseph E. Le Doux

W. M. Keck Foundation Laboratory of Neurobiology, Center for Neural Science, New York University, New York, New York 10003, USA

'New' memories are initially labile and sensitive to disruption before being consolidated into stable long-term memories[1–5]. Much evidence indicates that this consolidation involves the synthesis of new proteins in neurons[6–9]. The lateral and basal nuclei of the amygdala (LBA) are believed to be a site of memory storage in fear learning[10]. Infusion of the protein synthesis inhibitor anisomycin into the LBA shortly after training prevents
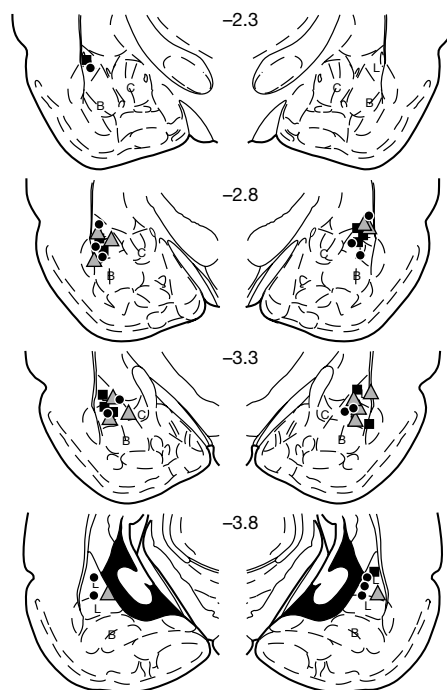

Figure 1 Schematic representation of the amygdala at four different rostral–caudal planes. The numbers represent the posterior coordinate from bregma. Injector placements in the LBA are represented by the filled symbols; black filled squares represent ASCF group placements, grey filled triangles represent the low-dose anisomycin, and black filled circles represent high-dose group. L, lateral nucleus; B, basal nucleus; C, central nucleus. The placements for subsequent experiments all demonstrate similar distributions as in this experiment and therefore are not shown.