



a, Frequency distribution of yield in an interspecific (*O. sativa*/*O. rufipogon*) BC₂ test-cross population, with phenotypes of *O. rufipogon*, V20B and V/64 (V20A×Ce64) indicated by arrows; b, chromosome maps (marker order and map distances based on published rice molecular-genetic map⁴) showing locations of putative yield-enhancing genes from *O. rufipogon*, *yld1.1* and *yld2.1*. *O. rufipogon* allele associated with increased yield at $P < 0.005$ (black shading); $P < 0.010$ (dark grey shading); and $P < 0.050$ (light grey shading).

yielded less than V/64, but a small percentage of the plots yielded as much as 50% greater than the elite hybrid. Overall, 15% of the BC₂ test-cross families outperformed V/64 with respect to yield, 14% with respect to grains per plant, and 56% with respect to 1,000-grain weight. Thirteen (4.3%) of the BC₂ test-cross families outyielded V/64 by at least 30%. These results suggest that genes coming from *O. rufipogon* can increase yield of an elite rice variety, even though *O. rufipogon* itself is inferior to cultivated rice varieties.

If *O. rufipogon* genes are contributing to the higher yield of certain BC₂ test-cross families, it should be possible to detect the presence of the segments of wild chromosomes containing such genes (quantitative trait loci or QTL) and to demonstrate a significant correlation between their presence and higher yield.

A high-density molecular-genetic map developed for rice⁴ has previously been used to map and characterize QTL conditioning heterosis⁵, biotic and abiotic stress

tolerance and various agronomic traits^{6,7}. In an effort to identify regions of the *O. rufipogon* genome that might be contributing to a yield increase, 100 informative restriction-fragment length polymorphisms and 20 microsatellite markers (S. R. McC. *et al.*, unpublished data), covering the entire rice genome at intervals of roughly 12 cM, were assayed on each of the 300 BC₂ test-cross families.

We conducted QTL mapping on BC₂ test-cross data by regression of field performance on marker genotype using standard analysis of variance procedures and assuming regular segregation of wild and cultivated alleles within test-cross families. In most cases, introgression of *O. rufipogon* alleles had either no significant effect on yield or were inferior to the cultivated alleles. However, *O. rufipogon* alleles at marker loci RM5 on chromosome 1 and RG256 on chromosome 2 were associated with enhanced yield ($P < 0.006$; see table on previous page), and were designated *yld1.1* and *yld2.1* (see figure). The phenotypic advantage of the lines carrying *O. rufipogon* alleles at these loci was estimated to be 1.2 and 1.1 tonnes per hectare (fig-

ures converted to field scale using conventional plant densities), respectively, which corresponds to an 18 and 17% increase over V/64 (see table).

The alleles *yld1.1* and *yld2.1* were both associated with a significant increase in grains per plant ($P < 0.005$), but had no detectable effect on 1,000-grain weight, plant height or growth duration.

Rice was originally domesticated by humans from wild stands of native plants⁸. Only a small portion of the genetic variation found in nature was captured in this domestication process⁹, and it is this limited genetic base that forms the foundation of all of our modern cultivars¹⁰. Many of the ancestors of cultivated crop species still exist in the wild or have been collected and maintained in germplasm banks. Although these wild species are valued as a unique source of genetic variation, they usually have low yields. Nevertheless, our results indicate that one of the closest wild relatives of cultivated rice, *O. rufipogon*, despite its overall inferior appearance, contains

genes that can substantially increase the yield of rice. The strategy we describe here is being used to search for yield-enhancing genes in other wild rice species, and could be extended to the genetic improvement of other crop species.

Jinhua Xiao
Silvana Grandillo
Sang Nag Ahn
Susan R. McCouch
Steven D. Tanksley*

Department of Plant Breeding & Biometry,
 252 Emerson Hall, Cornell University,
 Ithaca, New York 14853, USA
 e-mail: sdt4@cornell.edu

Jiming Li

Longping Yuan

China National Hybrid Rice Research and
 Development Center,
 Changsha, Hunan 410125,
 People's Republic of China

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*To whom correspondence should be addressed.

Origin of oscillons

SIR — The term ‘oscillons’, recently described in *Nature*^{1,2} and featured on the cover, was earlier used by us³ to represent strongly nonlinear electrostatic oscillations on a plasma boundary. These peculiar oscillations of surface fields are described by exact solutions of the cold electron fluid and Maxwell equations together with the boundary conditions. They have a unique spatial pattern and their frequency satisfies a simple algebraic dispersion relation involving the oscillon radius and peak amplitude.

Clearly, these oscillons are physically different from those recently discussed in *Nature*. But in all cases, strongly nonlinear anomalous oscillations of surface patterns are involved, and thus there is no fundamental conflict in the terminology.

L. Stenflo

Department of Plasma Physics,
 Umeå University,
 S-90187 Umeå, Sweden

M. Y. Yu

Institute for Theoretical Physics I,
 Ruhr University,
 D-44780 Bochum, Germany

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