

Shaping Taste: The Molecular Discovery of Rice Genes Improving Grain Size, Shape and Quality

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Modern-day human life is absolutely dependent upon the food that we derive from our crop plants. We eat grains, fruits, roots, tubers and other structures, all of which are constructed via coordinated organ growth. Whilst plant organ identity is first established in apical meristems (vegetative and floral shoot meristems and root meristems), and in other meristematic regions, the final size and shape of organs is defined by subsequent coordination of organ expansion in longitudinal and transverse axes. Key genes playing roles in the coordination of longitudinal/transverse organ growth have been identified through studies in *Arabidopsis thaliana*. Amongst these are the closely-related LONGIFOLIA1 (LNG1) and LONGIFOLIA2 (LNG2) proteins, which, when overexpressed, confer an elongated shoot lateral organ phenotype (e.g., narrow leaf blades of increased length), consistent with LNG1/LNG2 promoting longitudinal versus transverse organ growth¹. Subsequent work has shown that LNG2 targets TON1 (TONNEAU, a plant protein related to the human centrosomal protein FOP²) to cortical microtubules³ and that a protein complex including LNG2 and TON1 regulates preprophase band formation and spatial control of plant cell division⁴.

Recently reported independent discoveries from two laboratories have highlighted the central importance of LNG1/2-related promotion of longitudinal organ growth to human nutrition^{5,6}. Rice contributes up to 76% of the calorific food intake of the people of Southeast Asia. Whilst increasing rice grain yield remains a constant goal of plant breeders in the face of future population growth, grain quality is also of paramount importance. Although food quality preferences may vary from

culture to culture, rice grains that are relatively long and slender^{5,6} are highly prized in many parts of the world (Figure 1). Such grains tend to be transparent, and to lack the opaque patches that are associated with an unpleasant chalky texture and taste. Additional properties of long/slender-grained varieties, including increased levels of gene transcripts encoding starch synthesis enzymes in developing endosperms, result in better tasting rice. However, the dual requirement for increases in both yield and quality is a long-standing problem for rice breeders, because improvements in one are often associated with detrimental effects on the other.

The recent reports describe the molecular discovery of a gene regulating the long/slender rice grain phenotype^{5,6}. This gene, independently named *GL7*⁵ and *GW7*⁶ (because it underlies *GL7* and *GW7* QTLs), regulates rice grain length/width ratio by differentially affecting longitudinal versus transverse grain growth. Wang, S. *et al.*⁶ took a recombinant-mapping approach to identifying the gene responsible for the long/slender grain *GW7* QTL from a high-quality *indica* hybrid rice variety, Taifeng A. They found that this trait is caused by relatively high levels of expression of the transcripts of gene *Os07g0603300*, conferred by a particular variant gene promoter found in the *GW7* allele. Further work showed that *Os07g0603300* transcript levels are negatively regulated by the OsSPL16 transcription factor (shown by the same group to be the protein product of the gene underlying another grain-shape QTL, *GW8*⁷). These observations are particularly important because they for the first time link *GW7* and *GW8* within the same grain-shape regulatory molecular signalling pathway.

Using an alternative recombinant-mapping approach, Wang, Y. *et al.*⁵ identified the gene responsible for the long/slender grain *GL7* QTL from an *indica* rice landrace variety Ping13. They discovered that gene *Os07g0603300* (the same gene as underlies *GW7*) is the gene causal of the *GL7* QTL, and that, like in *GW7*, the increased grain length of Ping13 is due to an increased level of expression of this gene. However, in this (*GL7*) allele, increased expression appears to be due to a

copy-number variant that duplicates *Os07g0603300*⁵ as opposed to the gene promoter variant that causes the increased expression of the *GW7* allele⁶. Further work identified a neighbouring gene, *Os07g0603400*, 12kb upstream of *GL7*, which appears to function as a negative regulator of *Os07g0603300*⁵.

Thus both studies have molecularly identified variant forms of *Os07g0603300* as conferring the high-quality long/slender rice grain phenotype that is preferred by rice consumers in many parts of the world, and both have shown that increased levels of *Os07g0603300* transcripts are causally responsible for that phenotype^{5,6}. An obvious next question is: what is the biological function of the protein product of *Os07g0603300*? The fact that *Os07g0603300* encodes a TON1 RECRUIT MOTIF (TRM)-containing protein having 20-22% amino acid sequence identity with *Arabidopsis* LNG1/2^{5,6} (see above) suggests a function associated with the direction of cell division/expansion via recruitment of TON1 to cortical microtubule arrays. Consistent with this proposed function, the protein product of *Os07g0603300* was found to associate with rice TON1 and PP2A homologues (likely components of the protein complex identified above as regulating preprophase band formation) both in yeast and *in planta*⁶. In conclusion, the preferred high-quality long/slender grain trait is likely caused by an *Os07g0603300*-dependent alteration in the properties of preprophase band formation that favours longitudinal over transverse organ growth. It is particularly noteworthy that elevated expression of presumed homologues (LNG1/2 in *Arabidopsis thaliana*; product of *Os07g0603300* in rice) has parallel effects (promotion of longitudinal versus transverse growth in *Arabidopsis thaliana* leaves and rice grains) in such widely divergent angiosperms, suggesting that this component of organ growth regulation has been strongly conserved during angiosperm evolution (and possibly predates the angiosperm divergence from the land-plant lineage).

There are important additional reasons why, when considered together, these reports are remarkable. First, as pointed out by Wang, S. *et al.*⁶, QTL studies have identified a number of

distinct QTLs responsible for rice grain size/shape. Previously, many of these QTLs might have been thought to be specific to the particular different varieties used in different QTL-mapping experiments. However, the fact that two independent studies using widely divergent genetic materials have converged onto the same gene (*Os07g0603300*) means that this gene has had, and will continue to have, a major impact on rice grain quality in diverse breeding contexts. Second, both reports^{5,6} show that variant *Os07g0603300* alleles can be used to improve rice grain quality without compromising yield. Thus the frequently observed negative correlation between yield and quality that has been so troubling to rice breeders in the past can be broken by use of these alleles: combined increases in both quality and yield are now possible. Farmers will benefit from being able to grow high-quality high-yielding varieties, and rice consumers, amongst whom are some of the world's poorest people, will be able to eat high quality rice at reduced cost.

References

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Figure 1. Genetic control of rice grain size and shape. Long and slender rice grains (right) are preferred over short and broad grains (left) in many of the world's cultures and cuisines. Recent reports^{5,6} describe the independent molecular discoveries of variant forms of a rice gene that confer the high-quality long/slender grain trait, and that can now be used to enhance grain quality without associated yield penalties.