measurements. Even Li and colleagues' results are in disagreement: the values of *G* determined in the two current experiments, as well as values obtained in two previous experiments at the same laboratory[8,9], are statistically inconsistent with one another. The authors speculate that fibre anelasticity might be responsible, but they do not give a definitive explanation.

Because all four of these experiments were carried out at the same institution, it should be more straightforward to compare them than it would be to compare different experiments from various groups around the globe. An excellent opportunity exists, therefore, to uncover the causes of the discrepancy and, in turn, to learn more about the true value of *G*. Li *et al.* should be encouraged to take on this challenge. In the end, if we want to understand the measurements of *G*, we must find the reasons for the inconsistent results[10]. ■

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PLANT GENETICS

A new green revolution on the horizon

Manipulation of the transcription factor OsGRF4 can improve the efficiency with which some high-yielding cereal crops use nitrogen. This discovery has implications for sustainable agriculture. SEE ARTICLE P.595

FANMIAO WANG & MAKOTO MATSUOKA

The green revolution of the mid-twentieth century saw the development of high-yielding varieties of rice and wheat for use in agriculture. But to produce high yields, these green-revolution varieties require a large supply of nitrogen. Developing green-revolution varieties that use nitrogen more efficiently is an important goal for sustainable crop breeding. On page 595, Li *et al.*[1] report a previously unknown function for the rice transcription factor OsGRF4 in nitrogen use. By modulating the *OsGRF4* gene, the researchers produced plants that use nitrogen efficiently and have a high yield.

Proteins of the DELLA family inhibit plant growth, whereas hormones called gibberellins promote plant growth by triggering the destruction of DELLA proteins. Green-revolution varieties of rice and wheat harbour genetic mutations that lead to the accumulation of DELLA proteins. As a result, these plants are shorter than are normal varieties, and so are resistant to lodging[2,3] — the process by which plants are flattened by wind and rain. This lodging resistance is a fundamental mechanism for achieving increased crop yield in green-revolution varieties.

DELLA accumulation also inhibits nitrogen uptake and nitrogen-related growth responses — traits that are associated with the inefficient use of nitrogen[4]. Consequently, farmers have to apply large amounts of environmentally damaging nitrogen-based fertilizer to their crops to achieve high yields in green-revolution varieties. Although DELLA accumulation increases the yield, it therefore also has a negative impact in terms of sustainable agriculture.

Li *et al.* set out to overcome the negative impact of DELLA accumulation. They crossed varieties of the rice subspecies *Oryza sativa indica* that showed differing rates of nitrogen uptake. They then performed genetic analyses on the resulting plants, which had a range of yields. In doing so, they found that *OsGRF4* is associated with nitrogen uptake. *OsGRF4* has previously been found to regulate the size of rice grains[5–7] and the levels of growth molecules called cytokinins[8], both of which affect crop yield. But no relationship between *OsGRF4* and nitrogen-use efficiency has previously been described.

The researchers genetically engineered green-revolution varieties of rice to lack OsGRF4. Compared with control plants carrying the wild-type gene, mutants showed less nitrogen-dependent growth and reduced nitrogen uptake and assimilation (the process by which inorganic nitrogen from fertilizers is converted into useful organic compounds such

50 Years Ago

Mr J. H. Brazell of the Meteorological Office has compiled a book of weather statistics for the London area which promises to become a well-thumbed reference … The year 1841 … is the first year for which regular official meteorological observations are available … Mr Brazell has taken this opportunity to delve into earlier chronicles to find what London's weather was like before 1841 … A rare feature of London's climate has been the freezing of the Thames … During twenty-three winters between 1260 and 1814, the ice on the river was thick enough to allow pedestrians to cross from one bank to the other. It became the custom for frost fairs to be held on the frozen Thames, starting from small beginnings in the winter of 1309–10 when people danced around a bonfire built on the ice, to the great frost fairs of the 17th, 18th and 19th centuries, when the frozen river supported streets of shops and booths.

From *Nature* 31 August 1968

100 Years Ago

The July issue of *Science Progress* contains an interesting article by Sir Henry Thompson on the food requirements of a normal working-class family. A comparison is instituted between the physiological values of the diets reported upon by the Board of Trade in pre-war times and some data collected by the War Emergency Committee in 1917 … Sir Henry Thompson has employed a more liberal scale of requirements for children than the older standard of Atwater, which is now generally recognised to be unsatisfactory. The three diets do not differ greatly in respect of energy-value; the highest average is that of the urban working-class families (1913), yielding 3410 calories; the lowest, the 1917 sample, is 3160 calories, a reduction of but 250 calories.

From *Nature* 29 August 1918

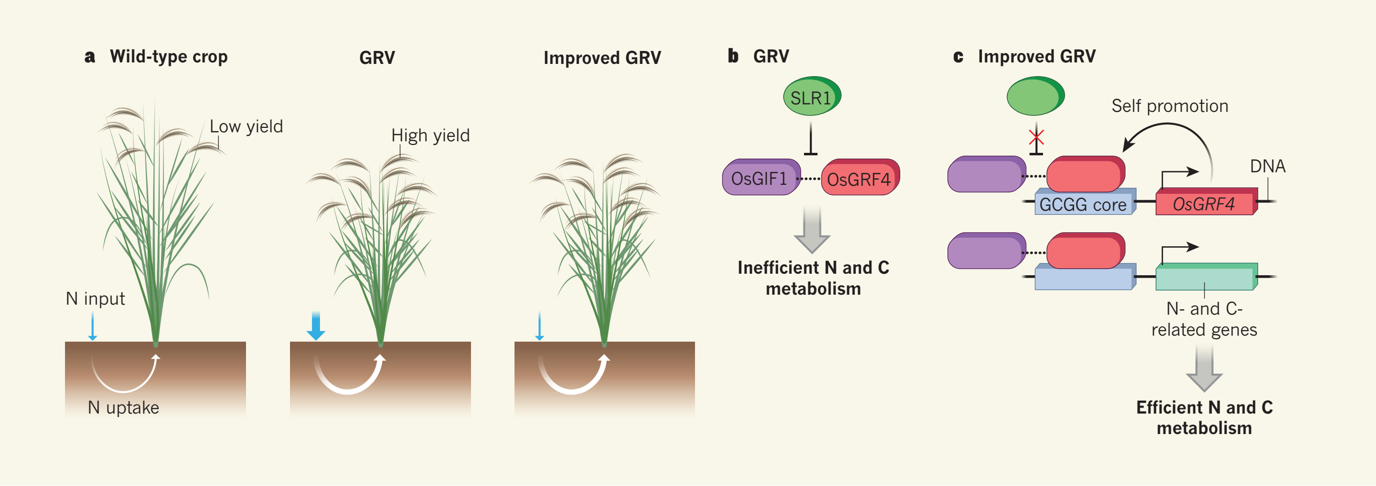

Figure 1 | Tipping the scales to improve plant yields. **a**, Nitrogen is a major component of fertilizers. The height of many wild-type crop plants makes them prone to flattening by wind and rain if they are grown under high nitrogen (N) input. Therefore, farmers cultivate wild-type crops under low nitrogen input, which decreases yield. Yields can be improved by generating short plants known as green-revolution varieties (GRVs), in which the growth-inhibiting protein SLR1 accumulates (not shown). However, GRVs take up and use nitrogen inefficiently, and so require high levels of nitrogen input to take up sufficient nitrogen to produce high yields. Li *et al.*[1] have generated improved GRVs that both have high crop yields and use nitrogen efficiently. **b**, The authors found that, in GRVs, SLR1 inhibits the interaction between two proteins, OsGIF1 and OsGRF4. This reduces the efficiency with which both nitrogen and carbon (C) are metabolized. **c**, The group bred plants that produced high levels of OsGRF4, thereby overcoming the ability of SLR1 to prevent OsGIF1–OsGRF4 interactions. In these improved GRVs, OsGRF4 binds to a specific DNA sequence (the GCGG core) to promote the expression of the *OsGRF4* gene, and of genes involved in nitrogen and carbon use. This leads to a feed-forward loop that increases the efficiency of nitrogen and carbon metabolism and results in higher yields.

as amino acids). By contrast, plants that were selectively bred to express *OsGRF4* at higher than normal levels showed an increased rate of nitrogen uptake. Thus, OsGRF4 promotes various nitrogen-related events.

Li *et al.* then demonstrated that OsGRF4 acts in opposition to the DELLA protein SLR1 in rice (Fig. 1). Transcriptional activation by OsGRF4 is known to be promoted by physical interactions between OsGRF4 and another protein, OsGIF1 (refs 5 and 6). The authors found that OsGRF4, promoted by OsGIF1, binds to a specific DNA sequence (the core motif GCGG) to drive the expression of genes that encode a range of proteins involved in nitrogen metabolism, uptake and assimilation. However, the accumulation of SLR1, as occurs in green-revolution varieties of rice, inhibits the interaction between OsGRF4 and OsGIF1, thereby suppressing the expression of the genes involved in nitrogen uptake and metabolism. This SLR1-mediated inhibition was relieved by the presence of gibberellin. Li and colleagues also showed that the expression of *OsGRF4* itself is activated by the OsGRF4–OsGIF1 complex. Therefore, *OsGRF4* transcription is suppressed by SLR1.

Next, the group discovered that OsGRF4 and SLR1 have the same antagonistic relationship in another key process in plant metabolism, carbon assimilation. Products of carbon and nitrogen assimilation act together to form the building blocks needed for metabolic processes in plants, and a balance between the two is therefore essential for optimal growth and yield. The authors showed that OsGRF4 promotes, and that SLR1 inhibits, the expression of various genes that are involved in three carbon-related processes: photosynthesis, sucrose transport and sucrose metabolism. Furthermore, the same relationship governs the expression of several genes involved in cell-cycle progression. Li and colleagues therefore propose that the antagonistic relationship between OsGRF4 and SLR1 provides a regulatory link that coordinates plant growth, nitrogen metabolism and carbon assimilation.

Finally, the authors used their findings to improve the yields of green-revolution varieties. They applied breeding strategies to generate rice plants that produce high levels of OsGRF4 but retain the short stature of green-revolution varieties. The resulting plants had wider leaves and stems, and showed an increased nitrogen uptake compared with normal plants. Consequently, crop yield was increased, even at low levels of nitrogen; an optimal carbon–nitrogen balance was attained; and the plants maintained their beneficial stature. Li *et al.* achieved a similar effect by increasing *OsGRF4* expression in the rice subspecies *Oryza sativa japonica*, as well as in green-revolution varieties of wheat. They have therefore successfully disconnected gibberellin-mediated control of plant height from regulation of nitrogen metabolism, producing plants that grow better without an increased risk of lodging.

> ***“The authors used their findings to improve the yields of green-revolution varieties.”***

Li and colleagues’ study raises the question of how increased levels of OsGRF4 can increase plant growth horizontally (by increasing leaf and stem width) but not vertically (through stem elongation). Answering this question will involve in-depth studies of nitrogen-related genes that are under the regulatory control of OsGRF4.

More importantly, the authors’ work not only reminds us of the disadvantages of green-revolution varieties, but also demonstrates that they can be overcome by implementing breeding strategies to increase levels of OsGRF4. By improving the efficiency of nitrogen use by green-revolution varieties, the amount of nitrogen-based fertilizers that are needed for agriculture could be reduced, which would improve our ability to grow crops sustainably. Li and colleagues’ research should also stimulate the discovery of other genes and molecules with roles in nitrogen use that are independent of gibberellin-regulated plant growth. Identifying fresh targets for breeding strategies in this way could usher in a new green revolution. ■

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