call thermal displacement by posing the same question that bothers an overheating fish: 'How far do I have to go to find conditions that are at or cooler than normal temperatures?' In other words, this metric quantifies the availability (or lack) of cooler temperatures in the waters surrounding a given point (Fig. 1a). The authors show that historical heatwaves have thermal displacements ranging from tens to thousands of kilometres (Fig. 1b), highlighting the scale of the disruption that MHWs can bring. In many cases, these displacements are on the same scale as, or on scales even greater than, the displacements expected to become the norm by the end of the century under many climate-change scenarios[9].

Thermal displacements offer a fresh perspective when looking into the future. Projections of this metric in a changing climate combine not only the distribution of temperatures in the ocean, but also differences in the rate of warming. As a consequence, future changes in thermal displacements have a complex structure and can be either positive or negative – in contrast to projections of MHW frequency and intensity, which largely reveal uniform increases[8]. Some regions can therefore be expected to show reductions in thermal displacement due to MHWs in the future, whereas others will see increases.

Nevertheless, as with any new tool, the limitations of thermal displacement need to be understood – in particular, how this metric of ocean-temperature data relates to biological responses. For example, the habitat of a marine organism is shaped not only by temperature, but also by factors such as water depth, proximity to the coastline and the nature of the sea bed. Moreover, finding and reaching a suitable alternative habitat takes time, which means that species displacements expected on the basis of the thermal-displacement metric might not always occur, especially for short-duration MHWs. That said, Jacox and colleagues' analytical approach is flexible enough to allow species-specific constraints on habitat and movement to be incorporated. Collaborations with biogeographers, who have well-developed models[10] of the environmental niches and distribution of marine organisms, might have great potential.

It should also be noted that thermal displacement is relevant only for species that have some capacity for active movement. Many marine organisms are location-bound and cannot or will not move, such as kelp forests or parents guarding their young.

Such limitations notwithstanding, the strength of Jacox and colleagues' advance is that it diversifies the toolbox for MHW researchers. Scientists can now tailor their approach to the questions and organisms at hand, using conventional metrics when thermal tolerance at a location is the main concern, and thermal displacement when

species-distribution shifts are a focus. The development of thermal displacement as a metric therefore expands our perspectives of MHWs and their potential impacts in a new direction. Discovering where this insight will lead us on the road to understanding these extreme events will be eagerly anticipated.

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Plant biology

Genetic drivers of high-rise rice

Julia Bailey-Serres & Laurentius A. C. J. Voesenek

Rice in deepwater paddy fields can survive a slow-rising flood by a remarkably rapid elongation of submerged stem sections. Two genes discovered to affect this process could aid targeted improvements in crop height and flood tolerance. **See p.109**

The height that a plant reaches during its life cycle is influenced by both its genetic inheritance and its environment. The agricultural revolution of the 1960s led to a rise in the productivity of rice (*Oryza sativa*) and wheat (*Triticum aestivum*) through the adoption of varieties with a genetic predisposition to having a short height through restrained stem elongation. This trait allows more of the carbon generated by photosynthesis to be allocated to flowers and grain production, rather than being directed to stem biomass. Moreover, these shorter, highly productive varieties are much less likely to topple over at maturity, or during driving rain, than are taller varieties. On page 109, Nagai *et al.*[1] describe the identification of genes that accelerate or decelerate stem elongation during specific phases of rice development.

The leaf blades and the floral 'spike' of grass species, including rice, develop from a compact shoot tip that expands upwards telescopically as the plant matures. This shoot tip produces a series of leaf blades that are each attached to the hollow stem by a 'collar' called a node (Fig. 1). Each node consists of a ring of tissue, including a patch of cells called a meristem that can divide to produce daughter cells; these elongate to form a stem segment called an internode[2]. The activation of this cell division and elongation process requires the growth hormone gibberellin. The number of internodes that elongate and their cumulative length determine the plant's ultimate height.

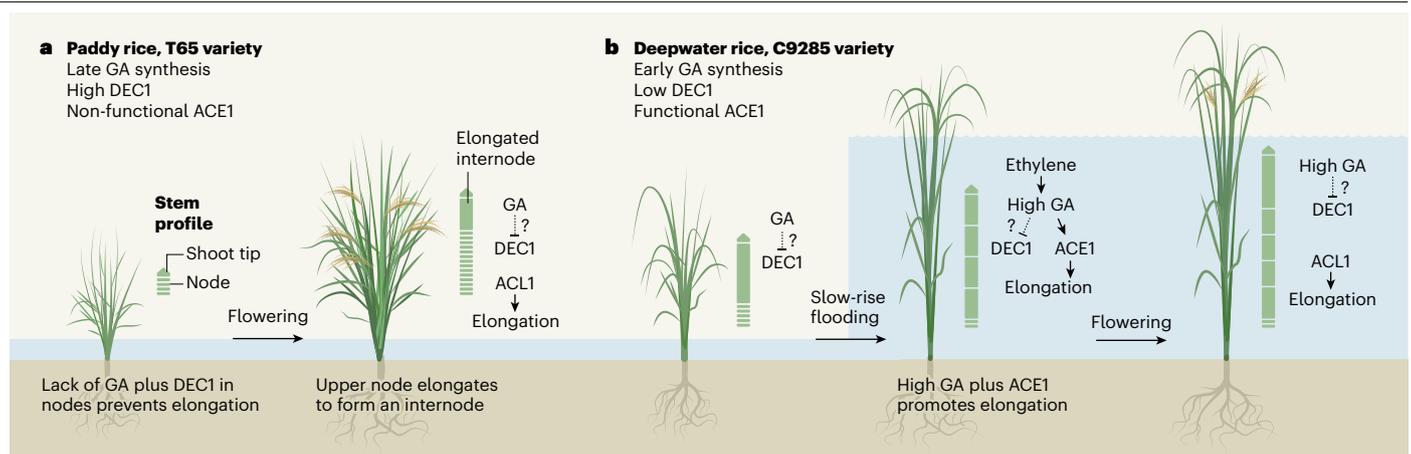Modern rice grown in shallow paddy fields

is short in stature because these plants have a defect in a gene called *SEMIDWARF 1* (*SD1*). This gene encodes the enzyme GA20 oxidase 2, which catalyses the production of highly active forms of gibberellin[3,4]. The lower stem nodes of these varieties make insufficient amounts of gibberellin to activate internode elongation. However, as these semidwarf plants transition from the juvenile (leaf producing) to the adult (flowering) phase of development, their uppermost node makes sufficient gibberellin for internode lengthening, enabling the flowers to extend above the leaf canopy. Mutations in other genes involved in the synthesis or perception of gibberellin are often responsible for the highly desired short stature of other grain crops.

More than 30% of all acreage planted with rice is susceptible to crop loss from floods[5]. The cultivation of deepwater rice allows farmers in south Asia and western Africa to integrate rice and fish farming in delta regions. Deepwater rice can escape submergence in a slow-rising flood by elongation growth of their stems at a rate of 25 centimetres per day[6].

Genes responsible for this elongating ability have been identified for the Bangladeshi deepwater rice variety C9285. One gene that is essential for this trait is a functional version of *SD1* termed *SD1^{C9285}*, which robustly produces growth-promoting gibberellins in stem nodes[7]. The aptly named *SNORKEL 1* and *SNORKEL 2* (*SK1/2*) genes further boost underwater internode elongation in this variety[8]. Plants sense submergence by means

a Paddy rice, T65 variety
Late GA synthesis
High DEC1
Non-functional ACE1

b Deepwater rice, C9285 variety
Early GA synthesis
Low DEC1
Functional ACE1

Stem profile
— Shoot tip
— Node

Elongated internode
GA ⊣? DEC1 ↓ ACL1 ↓ Elongation

Flowering

Lack of GA plus DEC1 in nodes prevents elongation

Upper node elongates to form an internode

GA ⊣? DEC1

Slow-rise flooding

Ethylene ⊣? High GA ⊣? DEC1 ACE1 ↓ Elongation

High GA plus ACE1 promotes elongation

Flowering

High GA ⊣? DEC1 ↓ ACL1 ↓ Elongation

Figure 1 | Flexible height control in rice. The hormone gibberellin (GA) drives elongation of the stem of a rice plant. Lower GA levels in stems are associated with shorter plants. **a**, Semi-dwarf rice varieties, such as T65, which grow in shallow water in paddy fields, have short stems owing to a deficiency in a key enzyme needed for the synthesis of forms of GA that promote elongation growth of stems. A profile of the stem components is shown for each scenario represented. Nagai *et al.*[1] report that the protein DEC1 inhibits node elongation, and that GA might limit the negative effect of DEC1. At the flowering stage, T65 plants make sufficient GA in the uppermost stem node to allow its elongation into an internode, which places the floral cluster above the leaf canopy. The authors report that the protein ACL1 aids elongation of the uppermost node during flowering. Nagai and colleagues discovered that the protein ACE1 (which is related to ACL1) aids stem elongation; however, the version of ACE1 in T65 is non-functional. **b**, Deepwater rice, such as the C9285 variety, produces GA in stem nodes early in development and has low levels of DEC1, enabling the uppermost node to elongate. These plants can survive a slow-rising flood by rapid stem elongation. This process is aided by accumulation of the hormone ethylene in submerged tissues, boosting GA production. This GA drives ACE1 to promote cell division in stem nodes, generating cells that elongate to lengthen the underwater internodes. The elongation of the uppermost internode at flowering in deepwater rice uses the same pathways as those found in paddy rice.

of the hormone ethylene — a gas that becomes trapped within minutes in cells of submerged organs owing to its slow diffusion through water[9]. A rise in ethylene is a signal that activates $SD1^{C9285}$ and $SK1/2$. In deepwater rice varieties, the rise in ethylene in submerged tissues drives the growth of underwater stem sections, enabling the upper leaves and reproductive organs to escape above the rising flood waters.

Nagai *et al.* looked for genes that control stem elongation in response to gibberellin production in the C9285 variety, and identified two, which they named *ACCELERATOR OF INTERNODE ELONGATION 1* (*ACE1*) and *DECELERATOR OF INTERNODE ELONGATION 1* (*DEC1*); these genes, respectively, boost and inhibit stem elongation. Neither is regulated by ethylene, but both influence gibberellin-activated cell division in stem nodes.

The authors report that a version of *ACE1* that acts early in plant development, together with gibberellin-repressed *DEC1*, are present in deepwater rice varieties and deepwater-adapted wild grasses of the *Oryza* genus. By contrast, a defective version of *ACE1* and a version of *DEC1* that acts early in plant development are characteristic of semi-dwarf rice varieties, such as the T65 variety, grown in shallow paddy fields, which can't survive a slow-rising flood. The inactive form of *ACE1* and the active form of *DEC1* were selected for during the domestication of paddy rice grown in shallow water. The DEC1 protein dampens internode elongation growth of T65 rice, and it is probably a negative regulator of transcription, with targets that are still unknown.

Nagai and colleagues report that expression during submergence of the version of *ACE1* present in C9285 (*ACE1^C9285*) rice initiates enlargement of the cell-division zone in nodes near the base of the plant, resulting in an increase in the total number of elongated internodes and greater plant height. The cellular function of ACE1 is unknown. Intriguingly, the authors find that the expression of *ACE1^C9285* is regulated by a gibberellin-activated transcription factor called SUBMERGENCE 1C (SUB1C), which is upregulated in response to submergence[10]. *SUB1C* expression is lower in varieties that carry the submergence-tolerance regulator gene *SUB1A-1*, which is closely related to *SUB1C*. Working in the opposite way to the flood-escape growth strategy of deepwater rice, varieties with *SUB1A-1* limit gibberellin responsiveness and the investment of carbon in the elongation of leaves, and such semi-dwarf varieties that have *SUB1A-1* suppress growth during flooding to enter a quiescent state that allows them to survive deep floods that are transient[11,12].

Internode elongation is enhanced only in the upper internodes of semi-dwarf varieties during reproductive development. The authors reveal that a gibberellin-upregulated gene (related to *ACE1*) that they call *ACE1-LIKE1* initiates this upper internode growth in deepwater or shallow paddy plants as they transition to flowering.

Antagonistic pathways and gene products that balance trait characteristics are frequently found in flowering plants. Such regulation provides flexibility in changing environments, but these regulatory capacities are often lost during crop improvements that focus on other characteristics in relatively stable growth environments. Nagai *et al.* demonstrate that genes related to *ACE1* and *DEC1* in rice are present and regulate cell division and the elongation or number of internodes in other grass species. This knowledge might enable the design of crops with height and growth characteristics that are suitable for cultivation in specific dynamic environments.

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