

of the observed growth in atmospheric methane in 2020.

Scientists often struggle to balance top-down and bottom-up methane estimates. Peng and colleagues' study is remarkable in that it successfully matches the two estimates in a geographically accurate analysis. The findings allow us to understand the relative contributions from changes in sources and the OH⁻ sink during the pandemic.

Despite these advances, some sources of uncertainty remain. For example, Peng *et al.* used only rough estimates for methane emissions from freshwater areas (lakes, reservoirs, ponds, rivers) and melting permafrost, which are thought to be major sources of natural emissions – arguably, just as important as wetlands². A more refined approach that considered, for example, the length of time for which lakes were covered by ice in 2019 compared with that in 2020 would have produced a more accurate emissions estimate. To be fair to the authors, there is still substantial uncertainty associated with estimates of methane emissions from these sources, making it difficult to incorporate such emissions into methane budgets.

Generally, it remains challenging to achieve a predictive understanding of the complex sources, sinks and feedbacks in the global methane budget. More field observations are needed to constrain bottom-up estimates, and more observations from networks of surface sensors and satellites are required to better constrain atmospheric-inversion models – particularly in Central and South Asia, the Middle East, Africa and tropical South America, as the authors recognize.

Peng and colleagues' findings imply that wetland methane emissions are sensitive to a warmer, wetter climate, and thus might fuel a positive feedback loop between methane emissions and global warming. The findings also suggest that future improvements in air quality, resulting in reduced emissions of carbon monoxide and nitrogen oxides, could extend the lifetime of methane in the atmosphere. Thus, a greater reduction in methane emissions than is currently targeted would be required to meet the goal of the United Nations 2015 Paris climate agreement to keep global warming to within 1.5 °C of pre-industrial levels.

The concentration of atmospheric methane surged again (see go.nature.com/3xm1dx4) to 18.2 ± 0.5 p.p.b. per year in 2021 – another mysterious acceleration without a clear cause, and the fastest rate of increase ever recorded. Further investigations into the sources and sinks of methane are clearly needed.

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Plant sciences

How roots go with the flow

Christa Testerink & Jasper Lamers

How do environmental cues steer the branching of plant roots? Insights into how water availability shapes root growth reveal an unexpected mechanism behind the hormone-mediated regulation of this process.

Plants need their roots to branch out in different directions so that they can explore the soil in their search for nutrients and water. Writing in *Science*, Mehra *et al.*¹ have uncovered the system that determines whether the main root of a plant invests in a new side branch for exploration or continues growing and waits for a better opportunity for side branching. The regulation of this process depends on water flow in the root.

In natural soils, plants experience variation in water availability. When root tips that are growing downwards lose contact with moist soil (for example, in an air gap), they respond by halting the formation of side (lateral) roots that branch out horizontally until contact of the root tip with moisture is re-established. The suppression of root branching in air gaps

“This principle might have relevance for other aspects of directed root growth.”

in soil is called xerobanching². This response was previously proposed to depend on the hormone ABA, which is made in response to drought. ABA inhibits both the initiation and the growth³ of lateral roots in many plant species, including the model plant *Arabidopsis thaliana*, maize (corn) and barley². The hormone auxin must accumulate in what are called the pericycle cells of the root for lateral roots to develop⁴. During xerobanching, ABA stops the formation of lateral roots by inhibiting auxin accumulation².

Mehra *et al.* confirmed that when the roots of tomato and maize plants cross an air cavity in soil, they need ABA for a xerobanching response – ABA-deficient plant mutants made lateral roots in air gaps. To predict how water flows through the root depending on external water availability, the authors carried out

simulations. Their findings indicate that when there is sufficient water, it flows in an inward direction, and when the roots are exposed to drought, the flow is reversed. In drought, a water-stressed root depends on water from shoots that reach the root tissues through a water-conducting internal tissue network called the vasculature (or vascular tissue). On the basis of these results, the authors hypothesized that ABA would travel with this water flow from the vasculature to the outer root tissues if the root crosses an air gap.

Previously, xerobanching could be studied only in soil, which limits the options for using *A. thaliana*, high-throughput analyses and tools such as plants with fluorescent markers because of the opacity of the soil. To overcome these constraints, the authors developed a laboratory approach to mimic root exploration over an air gap using an *in vitro* plate assay. Mehra and colleagues used this set-up to explore the role of ABA in *A. thaliana* seedlings that expressed a newly developed set of engineered proteins – ABACUS2 biosensors that offer a way to monitor ABA through use of an imaging process called fluorescence resonance energy transfer (FRET). These biosensors are reported⁵ to have a higher affinity for ABA than did the previous generation of ABA biosensors, and so provide greater sensitivity. This work revealed that ABA does indeed move from the vasculature to the outer root layers (Fig. 1a), showing that, on traversing the air gap, ABA gradually accumulates in the outer root tissues while becoming depleted in the vasculature.

Next, the authors investigated plants with signalling deficiencies in ABA arising from mutations in the *SnRK2* gene family. As was the case for plants with mutations affecting ABA production, the mutant plants did not show xerobanching. To elucidate which tissues require ABA signalling, Mehra and colleagues selectively restored ABA signalling in a *snrk2* mutant; they did this using engineered

plants in which expression of the SnRK2.2 protein was driven in a tissue-specific manner⁶. Intriguingly, restoring expression in any of the tissues outside the vasculature – namely, the epidermis, cortex or endodermis – could rescue the xerobranching response. This indicates that the response is not dependent on a certain cell layer, and that ABA signalling in any of these layers is sufficient for xerobranching.

ABA can induce the closure of pore structures, called plasmodesmata, that connect the cytoplasm between plant cells⁷. In the authors' studies, transport through plasmodesmata in the root was consistently reduced during xerobranching, in an ABA-dependent way. Moreover, mutants that were unable to close their plasmodesmata failed to mount a xerobranching response.

The authors report that ABA increased the expression of enzymes that produce the polysaccharide callose, which functions as a 'plug' to block plasmodesmata. Plants engineered to produce a higher than normal amount of callose overcame the ABA signalling deficiency and showed normal xerobranching, even in the context of *snrk2* mutation. By blocking water transport through plasmodesmata, ABA probably also blocks the inwardly directed transport of auxin. As a consequence, auxin cannot reach the inner root tissues, where it is required for lateral-root initiation, and branching is therefore inhibited if the root crosses an air gap.

These insights about the movement of ABA when water is limited, and its effect on auxin localization, might be relevant to other root responses that rely on ABA and auxin transport. One such response, called hydropatterning (Fig. 1b), occurs when one side of the root is in contact with water, but the other is not, resulting in the root branching only on the side that is in contact⁸. This response relies on the accumulation of auxin on the wet side of the root, but is independent of ABA, perhaps because the root would still be able to take up water from the soil through its wet side.

Other types of directed root growth during limited water availability are called hydrotropism and halotropism (Fig. 1b). Both rely on ABA and, in each case, the roots alter direction so that they are growing towards a more favourable environment^{6,9}.

Hydrotropism occurs when roots grow towards available water along a gradient, owing to an ABA-dependent asymmetry in the elongation of cells in the cortex layer of the root. It differs from xerobranching in that it requires ABA signalling in the cortex but not in epidermal or endodermal cell layers, and is an auxin-independent process. Hence, although ABA-mediated plasmodesmata closure is probably not involved in hydrotropism, Mehra and colleagues' findings might suggest that, during hydrotropism, water and ABA also move towards the side of the root with lower

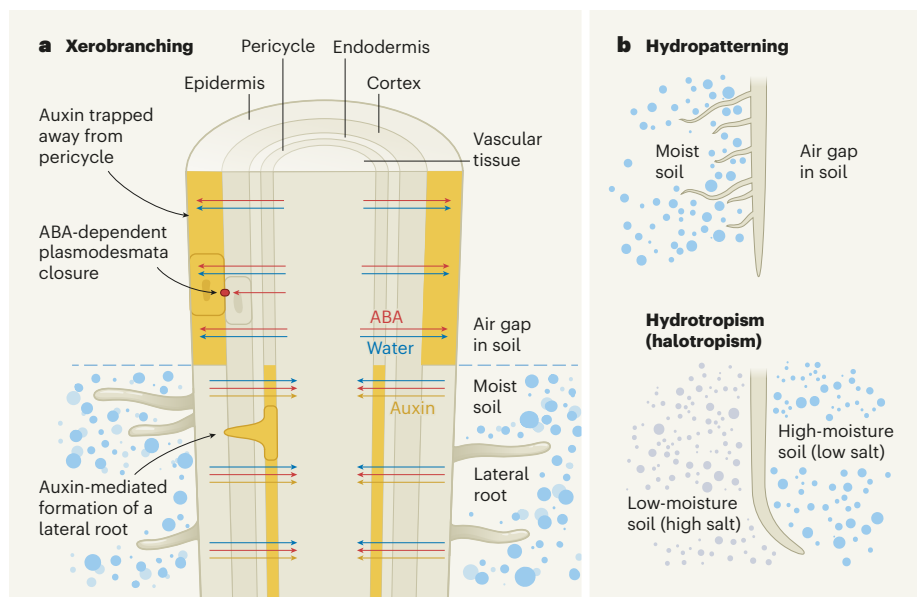


Figure 1 | How roots respond to water shortages. **a**, Mehra *et al.*¹ reveal how the growth of a type of side root called a lateral root is inhibited when water is scarce. Lateral roots initiate from cells in the root's pericycle layer by a process mediated by the hormone auxin (the other root layers are also labelled). When roots lose contact with moist soil (such as in an air gap), the usual inward direction of transport reverses and water moves outwards instead, taking the hormone ABA with it. ABA closes a type of pore called a plasmodesmata (red circle) that connects cells, preventing auxin from moving inwards. This reduces auxin concentrations in pericycle cells and inhibits lateral-root formation – such inhibition is called xerobranching. **b**, This principle might have relevance for other aspects of directed root growth, such as hydropatterning (lateral-root formation on one side of the root), hydrotropism (root growth towards soil with the highest levels of moisture) and halotropism (root growth away from a high concentration of salt).

water availability. This would result in differential ABA accumulation and thus could contribute to the observed asymmetrical cortical-cell elongation and the resulting change in the direction of root growth⁶.

In halotropism, roots grow away from high salt concentrations in the soil. The auxin-dependent part of this response is governed by sodium ions and is not affected by other ions or the level of water availability¹⁰. Yet because salts reduce water availability, similar processes that depend on water and ABA accumulation might cause plasmodesmata closure in this scenario. However, the model proposed by Mehra *et al.* would predict increased auxin accumulation on the salt-exposed side of the root during halotropism, whereas experimental data show that auxin accumulates on the other side of the root¹⁰.

These contrasting observations between xerobranching and halotropism might be a result of salt-induced changes in the location and abundance of auxin transporters. These transporters don't change their location in the context of xerobranching, as Mehra *et al.* report, but such relocations are essential for the halotropic response^{10,11}. It is possible that other effects of ABA on auxin production and transport are also relevant, reducing the need for the plasmodesmata-mediated transport control that is essential during xerobranching.

It will therefore be important to know whether the mechanisms that enable xerobranching also contribute to other processes that affect roots, allowing them to navigate a natural soil environment and optimize water uptake to support plant growth. The new generation of ABA biosensors now available will be instrumental in investigating how hormone transport through water flow contributes to other developmental responses of roots to water deficits.

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