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WUSCHEL: the versatile protein in the shoot apical meristem

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In vascular plants, almost all above-ground organs are derived from the shoot apical meristem (SAM). The developmental role of the SAM has been extensively studied, especially in the model dicot plant *Arabidopsis thaliana* (Aichinger et al., 2012). The SAM is spatially divided into three regions: the central zone comprising the stem cells and the organizing center (OC); the peripheral zone that can initiate lateral appendages such as leaves and flowers; and the rib zone that is located beneath the central zone and the peripheral zone. In the central zone, the OC provides signals to the stem cells and maintains their activity. In turn, the stem cells provide signals to restrict the number of cells in the OC. In addition, the SAM contains rib meristem activity, which is responsible for internode formation. Strikingly, the SAM is also a virus-free region. It is known that the accumulation of virus particles decreases toward the SAM, and this has led to the development of technologies to culture virus-free plants by SAM tissue culture (Morel and Martin, 1952). However, it is unclear why and how the SAM remains free of viruses. Recently, research groups led by Zhao and Tian have made great progress in determining the molecular mechanism of the virus-free nature of the SAM by characterizing the WUSCHEL (WUS) transcription factor (Wu et al., 2020).

WUS was the first gene to be identified in the *WUSCHEL-RELATED HOMEOBOX* (WOX) transcription factor family (Mayer et al., 1998). Mutations in *WUS* lead to a smaller and less active SAM. The *WUS* gene is expressed in the OC, and the WUS protein can move from the OC to outer regions such as the stem cells above the OC (Yadav et al., 2011). In the stem cells, WUS interacts with SHOOT MERISTEMLESS (STM) and promotes the expression of *CLAVATA3* (*CLV3*) to control stem cell activity (Su et al., 2020). In turn, CLV3 confines *WUS* expression to the OC through its signaling pathway, thus forming a feedback loop between stem cells and the OC (Fletcher et al., 1999; Schoof et al., 2000). Therefore, the WUS transcription factor appears to be a key regulator of cell identity in the central zone during SAM development.

Recently, Wu et al. (2020) made a great step toward understanding the anti-virus mechanism of the SAM by linking WUS to virus control. They observed that cucumber mosaic virus (CMV) could infect many tissues in *Arabidopsis*, but not the SAM or the floral meristem (FM). In the *clv3* mutant, in which *WUS* was ectopically expressed in the L2 cell layer, CMV could move upwards to the region beneath the tissues containing WUS. When CMV was introduced into the stem cells and the OC region of the *mp clv3* double mutant, which exhibited a large SAM, CMV particles were still able to spread into the region beneath the stem cells and the OC region, but did not accumulate in WUS-containing tissues. Ectopically accumulated WUS could inhibit CMV outside of the stem cells and the OC, and down-regulation of WUS resulted in the accumulation of CMV throughout the whole SAM. The WUS protein could also be induced by CMV infection in a broader region involving the peripheral zone and the FM. Therefore, the authors suggested that WUS may have a role in inhibiting virus accumulation, but not virus spread.

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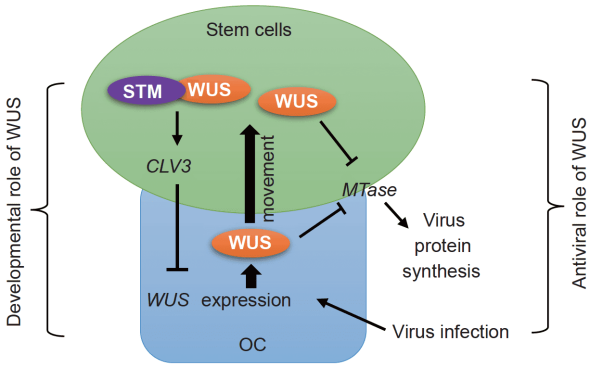

Figure 1 (Color online) Roles of WUS in the development of the SAM and its virus-free status. *WUS* is transcribed in the organizing center (OC), and then WUS can move to stem cells. WUS controls stem cell maintenance by forming a complex with STM and promoting *CLV3*, which in turn represses *WUS* expression. WUS also has anti-virus activity by repressing *MTase* expression, thereby inhibiting viral protein synthesis.

Next, the authors used tobacco and *Arabidopsis* assays to show that WUS could repress CMV protein accumulation via its function as a repressive transcription factor. Further molecular analyses revealed that WUS could repress the expression of genes encoding S-adenosyl-L-methionine-dependent methyltransferases (MTases), which are involved in ribosomal RNA processing and ribosome stability. Those results indicated that WUS could have a general role in the repression of protein synthesis mediated by MTases in the SAM. This hypothesis was tested by overexpression of an *MTase*, which led to blocking of WUS-mediated viral immunity. In summary, when viruses infect plants, WUS may inhibit viral protein synthesis, thereby providing broad-spectrum innate immunity to viruses (Wu et al., 2020).

The discovery that WUS can inhibit virus protein synthesis answers the old question as to how the SAM remains virus-free. Thus, it appears that WUS not only functions as a developmental controller, but also as a protector against viruses (Figure 1). On the basis of this discovery, many interesting questions arise. First, how is *WUS* expression regulated upon virus infection? WUS could be a key protein that balances virus inhibition and SAM development, but how this balance is regulated is unclear. It is possible that other factors are involved in the crosstalk between the development-controlling and immunity-controlling roles of WUS. Second, do other WOX proteins also have anti-virus properties? It is known that WUS-clade WOX proteins share many common functions in the regulation of stem cells. It is worth testing whether the anti-virus role of WUS to regulate *MTase* expression is a common feature of WUS-clade WOXs. Third, how can WUS be modified to generate a broad-spectrum tool for innate immunity to viruses? If WUS or the MTase pathway could be modified to increase anti-virus activity without affecting developmental control, it could be a new weapon to activate the SAM-related anti-virus mechanism throughout the whole plant. Fourth, are there other roles of the versatile WUS protein (or other WOX proteins) related to the special features of the SAM? Genome-wide identification of WOX targets may reveal multiple as-yet unknown functions in the regulation of meristems.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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