

Manuscript version: Published Version

The version presented in WRAP is the published version (Version of Record).

Persistent WRAP URL:

<http://wrap.warwick.ac.uk/132191>

How to cite:

The repository item page linked to above, will contain details on accessing citation guidance from the publisher.

Copyright and reuse:

The Warwick Research Archive Portal (WRAP) makes this work of researchers of the University of Warwick available open access under the following conditions.

This article is made available under the Creative Commons Attribution 4.0 International license (CC BY 4.0) and may be reused according to the conditions of the license. For more details see: <http://creativecommons.org/licenses/by/4.0/>.



Publisher's statement:

Please refer to the repository item page, publisher's statement section, for further information.

For more information, please contact the WRAP Team at: wrap@warwick.ac.uk

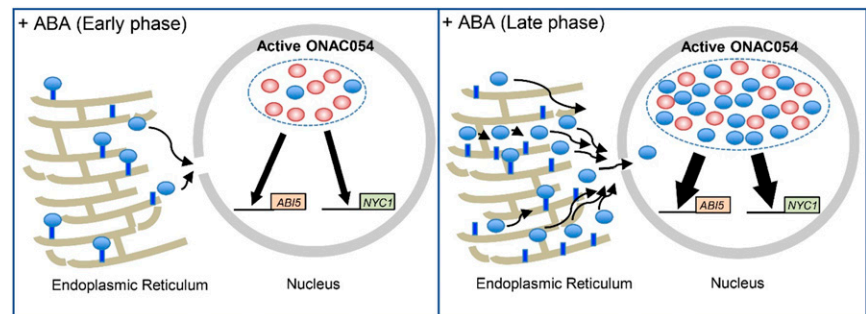
IN BRIEF

Make, Modify, Move: Multilayered Regulation of ONAC054 during ABA-Induced Leaf Senescence^[OPEN]

The word “senescence” originates from the Latin word *senescere*, to grow old. However, the process of leaf senescence is not simply the passive death of the leaf but instead represents an active and highly regulated process of nutrient remobilization from older leaves into developing parts of the plant to support further growth and reproduction. In crop plants an efficient senescence program is essential to maximize the carbohydrate and nutrient content of the seed, which ultimately impacts upon grain yield and quality. Postharvest senescence of fruit and vegetables is also a significant economic issue, negatively affecting shelf-life and nutritional value. Aside from being a developmental process, senescence can also be induced prematurely as an adaptive response to environmental stress conditions.

Several transcription factor (TF) families have been implicated in the regulation of leaf senescence, including the bZIPs, NF-Ys, WRKYs, and NACs (Breeze et al., 2011). Many of these TFs are also known to be involved in phytohormone signaling pathways supporting the existence of a complex regulatory network underpinning leaf senescence. Here, **Sakuraba et al. (2020)** describe the mechanism of action of one such senescence-induced NAC TF in rice (*Oryza sativa*), ONAC054, which promotes ABA-induced leaf senescence.

ONAC054 belongs to a subclass of NACs that are membrane-bound, frequently to the endoplasmic reticulum, by virtue of possessing a C-terminal transmembrane domain (TMD). Upon signal perception the TMD is proteolytically cleaved to release the active form of the TF that relocates to the nucleus (Kim et al., 2006). Sakuraba et al. (2020) demonstrated that ONAC054 (ONAC054 α), is indeed dual-localized to the ER or nucleus



Putative Model of ONAC054-Mediated Leaf Senescence upon ABA Perception.

In the absence of ABA, levels of the two ONAC054 splice variants, ONAC054 α (blue ovals) and ONAC054 β (red ovals), are low, with the former localizing exclusively in the endoplasmic reticulum and the latter in the nucleus. Upon ABA signal perception, levels of ONAC054 β rise initially, followed later by ONAC054 α , which is subsequently cleaved from its native membrane and translocated to the nucleus. This nuclear pool of ONAC054 then directly activates *ABI5* and *NYC1*. (Adapted from Sakuraba et al. [2020], Figure 10.)

depending on the presence or absence of a specific TMD. Moreover, they identified an alternative splice variant, ONAC054 β , in which a premature stop codon effectively eliminates the TMD resulting in the truncated protein being solely observed in the nucleus.

Loss-of-function *onac054* mutants exhibited a functional stay-green phenotype. However, while the concomitant increases in photosynthetic capacity can be associated with higher crop yield, in this case the mutants were observed to have a reduced fertility, which negated any such benefits. Microarray analysis of senescent leaves of the *onac054* mutant revealed that several genes associated with chlorophyll degradation (e.g. *STAY-GREEN1* and *NON-YELLOW COLORING1* [*NYC1*]), and with both ABA biosynthesis and signaling (e.g. *ABA-RESPONSIVE ELEMENT BINDING FACTOR4* and *ABA-INSENSITIVE* [*ABI5*]) were misregulated in comparison to wild type. Subsequent chromatin immunoprecipitation and protoplast transactivation assays confirmed that a subset of these putative downstream targets, namely *ABI5* and *NYC1*, were directly regulated by ONAC054

through the binding of the TF to a defined promoter motif. Consequently, ONAC054, in concert with other ABA-responsive NAC TFs, regulates the initial stages of chlorophyll degradation through the activation of the chlorophyll *b* reductase, *NYC1*.

Finally, the authors attempted to elucidate the precise regulatory roles of the two alternative splice variants in ABA-induced senescence. While the transcript levels of both ONAC054 α and ONAC054 β increased upon ABA treatment, ONAC054 β was upregulated more rapidly and to a greater extent, potentially through post-transcriptional regulation of the 3' untranslated region. Because ONAC054 β does not require posttranslational cleavage for activation, this suggests that this splice variant may be involved in early transcriptional responses to increases in ABA concentrations, with ONAC054 α transcription, processing, and nuclear import occurring later after more prolonged stimulation (see figure).

In summary, the membrane-bound TF ONAC054 is a key activator of ABA-induced leaf senescence, the activity of which is precisely controlled at the transcriptional, posttranscriptional, and posttranslational

levels. Such multilayer regulation offers multiple points of entry for potential manipulation, with the ultimate aim to develop an improved stay-green line offering higher grain yields. One possible strategy could be to “lock” the TF on its native membrane and thus prevent its nuclear relocalization, a tactic employed by pathogen virulence proteins (McLellan et al., 2013).

Emily Breeze
School of Life Sciences
University of Warwick
Coventry, United Kingdom

emily.breeze@warwick.ac.uk
ORCID ID: 0000-0001-5383-5448

REFERENCES

- Breeze, E., et al.** (2011). High-resolution temporal profiling of transcripts during Arabidopsis leaf senescence reveals a distinct chronology of processes and regulation. *Plant Cell* **23**: 873–894.
- Kim, Y.S., Kim, S.G., Park, J.E., Park, H.Y., Lim, M.H., Chua, N.H., and Park, C.M.** (2006). A membrane-bound NAC transcription factor regulates cell division in Arabidopsis. *Plant Cell* **18**: 3132–3144.
- McLellan, H., Boevink, P.C., Armstrong, M.R., Pritchard, L., Gomez, S., Morales, J., Whisson, S.C., Beynon, J.L., and Birch, P.R.J.** (2013). An RxLR effector from *Phytophthora infestans* prevents re-localisation of two plant NAC transcription factors from the endoplasmic reticulum to the nucleus. *PLoS Pathog.* **9**: e1003670.
- Sakuraba, Y., Kim, D., Han, S.-H., Kim, S.-H., Piao, W., Yanagisawa, S., An, G., and Paek, N.-C.** (2020). Multilayered regulation of membrane-bound ONAC054 is essential for abscisic acid-induced leaf senescence in rice. *Plant Cell* **32**: 630–649.