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EDITORIAL

Plant cell *harakiri*—programmed cell death in development

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The organisation of a multicellular organism requires that individual cells subjugate their needs for resources and their propagation under control of supercellular signals. The ultimate form of this cellular altruism is programmed cell death, a response that fulfils several basic functions in plants and other multicellular organisms: it participates in tissue differentiation and morphogenesis, plays a key role in the defence against different pathogens and stressors, and it safeguards genetic and physiological integrity of individual cells. The link between differentiation and cell death is actually very old and stimulated August Weismann to develop his concept of a developmental separation between the (immortal) germ line and the (differentiating and mortal) *soma* as a form of programmed 'genetic suicide' (Weismann 1892). A central element for Weismann's model is the observation of cell death as core element of initial differentiation events such as meiotic formation of germ cells in both animal and plants, the first zygotic division in plants separating the embryo proper from the suspensor which is doomed to death, or the asymmetric first division in somatic embryo that separates an embryogenic precursor from a vacuolate cell that will undergo programmed cell death but at the same time secretes a morphogenetic signal (a soluble arabinogalactan protein) required for the differentiation of its surviving sibling (McCabe et al. 1997). Two contributions in the current issue address the cellular aspects of programmed cell death in plant development and illustrate that developmental cell death does not occur as a "wild", free-running uncontrolled cellular degradation, but follows a prescribed and intricate pattern. This cellular suicide resembling in its complexity and sophistication the Japanase *seppuku* ritual (in the West better known as *harakiri*) allows to tune cell death with metabolic and differentation events of the dying cell to produce biological functionality of this terminal differentiation.

The work by Papini et al. (2011) investigates cellular details of meiosis-related death. Degeneration of three of four meiotic products is a common feature of eukaryotic oogenesis. In most angiosperms, the megaspores committed to undergo cell death are completely surrounded by callose, whereas the surviving megaspore maintains a callose-free window at the site adjacent to the chalaza, such that it can be supplied with nutrients and regulatory signals. The difference in developmental fate seems to depend on a gradient of the megaspore mother cell and becomes manifest, among other features, in an increase of mitochondrial density towards the chalazal cell pole (Ingram 2010). The abortion of the other megaspores shows the typical signature of programmed cell death such as terminal deoxynucleotidyl transferase dUTP nick end labelling (TUNEL)-positive nuclei and characteristic morphological changes of mitochondria and plastids, but a closer look reveals that this process is more complex. For instance, the first morphological indications of abortion are rather resembling autophagy and include the formation of autophagosomes, and the final stages leaving a lipid-rich cell corpse with swollen ER still surrounded by the callosic layer recall features of necrotic death.

The work by Zhou and Liu in the current issue investigates cell death in the context of excretion, an issue of high economic relevance. Plants utilise different routes to export their often valuable secondary compounds. In addition to exocytosis or passage of the plasma membrane into subcuticular excretion spaces (as found in glandular hairs or scales), they have developed routes that do not

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require the mechanistically difficult membrane passage. In this passage-independent route, the secretory active cell is simply dying such that the compound is released. The secondary compounds released by this so-called lysigenous excretion accumulate then in the space generated by the collapse of the secreting cell. Examples for this mechanism are the lactiferous ducts accumulating the protease papaine in the Papaya fruit or the extremely costly anticancer drug camptothecin in *Camptotheca acuminata* (Monacelli et al. 2005), but also the oil containers of citrus fruits, where the aromatic monoterpenes are collected. The authors ask whether the cell death generating the lactiferous duct in the latex-producing plant *Decaisnea fargesii* shows the features of programmed cell death. They describe a panel of degradative events including disintegration of vacuole and plasma membranes, misshapen nuclei coupled with degraded plastids in vacuoles, and nuclei enveloped by rubber granules. They also show that the nuclei of the secretory epidermal cells become TUNEL positive, which is indicative of DNA cleavage culminating in complete DNA degeneration. However, the DNA cleavage does not result in the typical electrophoretic ladder interpreted in terms of multiple internucleosomal sites, where digestion initiates. During the entire death process, the synthesis of the economically interesting rubber granules continues despite nuclear degradation supporting a model, where the execution of cell death even at the later stages remains tightly integrated into developmental functionality.

References

Ingram GC (2010) Family life at close quarters: communication and constraint in angiosperm seed development. Protoplasma. doi:10.1007/s00709-010-0184-y

McCabe PF, Valentine TA, Forsberg LS, Pennell RI (1997) Soluble signals from cells ldentified at the cell wall establish a developmental pathway in carrot. The Plant Cell 9:2225–2241

Monacelli B, Valletta A, Rascio N, Moro I, Pasqua G (2005) Laticifers in *Camptotheca acuminata* Decne: distribution and structure. Protoplasma 226:155–161

Papini A, Milocani E, Mosti S, Tani G, Brighigna L (2011) Megasporogenesis and Programmed Cell Death in *Tillandsia* (Bromeliaceae). Protoplasma. doi:10.1007/s00709-010-0221-x

Weismann A (1892) Aufsätze überVererbung und verwandte biologische Fragen. Gustav Fischer, Jena