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EDITORIAL

Activity in space

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How the scalar world of molecules is translated into developmental complexity that is ordered in time and space belongs to the most challenging topics of biology. The advances in fluorescence microscopy, along with the availability of non-destructive fluorescent markers, have revealed that this order is more dynamic than thought before. As a consequence, developmental concepts such as polarity, axis, or pattern can no longer be seen as static objects but have transmutated into descriptions of activities. Actually, this insight, although not adopted by many, is not new. Already more than five decades ago, in his famous textbook, Sinnott (1960) defined polarity as "specific orientation of activity in space". What we see as biological order is therefore just a snapshot of ordered activity. The questions, how the dynamic order of the "protoplasma" coexists and interacts with the stability of Mendelian inheritance (e.g. Nakazawa 1960) and how this order is generated and sustained by directional movement of molecules in response to chemical and physical gradients (e.g. Harold 1997), have been central also in this journal, giving rise to classical publications that are still worth reading today.

Three contributions in the current issue address how the temporal order of activity contribute to functional organisation at different levels of complexity: cells, organelles, and organs.

All eukaryotic cells contain acidic organelles that are often involved in degradation or digestion processes. In yeast cells, this acidic compartment is represented by the vacuole. The acidity is actively maintained by the activity of a proton ATPase. The function of this acidification is thought to provide a chemical environment favouring hydrolytic reactions. In their comprehensive study published in the current issue, Matsumoto et al. (2013) show that, in addition, acidification is relevant for the proper allocation of proteins into the vacuole. They block the vacuolar proton ATPase by the specific inhibitor concanamycin A and then examine the localisation of more than 70 GFP-tagged luminal and vacuolar membrane proteins by quantitative image analysis. About a quarter of these proteins lose their vacuolar targeting after treatment with the inhibitors. These include hydrolases, transporters, but also subunits of the vacuolar proton ATPase itself. This points to a scenario where initial acidity of the vacuole not only acts as attractor for the proteins destined to act in this acidic environment but also, in parallel, boosts the chemical reaction responsible for this acidity, which is a nice illustration of self-amplifying self-organisation at the subcellular level.

The dependence of protein function on subcellular distribution is also highly relevant for application, as carefully demonstrated by Pasare et al. (2013) in the current issue. Goal of their work was to improve the efficiency of metabolic engineering to generate potatoes that can be used as functional food because they contain elevated levels of nutritionally important carotenoids. The strategy to overexpress key enzymes of carotenoid biosynthesis, such as phytoene synthase and β-carotene hydroxylase, had not yielded consistent success during previous work. This led the authors to ask whether differences in suborganellar localisation of these proteins in amyloplasts versus chromoplasts might be relevant. They used fusions of the two key enzymes with red fluorescent protein and investigated their localisation after stable transformation either in *Nicotiana benthamiana* (leaves) or in potato (tubers). They observed that the localisation of the two key enzymes differed depending on the type of plastid. In leaves, the β-carotene hydroxylase was found in the stroma, whereas in tuber amyloplasts, it was sequestered in small vesicles. In contrast, the phytoene synthase localised to focal dots at the thylakoid in leaves, whereas it was stromal in the amyloplasts. This finding not only highlights the importance of subcellular distribution for the success of transgenic strategies but also

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demonstrates very clearly that it can be misleading to infer subcellular localisation from convenient experimental models (such as transiently transfected leaves of *N. benthamiana*) to the real situation in different organs (such as tubers). It further demonstrates that functionality of compartmentalised metabolism can be controlled even on the level of suborganellar organisation.

The third contribution by Qi et al. (2013) in the current issue investigated the molecular events underlying the characteristic flower pattern of the broad-leafed grape hyacinth (*Muscari latifolium*). The inflorescence of this flower is pale blue in the upper and purple in the lower domain. To understand the reason for this peculiar gradient, the authors measured vacuolar pH with a microelectron as well as content of metal ions by inductively coupled plasma mass spectrometry. None of these factors were significantly different. Nevertheless, the upper flowers contained exclusively delphinidin, whereas in the lower flowers, the delphinidin was accompanied by cyanidin. When they analysed the transcript levels of the key enzymes, they discovered that a specific isotype of dihydroflavonol 4-reductase (DFR2) was especially elevated in the lower flower along with flavonoid 3′,5′-hydroxylase and flavonoid 3′-hydroxylase genes. These molecular differences were linked with a different tissue distribution of the pigments: in the upper flowers, only the palisade cells were coloured (blue), whereas in the lower flowers, this blue pigmentation in the palisade was accompanied by purple pigments the spongy parenchyma and in epidermal cells. The primary cause for these differences in tissue-dependent activation of anthocyanin synthesis and different have not been addressed, but since the lower flowers have been generated before the upper flowers, the gradient might simply be the manifestation of a developmental maturation—in young flowers, anthocyanin synthesis is triggered in the palisade parenchyma. With progressive maturation, DFR2 along with its companions is activated in other layers of the leaf (spongy parenchyma, epidermis, but also in the palisade), such that the blue colour turns progressively purple. Again, a spatial gradient seems to be the manifestation of ordered activity in the expression of key enzymes.

Conflict of interest The author declares that there is no conflict of interest.

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