

## Significant signals—versatile interpreters

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Signals do not convey information a manner that is absolute; their information depends on the context. Many biological signals are simple molecules or simple molecular events. It is the *competence* of the receiver cell or tissue that confers a specific, often diverse, “meaning” to these signals. In multicellular organisms, the spatial or temporal distribution of signalling is a key element of coordination. For instance, neural systems are based on a tight control of electrical fluxes along the axons that is complemented by tight spatial constraint of secretion events in the synapses. However, rather than patterning the signal itself, spatial and temporal patterns can also be generated by patterning the competence of the cells that perceive and interpret a signal. For the totipotent plant cells with their lack of hierarchy, such *patterns of competence* (Steinitz et al. 1976) are crucial. When signal competence is the key factor for coordination, there must be versatile and diversified ways to perceive signals. During plant evolution, the group of leucine-rich repeat (LRR) receptor-like kinases has been extended with more than a thousand members identified in the genomes of model plants such as *Arabidopsis* or rice. Three reviews in the current issue shed light on the versatility in molecular structure and biological function of this protein class and simultaneously draw the attention to a core element of signal competence.

The review by Robatzek and Wirthmüller (2013) in the current issue updates the state of the art for FLS2, the central receptor for the basic innate immunity of plants. This member of the LRR binds a conserved motif in bacterial flagella and therefore can efficiently trigger a general defence response against bacterial infections. This receptor has to form dimers with a further LRR, BAK1, to activate defence. BAK1 is important for signalling through the brassinosteroid

phytohormones. Both receptors can interact with a third LRR, normally activated by attack of the necrotrophic oomycete *Botrytis*. Depending on the defence context, these LRR can phosphorylate each other and thus control the preference of heterodimer formation. This preference, in turn, determines which signal pathway is switched on. In this example, the molecular correlate of competence would be the dynamic interaction of different LRR types depending on specific patterns of kinase activities.

An alternative mechanism to regulate competence pattern is highlighted in a second review by Carvalho et al. (2013) in the current issue. They discuss the fact that a great number of plant genes (the estimate for *Arabidopsis* is 60 %) undergo differential splicing and investigate the function of this splicing for various physiological processes such as photosynthesis, hormonal signalling, germination, root growth, flowering and stress signalling. In this context, they also treat the role of differential splicing for LRR-dependent defence. A large group of LRR receptors falls into the class of resistance genes with a toll/interleukin-1 receptor domain. By differential splicing, truncated versions of these receptors are generated that can interact with the full-length versions and modulate their signal activity. Competence for this mechanism would here be the pattern of splicing activity.

Defence is launched by external signals and therefore has to be perceived in the periphery, either in the plasma membrane or even in the apoplast. However, external signals are also a core element of developmental coordination. This is most evident for plant cells and the issue of a third review on the genetic control of planar tissue growth in plants by Enugutti et al. (2013) in the current issue. The characteristic composition of plant organs from radial cell layers requires that cell divisions have to be aligned with respect to the plane of the layer culminating in planar growth. The orientation of cell division is governed by the spatial organisation of plant-specific

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microtubular arrays such as preprophase band and phragmoplast and follows simple and universal rules (for a recent review, see Müller 2012). Planar growth requires that signals from neighbouring cells have to be fed into this microtubule-based geometry sensing. This link requires again a peripheral sensory system. One pathway seems to involve trimeric G-proteins that through inositol-phosphate signalling, especially based on the activity of phospholipase D connected to cortical microtubules. However, trimeric G-proteins that have diversified during animal evolution seem to be constricted to one member in plants. Kinases of the plant-specific AGC VIII family seem to be important as pointed for the novel member UNICORN. In addition, Crinkly type kinases, a sister clade of LRR, have been shown to control planar organisation in the layered tissues of ovules, sepals and leaves as evident from mutants with irregular protrusions and interrupted layer continuity.

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

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