microenvironment into stem cells (Figure 1). This mechanism has far-reaching implications; in the maize SAM, for example, feedback signalling of *ZmFCP1* from young leaf primordia might have consequences for the asymmetry of cell divisions that release daughter cells for differentiation into the PZ, which might relate to the alternate leaf phyllotaxy. A more important consequence is the potential to increase yield, because the fasciated ear phenotype of weak *fea3* alleles in hybrid maize backgrounds led to enhanced yield traits. This has especially exciting implications for agriculture, particularly if weak orthologous *fea3* mutations could increase sink strength in rice grains and other cereals. The study of Je *et al.* also nicely epitomises the utility of using parallel model species; in this case, the conceptual mutual transfer of knowledge between the maize and arabidopsis studies, which will benefit further from extending analyses to other species.

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Forum

Vision in Plants via Plant-Specific Ocelli?

Frantisek Baluška[1] and Stefano Mancuso[2,*]

Although plants are sessile organisms, almost all of their organs move in space and thus require plant-specific senses to find their proper place with respect to their neighbours. Here we discuss recent studies suggesting that plants are able to sense shapes and colours via plant-specific ocelli.

Motto

The more I study nature, the more I become impressed with ever-increasing force with the conclusion, that the contrivances and beautiful adaptations slowly acquired through each part occasionally varying in a slight degree in many ways, with the preservation or natural selection of those variations which are beneficial to the organism under the complex and ever-varying conditions of life, transcend in an incomparable degree the contrivances and adaptations which the most fertile imagination of the most imaginative man could suggest with unlimited time at his disposal. (Charles Darwin)

Haberlandt's Plant Ocelli

In 1905, Gottlieb Haberlandt elaborated the concept of plant ocelli [1] according to which the upper epidermal cells of many leaves are shaped like convex or planoconvex lenses capable of bringing convergence of the light rays on the light-sensitive subepidermal cells (Figure 1). This concept, although favoured by Francis Darwin [2] and strongly supported by experiments performed by Harold Wagner [3], was almost completely forgotten. What evidence is there that this is something more than just a brilliant hypothesis? First, as a rule, the most superficial layer of cells lacks active green chloroplasts that would obviously interfere with the optical lens-like features of the epidermal tissue. With the exception of guard cells, which are the only cells within a leaf's epidermis containing chloroplasts, this feature is well known in numerous plants. This phenomenon it is not easy to rationalise. Leaf epidermal cells would be perfectly suited for photosynthesis as they receive optimal amounts of light. Second, upper epidermis leaf cells may act as a lens focusing sharp images in cells with the right focal length [1].

Evolution of Plant Ocelli

Two recent reports are bringing this concept back into the spotlight of scientific inquiry. The prokaryotic cyanobacterium *Synechocystis* sp. PCC 6803 measures light intensity and colours via several photoreceptors to control type IV pilus-driven movements [4]. Small cells of *Synechocystis* use directional light sensing to measure their precise positions with respect to a light source. The cells act as microlenses to navigate their movements towards light. More precisely, a high-resolution image of the light source is projected on the cell edge opposite to the light source, triggering movement away from the focussed spot [4]. On a higher level of cellular complexity, dinoflagellates – single-celled eukaryotes – assemble chimeric ocelloids from plastids and mitochondria [5,6]. This dinoflagellate ocelloid shows a remarkable resemblance to the multicellular camera-type eye as it contains retina- and lens-like structures [6].

Vision in Higher Plants?

Recently, two additional papers have suggested that even higher plants may experience a sort of vision using plant-specific ocelli, as proposed by Gottlieb Haberlandt. (i) The climbing wood vine *Boquilla trifoliolata* was demonstrated to modify the appearance of its leaves according to the host plant, perfectly mimicking the colours, shapes, sizes, orientations, and petiole lengths of the leaves [7]. (ii) Arabidopsis (*Arabidopsis thaliana*) seedlings distinguish their neighbours via photoreceptor-mediated recognition of their body shapes [8]. This light-based kin recognition of arabidopsis seedlings would implicate some kind of plant-specific vision (perception of body shapes of neighbouring plants) via a specific sensory system capable not only of sensing but also of decoding projected images. Considering that the leaf upper and subepidermis comprise cells suitable to act as ocelli (Figure 1), this concept would provide a satisfying explanation to the puzzling observations of leaf mimicry in climbing plants [7] and photoreceptor-mediated kin recognition of arabidopsis seedlings [8]. Both of these reports seem to suggest that plants are able to gather information about their environmental setting through vision-based inputs. Although this might sound improbable, and the authors of the two papers preferred not to entertain this possibility, there are several lines of evidence that seem to support Haberlandt's concept of plant-specific vision via plant ocelli.

Masters of Plant Mimicry

The most fascinating aspect of the *B. trifoliata* leaf mimicry is that vine leaves mimic all of the diverse morphological features of different leaf shapes and sizes of various host trees. Ernesto Gianoli and Fernando Carrasco-Urra recorded up to three different host plants supporting a single plant of *B. trifoliata* [7]. One

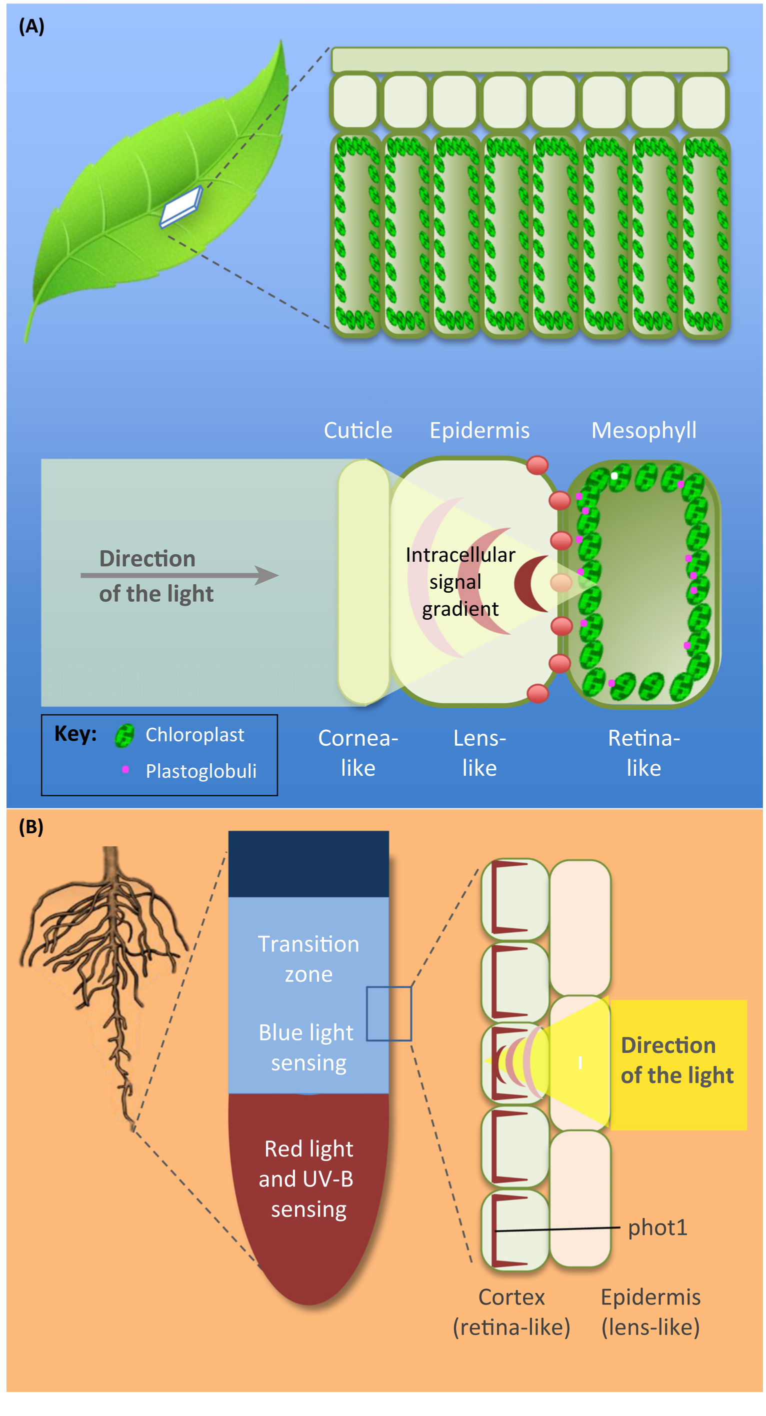

Figure 1. Schematic View of Plant Ocelli. (A) In the upper epidermis, cells of many leaves are shaped like convex or planoconvex lenses to allow the convergence of light rays on the light-sensitive subepidermal cells. Epidermal cells are predicted to express light-sensing molecules on their inner faces (red dots). The light-sensing role can also be accomplished via plastoglobuli in epidermal amyloplasts (not shown) and subepidermal chloroplasts (pink dots). The cuticle is proposed to act as a cornea-like structure while cytoplasm-dense epidermis cells serve as the lens-like component of Haberlandt's plant leaf ocelli. (B) Root apex ocelli comprise lens-like epidermal cells and subepidermal cells expressing the blue-light photoreceptor phot1, which has a polar subcellular distribution. For more details see [1,9].