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68 Hills Road
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Strange morphogenesis – organ determination in *Monophyllaea*

The achievement of adult form by plants can be seen as a series of developmental choices made by meristems and their products. The mature embryo, with radicle, hypocotyl, shoot apical meristem and (in dicotyledons) two cotyledons, is one of the simplest plant systems as a starting point for study. However, these particular organs are generally already determined, and only later on in a plant's life history are developmental choices made – for example, the choice between floral and vegetative meristems. However, a recent paper¹ exploits a new 'model plant', *Monophyllaea*, to study organogenesis. *Monophyllaea* does not have a shoot apical meristem, and the cotyledons make the developmental choice between continued growth and suppression. This plant may well prove of further use for studies of the control of organogenesis and the study of the regulation of the shoot apical meristem.

The one-leaf plant

The family Gesneriaceae, which, in addition to *Monophyllaea*, includes the familiar African violet and Cape primrose, is known to show unequal growth of the cotyledons (anisocotily). This condition is present in almost all the Old World species, but is generally absent in the New World Gesneriaceae. In anisocotylous plants, almost all the early above-ground growth of the seedling takes place in one cotyledon, and the activity of the shoot apical meristem is delayed. This may have adaptive significance: the seeds of anisocotylous plants are minute and have no endosperm, and the plants generally grow in shady habitats – continued growth of the cotyledon would serve to maximize the rapid production of photosynthetic area over support tissue².

In *Monophyllaea*, and some species of *Streptocarpus*, anisocotily is taken to extremes. These plants do not just delay the growth of the shoot apical meristem, they lack this meristem entirely. Instead, the one cotyledon continues to grow, and in some species of *Streptocarpus* may reach a length of 1 m. The single cotyledon becomes

the entire vegetative part of the plant, which is known as a 'unifoliate' or one-leaf plant. Inflorescences are borne on the cotyledon midrib, produced from a 'groove' meristem. Continued growth of the lamina is provided for by a basal meristem, and a third meristem ('rib' meristem) is responsible for petiole growth. At this point, the terms cotyledon or leaf begin to appear inadequate, because the structure is actually the product of a nexus of three meristems. For this reason the term 'phyllomorph' has been proposed³, to include the stalk ('petiolode') and the lamina.

A further complication arises when other phyllomorphs arise from the base of existing phyllomorphs to produce a 'false' rosette, a type of construction termed 'rosulate' to distinguish it from the unifoliate. The Cape primrose is a rosulate *Streptocarpus* of this type, lacking any shoot apical meristem. Rosulate and unifoliate *Streptocarpus* species can be crossed, and the progeny segregate in a manner that suggests that repeated phyllomorph iteration is controlled by two loci⁴. *Monophyllaea*, from Southeast Asia, has identical construction to the unifoliate African *Streptocarpus*, except that rosulate plants are unknown in *Monophyllaea*.

Establishment of novel plant organization

The onset of anisocotily and the establishment of the unifoliate condition in *Monophyllaea* has recently been investigated by Hirokazu Tsukaya¹. Meristematic activity was monitored in seedlings by immunodetection of incorporated 5-bromodeoxyuridine to determine DNA synthesis. This confirmed that a shoot apical meristem is never present. However, a basal meristem is present from the earliest stages in both cotyledons. The cotyledons are initially physiologically equivalent, but meristematic activity later disappears in one of them. To analyze how this change is determined, a series of simple but elegant excision experiments were conducted to show that the fate of the cotyledons is determined during development and becomes irreversible. However, if one

cotyledon is excised at an early stage, when both cotyledons are still physiologically equivalent, the remaining cotyledon continues to grow. Similar experiments had been conducted by Oehlkers⁵, but this early work gave equivocal results.

To explain the findings, Tsukaya has proposed a hypothesis of 'competitive organogenesis'. Competition between organs, as opposed to meristems, has never been reported before. However, as these cotyledons contain meristematic regions, competition between them – in a manner analogous to apical dominance – is probably inevitable. Competitive organogenesis amplifies any chance differences in growth between originally physiologically equivalent organs. Thus anisocotily may simply be an inevitable consequence of delayed or absent shoot apical meristem activity and the transfer of meristematic activity to the cotyledons. These studies are part of a wider research programme, coordinated by Masahiro Kato, to develop *Monophyllaea* as an experimental system. Phylogenetic studies on *Monophyllaea* and efforts to produce transgenic *Monophyllaea* plants are all under way.

Meristem evolution

The odd morphology of *Monophyllaea*, lacking a shoot apical meristem, provides an 'evolutionary mutant' with which to study the meristem. Tsukaya¹ points out the apparent similarity between *Monophyllaea* seedlings and *Arabidopsis* mutants that lack a shoot apical meristem⁶⁻⁸, and it is interesting to consider the relationships between the two systems. The *stm* ('shoot-meristemless') mutation results in loss of function at a locus whose expression appears to be a marker for the apical meristem⁹. One explanation for the unifoliate morphology is that a similar loss-of-function mutation of the *stm* homologue in Gesneriaceae has occurred. However, this is unlikely as certain species that normally possess a typical shoot can become unifoliate under certain environmental conditions. Furthermore, experiments with exogenous hormone applications have

succeeded in producing a stem in phyllo-morphic species¹⁰.

An alternative hypothesis is that the site of expression of meristem-determining genes (which may include the *stm* homologue) has been generalized to include the base of the cotyledons, so accounting for the delayed activity of the shoot apical meristem and the continued growth of the cotyledons. In unifoliate plants, expression of meristem-determining genes may accordingly have been eliminated entirely from the region between the cotyledons, resulting in the complete absence of a shoot apical meristem. If the Gesneriaceae *stm* homologue could be isolated, an examination of its expression pattern by RNA *in situ* hybridization would help to clarify the point.

The novel morphology of *Monophyllaea* need not involve a single major developmental mutation, but may have evolved gradually through incremental changes in the location of meristematic tissue. Even so, such changes appear to be rare. Molecular phylogenetic work on *Streptocarpus* suggests that the rosulate and unifoliate types represent unique clades, and that these growth forms have each arisen only once in Africa¹¹.

The enlarged, meristematic, inflorescence-bearing cotyledon of *Monophyllaea* has characteristics of both leaf and shoot. The neutral term phyllomorph is therefore preferable, as it is an organ with 'fuzzy morphology'¹². As it seems to show partial homology with both leaf and shoot, genes characteristic of both organ systems may be expressed there. The recent development of

Monophyllaea as an experimental system is welcome, because it opens the way to a more critical and process-based understanding of this morphological complexity.

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Quentin Cronk*

Institute of Cell and Molecular Biology, University of Edinburgh, Kings Buildings, Mayfield Road, Edinburgh, UK EH9 3JH and the Royal Botanic Garden, 20A Inverleith Row, Edinburgh, UK EH3 5LR

Michael Möller

Royal Botanic Garden, 20A Inverleith Row, Edinburgh, UK EH3 5LR

*Author for correspondence
(tel +44 131 552 7171;
fax +44 131 552 0382;
e-mail q.cronk@rbge.org.uk).

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