

An Examination of Leaf Morphogenesis in the Moss *Physcomitrella patens*

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Leaves are prominent attributes of most land plants, exhibiting common features such as lamination and laterality that maximize photosynthetic capacity. Leaf form and size, however are extremely diverse among taxa. Furthermore, the leaves of an individual plant may vary in form and size depending on such factors as the insertion point on the stem, the developmental stage, and the age of the leaf.

Descriptions of leaf morphology in mosses exist but leaf development has not been described in detail for *Physcomitrella patens*. In contrast to the leaves of most plants, the leaves of *P. patens* are unistratose except for the midrib. Detailed study of, for example, the number and size of leaf cells is possible.

The first two or three leaves that emerge on the shoot are picket-shaped and lack midribs. These leaves consist of cells that are approximately rectangular in shape except for an ellipsoidal cell at the leaf apex. Mature upper leaves are lanceolate. The distal portion of the leaf broadens before narrowing to an acute tip. Each mature leaf is larger and consists of more cells than the previously emerging leaf. Long shoots may bifurcate and produce elliptical leaves with acute tips.

A plastochron (P) number is used to designate each leaf as it emerges and develops. P₀ indicates a leaf primordium that is not yet visible but consists of differentiated leaf primordial cells. P₁ designates the newest visible leaf and so on.

Differential rates of leaf cell division and cell expansion in various regions along the proximo-distal axis of the leaf contribute to rapid and substantial changes in leaf form and size as well as cell shape and size beginning at P₁ and continuing until the mature leaf form is attained by P₅ or P₆.

Emergent upper leaves (P₁- P₂) are approximately triangular with a rounded cell at the apex. This cell quickly expands to an elongated, ellipsoid shape. Expansion, particularly along the proximo-distal axis, of 5-10 marginal and interior cells subtending the cell at the apex occurs rapidly. The marginal cells become ellipsoidal, and similar expansion of the remaining marginal cells proceeds from the distal end toward the leaf base. Thus, at the P₂- P₃ stage, the leaf is ovate with an acute tip consisting of a small number of cells that have attained their mature shape. The base of the leaf consists of numerous small cells.

Expansion of the interior cells proceeds toward the leaf base. Several tiers of cells at the base of the leaf expand rapidly during P₄-P₆. These cells become large and rectangular, their length (along the proximo-distal axis) being twofold, or more, greater than their width.

Both cell division and cell expansion continue throughout the life of the leaf, albeit at a greatly reduced rate. After P₅- P₆, the number of cells may increase twofold or more. The length of individual cells may double, while increases in width are generally less. Overall increases in leaf length and width after P₅- P₆ are generally less than twofold, however.