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Review

Leaf shape diversity with an emphasis on leaf contour variation, developmental background, and adaptation

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ABSTRACT

Leaf shape varies markedly. Here I focus on the diversity in leaf contour, which can be considered marginal variation in curvature if we omit detailed marginal structures such as serrations. This curvature can be described by a combination of sigmoids: a curve for the apical half and a curve for the basal half connected with or without an interval. Marginal curvature is determined by the position of the leaf meristem, the acceleration and deceleration of cell proliferation in the leaf meristem, and the angle of directed cell proliferation. Several key factors contributing to this variation have been revealed to date, but the majority of the underlying genetic mechanisms are unclear. Here I provide an overview of current knowledge and propose future directions for the field.

Contents

1. Introduction

Shape is important for organisms to maximize their ability to live in the wild. This is, of course, also the case for plants. Among angiosperms, the major clade of land plants worldwide, leaves are the most diversified organs. Flowers are also highly diversified,

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but their basic components, the floral organs, are modified leaves. Stems and roots also show species-specific characters, but their diversity is less rich than that of leaves. Branching patterns are also important and diversified characters, but again the diversity is less than that of leaf shape. Leaves are so diversified in shape and form partly because they are the site of photosynthesis. Photosynthesis requires efficient absorption of light energy and the exchange of CO_2 for O_2, and temperature and water content must be maintained within a certain range. Because the most productive form can differ according to environmental conditions, leaf shape varies among species and can be influenced by biotic or abiotic stresses. For example, flat leaves are metamorphosed into spines in desert plants.

Considering the rich diversity of shape and form in leaves, this review article focuses on leaves, in particular on leaf contour. Although the difference between simple and compound leaves is also an important factor in terms of diversity, it is omitted here because the morphological unit of compound leaves, the leaflet, can be considered a simple leaf in terms of its contour. One difference between compound and simple leaves is whether repetitive morphogenesis occurs; this has been reviewed by others [8,2]. Determinacy or indeterminacy is also omitted here because it contributes to leaf size but not shape [57–59] Tsukaya (2014, in press). Finally, variation in marginal structures, namely, the absence or presence of marginal dentations/serrations, is outside the scope of this review, which focuses on leaf contour. I wish to emphasize that the function of marginal serrations in leaves is controversial (see [11,58]).

2. Contour variation from the viewpoint of curvature

Most leaf contours can be described by a smooth curve if we omit the absence/presence of digitations/serrations along the margin. This curvature can be described by a combination of sigmoids: a curve for the apical half and a curve for the basal half connected with or without an interval (Fig. 1). Many taxonomic characters of leaf shape can be attributed to the nature of the curvature. The nature of the apical tip, which can be caudate (tailed), acute (pointed), apiculate (tapered to a short slender point), acuminate (tapered to a long point), obtuse (blunt), rounded, or emarginate (slightly indented), is mediated by differences in the curvature of the upper half (Fig. 2). Differences in overall form—such as lanceolate, ovate, orbicular, or deltoid (triangular over the entire leaf)—are also dependent on curvature. This also applies to features of the basal part, which can include cuneate (wedge shaped), truncate (end squared off), cordate (spade shaped), auriculate (with ear-shaped appendages), or sagittate (arrowhead shape over the entire leaf) features (Fig. 2). The nature of the curvature in the apical and basal halves is usually different, and they do not mirror each other. The joint of the apical and basal halves also varies: Some leaf shapes seem to be made by a direct joint between the two halves, whereas others have an intermediate part that manifests as elongated oblong leaves with parallel sides. Other leaf shapes, such as reniform (kidney shaped) and obcordate (heart shaped), are the result of combinations of different curvatures in the apical and basal halves. Sickle-shaped or falcate leaves have asymmetric curvatures on the left and right. Ensiform, or stick-like, thin leaves are an extreme case of diversified curvature, i.e., no curvature.

These morphological characteristics are used for taxonomic description/identification of plant species. What is the physiological or adaptive meaning of these morphologies? How did this diversity evolve? Which mechanisms underlie it? In the following sections I provide an overview of current knowledge on these issues. First, how does this variation come about?

3. Developmental basis of variation in leaf contour

From the standpoint of developmental biology, variation in leaf contour can be attributed to changes in the acceleration and deceleration of cell proliferation in leaf primordia. This is not pure cell proliferation per se, but rather 'proliferative growth' or 'growth coupled with cell proliferation'. Although genetic controls of polar cell elongation and polar cell distribution/proliferation contribute to an altered leaf index in the model plant *Arabidopsis thaliana*

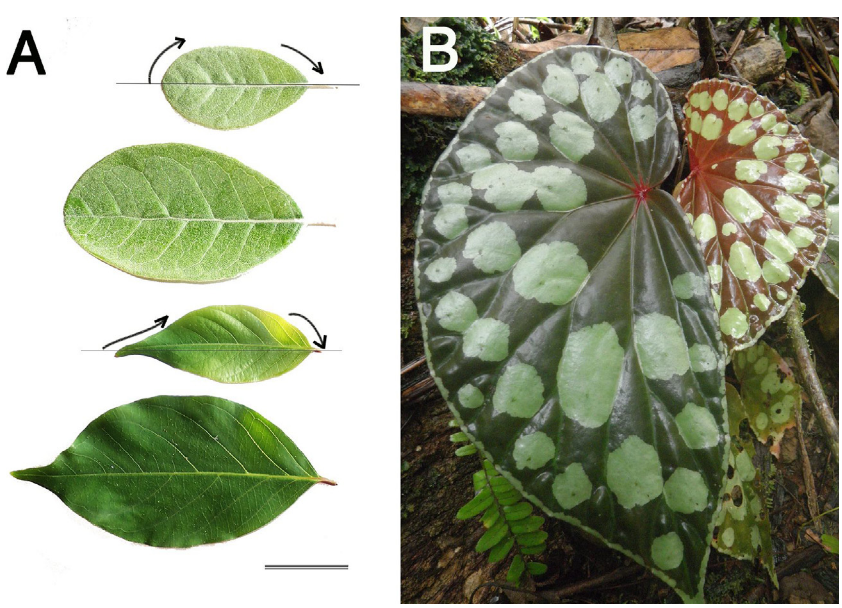

Fig. 1. Leaf contour can be described by curvature.
A, Upper two panels: Young leaves of *Feijoa selowiana*, which has ovate, base rounded, apex obtuse leaves. A, Lower two panels: Young leaves of *Lagerstroemia subcostata*, which has ovate-lanceolate, base broadly cuneate, apex acuminate leaves. If leaf organogenesis occurs from the apex to the base, as indicated by the lines and arrows, acceleration and deceleration of cell proliferation must differ between these two species. B, A species of the genus *Begonia*, which typically exhibits an asymmetric leaf shape. This type of asymmetry is generated by differing deceleration between the right and left sides of the leaf. Photographs in panel A were taken in my garden, and photograph of panel B was taken in Betung-Kerihun National Park, West Kalimantan, Borneo, Indonesia.

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