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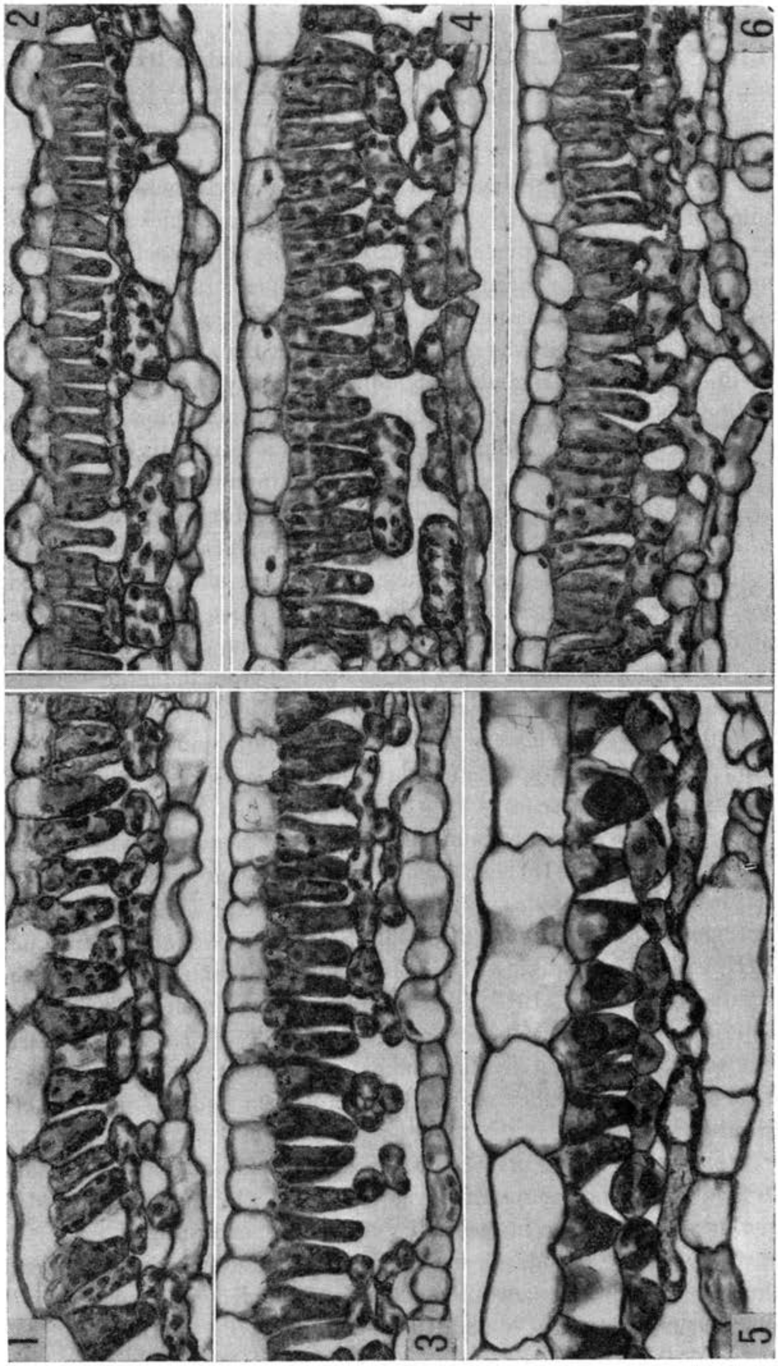
The number of cell-layers in leaves of dicotyledons varies considerably but within fairly definite limits. Extreme thickness of epidermis or mesophyll presently retards photosynthetic activity and is usually restricted to succulents and desert types. In connection with studies of leaves representing a large number of species of dicotyledons, no mature leaf was noted having fewer than five cell-layers in the blade. The list included, in addition to many species from Iowa, a liberal collection from southern Florida, samplings from the Pacific coast states, a number from Fiji and a fairly large collection from North Island, N. Z. with scattered numbers from various southern and eastern states. The series therefore included plants which were widely diversified in their geographical, taxonomic and ecological relations. Among these, numbering about five hundred species, only ten were noted having as few as five cell-layers in the blade. The names and general structure of nine of these are given in Table 1; the tenth, *Begonia rex*, is omitted from the table because it is a succulent, grown usually in planthouse, and is not comparable with the others which were growing out of doors under natural conditions. These ten represent eight families, one species each except three for the Urticaceae.

Earlier workers have included drawings of mature leaves of this type. Two species of herbaceous plants, having leaves with five cell-layers in the blade, were figured by Clements (1905); Fig. 2b, *Polygonum convolvulus* and Fig. 3b, *Bidens Bigelovii*, both on Plate VIII. Also, two species of woody plants with similar leaves were figured by Hanson (1917); Fig. 4, *Acer saccharum* and Fig. 8, *Tilia americana*. All of these were reported from deeply shaded habitats, but without comment by the authors as to their special structure. This raises the number of species to fourteen and the number of families to eleven.

It should be stated that in the present study no attempt was made to find leaves having such reduced structure. On the contrary, only sun leaves were taken in the earlier collections, excepting about forty species used in a study of sun-shade differentiations. Later collections included herbaceous plants and these yielded eight species having the simpler type of blade structure.

PLATE I



The first instance noted in this laboratory was a leaf from a deeply shaded branch of *Acer platanoides;* this is shown, Fig. 5, in a recent paper in the Academy Proceedings (Wylie, 1949). A moderately shaded leaf of *Quercus Muehlenbergii* added another woody plant but the others are herbaceous. In no instance does measurement or figure in this paper relate to an area of blade within the marginal-taper where tissues and cells are often highly modified.

A glance at Plate I shows that the six species there illustrated (using common scale of enlargement) all have specialized palisade and spongy mesophyll. A similar situation prevails in the species not included in this plate (*Oxalis stricta, Laportea canadensis, Begonia rex* and *Acer platanoides*). This was rather unexpected because many sun leaves have partly vertical spongy tissue and herbaceous leaves often have less specialized palisade.

Table 1 gives various measurements for nine of these species and shows a mean blade thickness of 77 μ. Each had a single layer of palisade and two layers of spongy mesophyll. *Begonia rex,* with the same number of cell-layers, was 272 μ thick, half of which was contributed by the epidermal layers. Blade thickness alone does not indicate the type of blade organization; others with blades of similar thickness had three layers of spongy mesophyll.

The epidermal cells in these leaves are slightly convex, seen in transections (Plate I), with the exception of *Pilea pumila* (Fig. 5), which, like *Begonia rex,* has greatly thickened cells that show as rectangles in these sections. However, the face view of these epidermal cells, as seen in paradermal sections, shows a very different picture. All of the herbaceous species have large epidermal cells with sinuous lateral walls in both epidermal layers, and this appears also in the lower epidermis of *Acer platanoides.* Some of these cells are so deeply lobed as to be almost branched and the entire boundary wall is sinuous. This gives a much greater area of lateral contact between epidermal cells and perhaps offers some mechanical advantage. The lower epidermis carries all stomata, and all herbaceous species excepting *Leonurus sibiricus* had chloroplasts in one or both covering layers.

The palisade cells taper abruptly in *Pilea, Begonia* and *Oxalis* but in others are relatively long and closely associated. Palisade cells

Description of Figures

Figs. 1-6. Transections of leaves of dicotyledons having blades with five layers of cells. All figures have the same scale of enlargement. Fig. 1. *Hypericum punctatum.* Fig. 2 *Phyllanthus lathyroides.* Fig. 3. *Parietaria pensylvanica.* Fig. 4. *Quercus Muehlenberghii.* Fig. 5. *Pilea pumila.* Fig. 6. *Leonurus sibiricus.*

Table 1
Organization of leaves having five cell-layers in the blade.
(Measurements in microns)

Species	Blade Thick-ness	Total Epider-mis	Pali-sade Mes.	Spongy Meso-phyll	Tissue Ratio SEE/P	Vein Spac-ing
Acer platanoides	77.0	34.2	22.4	23.9	2.59	227
Hypericum punctatum	63.4	29.4	20.0	14.0	2.17	138
Laportea canadensis	92.8	35.2	35.2	22.4	1.64	168
Leonurus sibiricus	67.6	23.4	22.4	21.8	2.02	124
Oxalis stricta	110.2	48.0	32.0	30.4	2.45	168
Parietaria pensylvanica	70.4	30.1	23.7	16.6	1.97	134
Phyllanthus lathyroides	59.5	19.8	19.2	20.5	2.10	84
Pilea pumila	85.8	42.2	23.0	20.2	2.71	345
Quercus Muehlenbergii	69.4	19.2	25.6	24.6	1.71	112
Means	77.34	31.28	24.83	21.60	2.15	167

are always united laterally in the plane of their junction with the supporting upper epidermis and at lower levels are usually isolated. This lessens lateral contacts in the palisade zone and results in considerable open space for this layer. Most of the chloroplasts are in the palisade and its cells often project into the open meshes of the spongy mesophyll below.

In all of these species the cells of both layers of spongy mesophyll are meshed, enclosing open spaces, which in the lower layer may be very large. In some, these meshes are 80-90 μ across; the result is the inclusion of much intercellular space in this tissue. All cell-layers of the blade, with the partial exception of the palisade, are in contact, thus permitting vertical transfer of materials. The epidermal and spongy mesophyll cells have greater areas of contact in the plane of the blade which favors translocation in that direction.

For each of these species the tissue-ratio was determined by dividing the combined volume of epidermis and spongy mesophyll by the volume of the palisade layer. This ratio has been shown, for larger groups of species, to be positively correlated with the vascularization of the blade. A higher ratio (which results from a greater proportion of the blade tissue having cells united and often elongated or expanded in the plane of the blade) is often associated with a wider spacing of the vains. The highest R-values were found in *Pilea* and *Begonia* which species had also the widest vein-spacings.

The mean vein-spacing, or intervascular-interval, was determined for each of these species and these are recorded in Table I. As might be expected the vein-spacing is relatively wide in these plants which means of course a lower degree of vascularization. The mean interval between veins for the nine species was 167 μ, while that for about one hundred northern woody plants was 142 μ, and 94 species of herbaceous dicotyledons was 184 μ.

Discussion

Within limits the dicotyledon is advantaged by having a multi-layered leaf, with as much chlorenchyma as can be adequately protected and illuminated. This is well illustrated by the broad-leaved evergreens, which are so conspicuous in many tropical and temperate areas. These generally have relatively thick leaves which are sufficiently xeromorphic to withstand the hazards of the entire year. In other regions where conditions in the alternate season force or invite the deciduous habit, blades are thinner and somewhat mesomorphic.

Of interest in this connection are a few comparative figures for groups of dicotyledons in different geographical areas. For 84 species of northern deciduous plants the mean blade thickness was 159 μ and the number of cell-layers was usually 6-8. For 43 species of dicotyledons from southern Florida, chiefly broad-leaved evergreens, the mean blade thickness was 205 μ, with generally 8-12 cell layers, though some were much thicker. For 26 species of forest and chaparral species from coastal southern California the mean thickness was 336 μ, with a mean depth of 5.49 μ for the upper cuticle (Cooper, 1922, P. 98). In many of these the number of cell-layers in the blade was 10-12, occasionally much higher. Among 45 species of woody dicotyledons from North Island, N. Z., chiefly broad-leaved evergreens, the mean blade thickness was 384 μ and the number of layers in the blade usually 10-12 or considerably more in some. It seems that the optimum blade thickness varies with geographical and ecological conditions but an upper limit is soon reached which is exceeded chiefly by desert types with survival at stake.

Well known also is the considerable variation in blade thickness with a given number of cell-layers in the lamina. To cite but a single instance,—among the sun-shade leaves on an isolated tree (Acer platanoides) blade thickness ranged from 198 μ to 77 μ while the number of cell-layers decreased but one, from six to five (Wylie, 1949).

The lower range reported for leaves of dicotyledons appears to be a lamina having five cell-layers. The chief reason for this limit appears to lie in the method of origin and early growth of the blade. Numerous investigators have shown that the growth of the blade is chiefly by the activity of "marginal meristems" which launch a lamina with an initial number of five or more layers of cells. (Foster, 1936). A paper by Smith (1934) showed that the young leaves of seventeen species of deciduous trees had five or more cell-layers in the blade; six others had six or more layers and one species seven or eight layers at the bud-stage. All of these species usually increase the number of layers as the leaf matures. It seems, however, that the earlier number of layers may be retained under certain conditions, including deep shade and perhaps greater humidity.

In the present survey the writer noted five cell-layers in blades of ten species of dicotyledons and included here are four additional species, figured by others. Of these fourteen, ten are herbaceous and four are woody species; they represent eleven families. These considerations suggest that this reduced type, with five cell-layers in the blade, will be found occasionally on dicotyledons growing completely or in part in deep shade, with accompanying changes in local environment. Of greater interest would be records for terrestrial dicotyledons having four or fewer cell-layers in the lamina of mature leaves.

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