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SOME WOUND RESPONSES OF FOLIAGE LEAVES

ROBERT B. WYLIE

The leaves of plants are their most exposed organs. The thin summer foliage of herbaceous plants and deciduous trees generally suffers so severely that one rarely finds an uninjured leaf. While the degree of wounding is less serious in the evergreens, since they are tougher and offer greater resistance, lesions are not uncommon on these especially on the broader leaved evergreens. The plant's ability, therefore, to deal with such frequent accidents must be highly developed to meet these daily needs for renewed cortex.

Recalling that the leaf is usually an organ of definite growth, its tissues quickly passing into functional maturity, and that wounds expose many layers of living cells remote from all growing tissues, the writer has often remarked the apparent efficiency of the leaf in dealing with its wounds. Infections through lesions in leaf tissue seem relatively unimportant in relation to plant diseases while wounds on stems commonly contribute to the liability of infection. Leaf wounds though most numerous of all types of lesion in plant tissues apparently have relatively the least to do with plant diseases.

While leaves have been studied intensively from many viewpoints their normal tissue responses to traumatic stimuli have received relatively little attention from botanists. This is in itself proof of the marked efficiency of the leaf to take care of its wounds. When galls are produced such have invited special investigation and their literature is extensive. Very few papers, however, discuss the morphological changes in consequence of lesions in a foliage leaf unless followed by abnormal growths. Since no paper at hand seems to bear directly on these morphological responses it seems best to defer the discussion of all papers that might find a place in the summary of literature to a later paper in which the writer traces the development of the cicatrice in certain leaves.

The work of the foliage leaf compels a structure that invites animal attack and also renders the leaf liable to mechanical injury. Photosynthesis is possible only as light enters the leaf,

and this condition inhibits the development of cortication that would markedly cut down the interior illumination. Neither cork nor bark may be regularly employed, so foliar organs are denied the major defenses of stems. Examination of leaves always suggests that the protective covering is reduced to the minimum so as to favor the utmost light relation. It may be that the marked efficiency of the deciduous trees is due to their large, thinly covered leaves which while most efficient through the summer become a menace in autumn and are frankly abandoned at the end of the growing season. Such tropophytes possessing a rhythmic foliage in harmony with the seasonal changes have leaves that are most susceptible to injury.

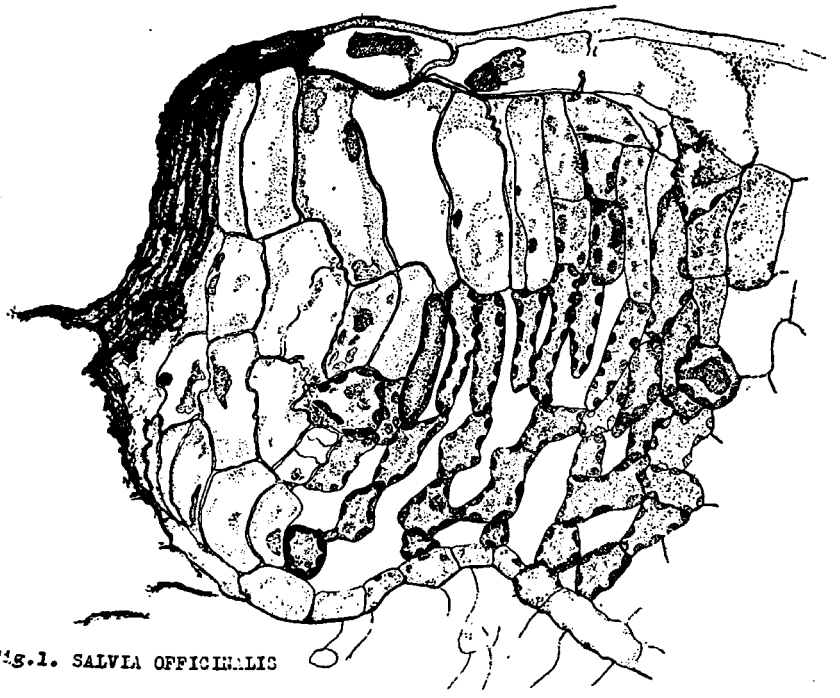

Fig. 1. SALVIA OFFICINALIS

To determine the nature of the healing tissues employed, wounded leaves were collected in early September from a number of plants, the injured areas were cut out together with a margin of normal blade, and the pieces prepared for sectioning. This material was killed in 1% chrom-acetic acid, imbedded in paraffin, and sections prepared 12 micra in thickness. Serial sections were used as large numbers of cuts had to be studied to find one showing what might be an average condition for the plant in question. Not only are the sections modified through any obliquity to the surface or margin but the structure of the blade and the nature of the cicatrice vary with relations to veins and islet-borders.

In this preliminary report are recorded the conditions found in a few of these leaves, Sage (*Salvia officinalis*), Honey-suckle (*Lonicera Sullivantii*), *Bryophyllum* sp., Red Clover (*Trifolium pratense*), Horse-radish (*Nasturtium armoracia*), *Pittosporum* sp. As may be noted there are included forms of diverse habitat and the series involves both herbaceous and woody plants. Included with plants growing here are *Pittosporum,* with firm evergreen leaf, mailed to me from Santa Monica, California, by Mr. N. D. Knupp; and also the thick leaved *Bryophyllum* cultivated in plant

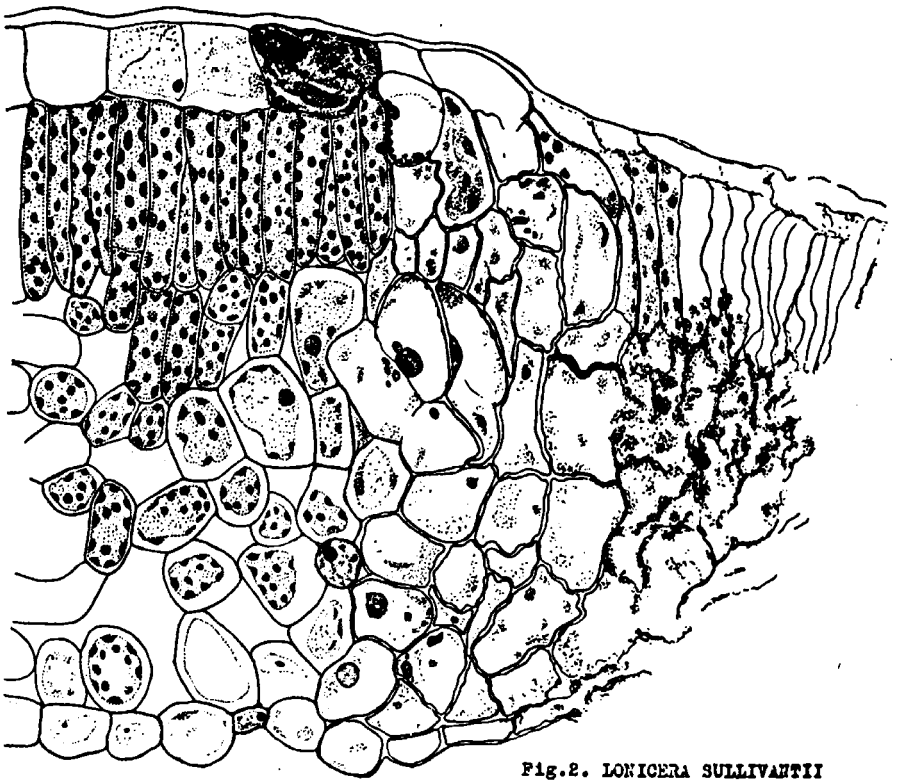

Fig.2. LONICERA SULLIVANTII

houses. With one exception the leaves had been wounded through natural causes and were from plants growing out of doors. The *Bryophyllum* leaf was from a plant in the green house which had been wounded 72 days before collection. The cicatrices shown in the figures are all apparently mature. All figures are drawn to common scale.

Following the injury of a leaf there is probably a temporary covering over the open edge due in large part to the collapsed and dried mesophyll cells which die back for some distance from the cut edge. This is often aided by over-folding of epidermal layers, particularly in the case of the softer leaves (figs. 1, 3, 4, 5).

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Fig.3. BRYOPHYLLUM SP.

In the thicker ones such as *Pittosporum* (fig. 6), the double upper epidermis seems to curve outward rather than inward, but probably most of the thinner leaves would show incurved epidermal margins. The combination of collapsed mesophyll cells and infolded epidermis thus partly protects the raw edge until by modification and mitosis cells are established which can provide the permanet recortication.

The cicatrice is usually clearly differentiated even in unstained free-hand sections. This is due in part to the modification of its walls, which are often brownish, and in part to the death of cells with consequent loss of contents. With reagents and stains

the cicatrice generally reacts differently from the uninjured cells. Especially marked is the positive reaction for lignin with phloroglucin. Tests for cutin, and suberin gave less positive results in most cases.

In contrast to the single epidermal layer found covering most leaves their cicatrices show a considerable thickness involving always more than one layer of cells and commonly several. The cicatrice itself, moreover, shows a general correlation with the structure and thickness of the leaf concerned. Disregarding the collapsed dead leaf cells the healing tissue often approximates one-third the thickness of the blade; but observation, even with the limited number studied, shows wide variation with leaves of different habitats.

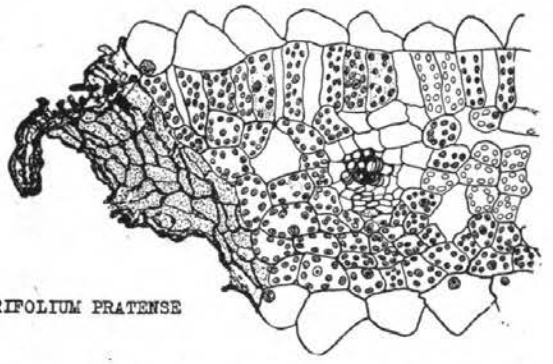

Fig.4. TRIFOLIUM PRATENSE

The nearest approach to agreement seems to be between the width of cicatrice and depth of palisade layer. In many cases the actual thickness of the cicatrice is nearly the same as that of the palisade of the same leaf (figs. 1, 2, 4, 6). In leaves where the mesophyll shows less differentiation the cicatrice is simpler and relatively thin (figs. 3, 5).

The thickness of the walls of the scar-tissue also shows general agreement with those of the epidermis. If there is a heavily cutinized epidermis the leaf is likely to develop a thicker walled cicatrice. It should be noted that in the latter such thickening is not limited to the outer walls of the cicatrice and is in no sense a reconstructed epidermis. *Pittosporum* (fig. 6) and *Lonicera* (fig. 2) present sharp contrast with Red Clover (fig. 4) or *Bryophyllum* (fig. 3).

This seeming correlation in width between palisade and cicatrice, and in character of walls between epidermis and cicatrice, might be expected on general grounds. A thick cicatrice with heavier walls would be demanded under conditions inducing much palisade and heavier epidermal walls.

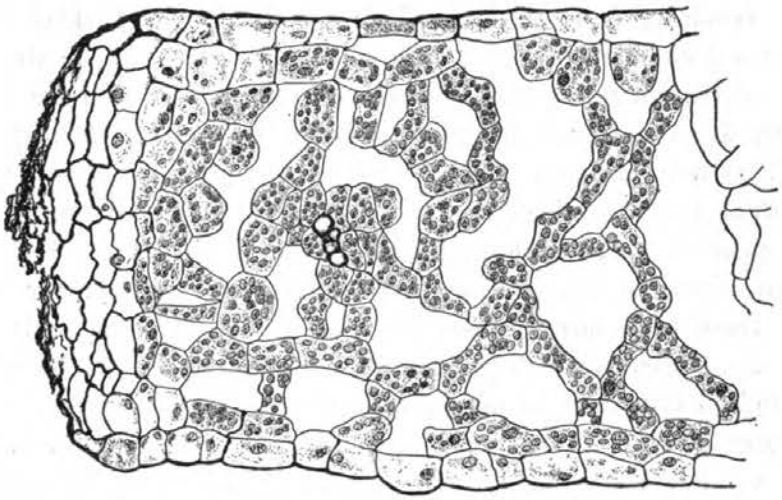

Fig.5. NASTURTIUM ARMORACIA

Certain cells of the protective tissue may become considerably enlarged as in *Salvia* (fig. 1) or *Lonicera* (fig. 2), or its tissue may remain about the same size as the average interior cells of the leaf, *Pittosporum* (fig. 6) or Horse-radish (fig. 5).

The wound tissue is largely formed by the development of new

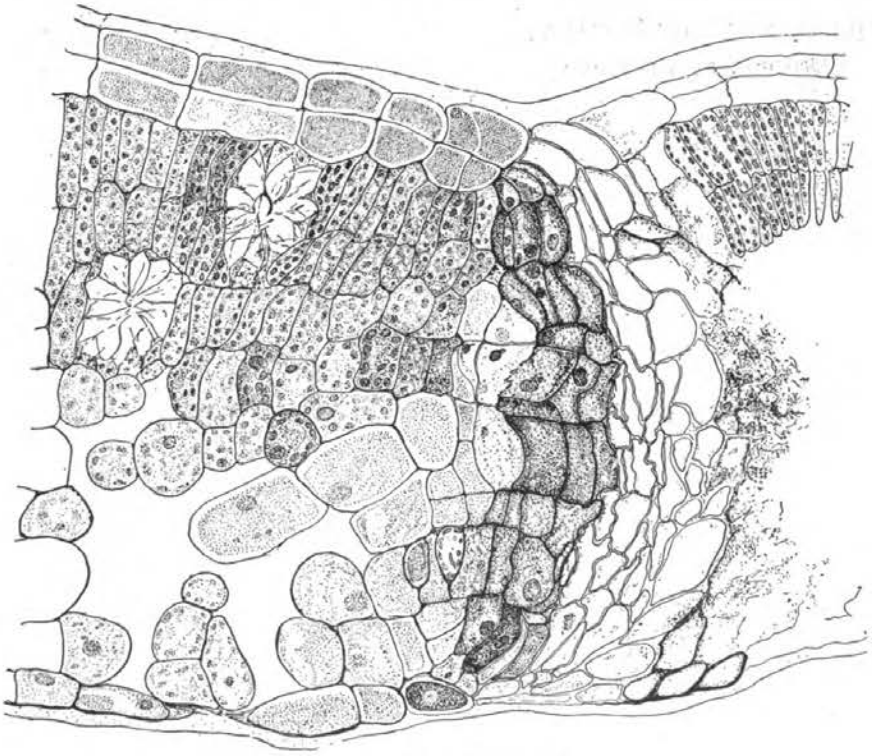

Fig.6. PITTOSPORUM SP.

cells resulting from mitoses which establish walls parallel to the wounded edge of the leaf. All cell-layers of the blade share in this work, including the epidermis in case its cells are large. There are occasional divisions of epidermal cells in *Pittosporum* (fig. 6) and *Lonicera* (fig. 2) and numerous divisions in *Bryophyllum* (fig. 3) where several cells may be derived from either an upper or lower epidermal cell.

The palisade cells divide first transversely into shorter units, and these may later divide at right angles by periclinal walls (fig. 2). Meanwhile divisions have closed the spaces in the spongy mesophyll thus completing the zone of healing tissue.

Quite striking is the appearance of a section through a porous leaf of the Horse-radish type (fig. 5), where the solid cicatrice offers strong contrast to the loose mesophyll of this leaf. Equally remarkable is the regular series of new cells bordering the wounded edge of *Bryophyllum* leaf (fig. 3) and extending from surface to surface across all of its tissues.

The completed cicatrice reveals the cambium-like behavior of those cells which by mitosis established the healing layers. Such activity seems strangely foreign to a leaf long since passed to its functional maturity.

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