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FORM AND FUNCTION OF THE LEAF -- FROM THE POINT OF VIEW OF A HERETIC

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Leaf Form and Function

Leaves are very obvious structures and have some very obvious functions. Chief among these functions are: the capturing of solar energy, during photosynthesis, with the leaf acting as the powerhouse of the plant; and gaseous exchange involving CO_2 , O_2 and water vapour, providing the raw materials of photosynthesis from the surrounding air or by the transpiration stream.

Leaves and roots are the two main interfaces of plants with their environment, in close contact, and, one hopes, closely adapted to ambient conditions. Even if we restrict ourselves to flowering plants, the range of form of leaves is enormous. Many of these variations in form can now be fairly certainly related through physical laws to function: for example, the size of a leaf can represent a trade off between the heat balance (with strong day and night differences), the need for gas exchange, and its physical strength. The physics of this is now well

worked out, and can be applied to plant breeding - an obvious example is that theory, reinforced by practice, indicates that plants with broad leaves are not suitable for hot, dry regions, or, conversely, for cold regions.

Another area of investigation that has made dramatic advances in recent years is the biological complex of interrelations between phytophagous animals - the main examples being insects - and plants. This has uncovered a wide range of plant defence mechanisms, many, because of the 'exposed' nature of leaves, expressed through leaf structure and function. The feature of glandular hairs, from wild species is used in potato breeding to introduce pest resistance. Tobacco leaves are always covered with dead insects, trapped by the sticky hairs. Disease infection is related to the position of stomata or thickness of cuticle. Plant chemical defenses, the loss of which has been critical in the evolution of crops, are perhaps even more varied and interesting.

A particular interest of mine has been the use - if I may so term it - of ants by plants as a protection device. In its simplest form ants are lured onto plants by the offer of food, and, once on the plant, remove plant-eating insects. In the simplest examples of this relation, plants produce extra-floral nectar - usually by foliar nectaries, and ants regularly visiting the nectaries keep the leaves relatively clear of destructive insects. This is found in cotton and castor-bean (and in many other plants with palmately lobed leaves, but not cassava) and very obviously in the African Tulip tree. The most sophisticated example I know of is in Cecropia. This is a secondary forest tree with large, lobed leaves. The hollow pith of the stem provides a nesting site for ants, with an access hole covered by a thin membrane. The leaf base regularly produces food-bodies containing glycogen (normally an animal product) which are rapidly removed by the resident ants. The pith is lined with a layer of cells with large concentrations of tannin - which acts as a bacteriostat to stop the debris in the nest rotting and the surfaces of the stem and leaves are covered with minute hooked hairs which provide a very secure footing for the ants - a botanical 'velcro'.

All this is interesting, possibly important, but in no way heretical. What I want to do now is to change gear, to move rapidly into an area of speculation unsupported (and possibly unsupportable) by experimental evidence and to present models for what I think are two greatly neglected properties of leaves - models that could be of great practical value in crop plant breeding, if and when they are tested.

Some years ago I was working as a taxonomic botanist on a revision of a very diverse and attractive genus from S.E. Asia, mainly herbaceous, in the family Gesneriaceae. At the level of species, a taxonomist is often working with morphological and, increasingly now, with anatomical features, including those of leaves (the diagnostic features of genera and families are usually floral characters; of species, very often leaf characters). Fortunately the herbarium was in a large botanic garden, and I began to work with the living plants in the collection (and not with the more usual dry herbarium specimens) and increasingly tried to relate the differences in leaf structure to what I knew of the habitat of each species. There were some puzzles: why did some species have a toothed leaf margin, and others an entire margin? Why were some species hairy, even when growing in the continually moist tropical montane forest? What was the function of the distinct capitate glands on the leaf surface (by the form of which you could determine whether a species came from the Americas or Asia)?

To take the first problem: how can a toothed leaf margin be an adaptive advantage to the plant? Some naive experimentation of mine established that a toothed margin increased the surface water-holding capacity of the leaf and that water could be absorbed through the pores over the vein endings at the tip of each tooth (the so-called hydathodes - thought to function as exit pores for 'excess' water leaking out of the leaf - known as guttation). The tooth/hydathode unit can act as a water holding/absorbing structure.

An advantage of this type of water absorption mechanism is obvious - liquid water enters a small pore rapidly during rain and subsequent loss, which must take place through the vapour state, is relatively

very slow. A crude analogy is what happens when you walk through a puddle of water with a small hole in your shoe: you quickly get a wet foot, and would find it a very long process waiting for your foot to dry by means of the same hole.

It can also be argued that the combination of hairs and glands on the leaf surface in the Gesneriaceae represents a water absorption system.

Hairs can serve to hold and spread water on the leaf surface (Challen, 1962). The hairs themselves or the associated glands seem capable of absorbing water. Dilute stain applied to the leaf concentrates in glands, indicating a low resistance pathway into the leaf. Some of the plants studied had a type of gland I had never seen described in the literature: when a leaf was placed in water the 4 cap-cells of each gland extruded a vesicle - apparently of protoplasm - through a microscopic pore. On drying the leaf, these vesicles retreated into the gland. It would be difficult to design a structure better adapted to water absorption. Apart from the observation that glands of this type stained, I had no experimental evidence of water actually passing into the leaf.

For the small group of plants for which I was making taxonomic revision, I had now convinced myself that the leaves showed an adaptive syndrome for water absorption: this included water holding teeth, with the associated hydathode, and water spreading hairs, with absorptive glands. This is my first model.

A wider survey, on the Dicotyledons of Trinidad, showed that hairs on the upper surface of leaves, and marginal teeth, were positively associated.

	<u>Hairs Absent</u>	<u>Hairs Present</u>
Teeth absent	524	114
Teeth present	100	152
	$\chi^2 =$	153.4

What than was known previously of foliar water absorption? A literature search showed that it was generally accepted that water, and nutrients in solution, could pass into leaves. Foliar water absorption was demonstrated as long ago as 1727 by Hales, but the potential significance of Hales detailed experiments has been ignored. In fact, foliar application of nutrients is now common commercial practice.

However, except in special cases such as epiphytes (e.g. Bromeliaceae), insectivorous plants, and aquatics with submerged leaves, there seems to have been no suggestion made that plants have leaves specifically adapted to absorb water.

The information about foliar nutrient absorption is useful, as it provides a possible explanation for why a leaf, growing in the lower layers of moist tropical forest, has water absorbing structures. The tropical forest soils are notoriously nutrient deficient, but, as a result of foliar leaching from the canopy, the rainfall passing through the canopy contains nutrients sufficient to maintain many types of epiphytes. Herbs and shrubs of the ground layer which have hairs on the upper leaf surface and/or toothed leaves commonly include members of the Gesneriaceae, Piperaceae, Melastomataceae and Begoniaceae.

The possession of marginal teeth, as part of a water absorbing structure, is an easily visible marker for comparing different vegetation types.

British evergreen and winter-deciduous species show a very highly significant difference in presence or absence of toothed margins.

	<u>Toothed</u>	<u>Entire</u>
Deciduous	79	19
Evergreen	5	23
	$\chi^2 =$	36.05

We can explain this simply by noting that the evergreen species tend to be found in the wetter, western regions of Britain, and may not

have the need for foliar water absorption.

Entire leaf margins seem to be the rule in tropical forest trees - at least in those trees that are part of the canopy - for example, out of 34 species of swamp forest in Sarawak, none had a toothed leaf margin. Again, as for temperate evergreens, we can explain the lack of foliar absorptive structures in tropical trees by assuming such trees do not need water in addition to the supplied by the roots. But - and this is a very big but - leading to my second major proposition, - we are repeatedly told in text-books (Richards, 1966, P. 244) that the leaf structure of tropical forest trees is 'xeromorphic' - a result of 'physiological drought', possibly associated with extremely poor soils. Why then, are water absorptive structures not found in such leaves?

The dogma of xeromorphy has been with us since Warming proposed it in 1909. Schimper (1903) has previously suggested the idea of physiological drought to account for the supposedly xerophytic features in plants of wet environments, roughly comparable with using the retrograde motion of the planets as evidence for an Earth-centered universe.

I propose, quite simply, that the supposed xeromorphic features of leaves have little or nothing to do with drought, but are adaptations to reduce the loss of nutrients from the leaf through foliar leaching during rain. Put in another way, plants growing in reasonably high rainfall areas and in nutrient poor soils will have evolved leaf characters to reduce foliar leaching. The previous leaf model was established by looking at individual characters and searching for an explanation of function that could explain the association of characters; that is, arguing from structure to function. For the second model, we'll follow the opposite approach, arguing from function to structure.

How should we go about designing a model leaf adapted to reduce foliar leaching (while maintaining the necessary ability for gas exchange and energy capture)? Features of my first model - teeth, hydathodes, glands and hairs, at least on the upper surface - would

be excluded, as these features permit water holding and absorption by the leaf, and this would increase the chance of leaching loss of nutrients.

We could expect at least some of the following features:

- entire margin
- vein system closed, that is, without hydathodes
- absence of hairs, at least on the upper surface
- absence of (absorptive) glands
- thick cuticle, possibly waxy
- low surface to volume ration, that is, a relatively thick leaf
- stomata on lower surface only (to protect the physiologically active guard cells from contact with water)
- erect or hanging leaves to reduce rain interception (this obviously has to be balanced against the light requirements of the plant)
- evergreen (to phase the loss of nutrients by litter fall throughout the year)

To complete the circular argument: are these leaf characters found in vegetation known to grow on nutrient poor soils?

Tropical Rain Forest

A comparison of 42 tree species of Evergreen Seasonal Forest with 40 weedy species in Trinidad showed the following:

	<u>Forest</u>	<u>Weedy</u>
Stomata on upper surface	0%	80%
Hairs on upper surface	5%	72%
Glands on upper surface	5%	50%
Marginal teeth	5%	55%

The forest and weed leaves respectively, would correspond closely to my model 2 and model 1 leaves. The suggestion here is that model 2 leaves, in wet, nutrient deficient conditions, are adapted to resist foliar leaching, while model 1 leaves (here on good agricultural land)

will have access to sufficient soil nutrients and will be adapted for foliar absorption of rainfall (model 1 leaves of the ground layer of forest, on nutrient poor soils, will be adapted for foliar absorption of nutrients contained in the throughfall).

British Evergreen Trees

We can now return to the predominantly entire-margined evergreen flora of Britain and offer a revised explanation that the evergreen leaf structure is an adaptation to soil nutrient deficiency in the wetter, western areas favoured by evergreen vegetation.

Australian Sclerophyll Scrub

This is thought to have evolved in conditions of aridity and of low phosphate. Described by Schimper as "evergreen, composed chiefly of shrubby plants with stiff, dry simple, entire leaves, which are arranged obliquely or even parallel to the light, and possess a dull bluish upper surface, usually due to particles of wax or resin: if they display hairs at all, these are usually on the undersurface only".

Although the plants are growing in arid conditions the description fits fairly well with the model indicating that leaching may be important even with low rainfall.

There are other points of interest about Australian vegetation. Many Australian acacias have phyllodes, mimicking entire leaves, instead of the bipinnate leaves characteristic of the sub-family and found in all African acacias. One assumes that a feathery, bipinnate leaf is not easily adapted to resist foliar leaching. This may explain why Leucaena does not grow well on acid, nutrient poor soils.

Eucalypts can have vertically hanging leaves, with minimum rainfall interception. Such leaves are slightly sickle shaped, to reduce flapping in the wind. I think the enormous success of Eucalyptus outside Australia is not due to their drought tolerance, but to their

resistance to foliar leaching, which gives them the ability to grow on poor soils.

From the only 18 flowering plants known from the end of the Cretaceous, 7 are of the families Ericaceae, Casuarinaceae and Myrtaceae, which characteristically have my model 2 leaves, suggesting that even in the Cretaceous, plants were growing on nutrient poor soils.

Cerrado

I have not looked at cerrado vegetation, characteristically growing on nutrient poor soil, but as a prediction, model 2 leaves should be found.

We now have a house build of loose bricks, some of dubious quality, needing the cement of experimentation to hold it together. But is meaningful experimentation possible? A thick cuticle which reduces foliar leaching will reduce water loss. A marginal hydathode that absorbs water will also allow water out during guttation. There will be many habitats where the extreme types are not found, leading to problems of the interpretation of intermediates.

If these ideas have any merit whatever, then what are the implications for plant breeding?

There may be conceptual errors in present breeding strategy. Some examples show how this can happen. If selection for drought resistance is through attempting to increase the hairiness of leaves, the result may be less ability to grow in dry conditions, if the hairs are of the type in leaf model 1. These hairs are considered to be water holding and associated with other water absorbing features. These will provide pathways for water loss from the leaf and only in certain circumstances (regular light rain, mist or dew) will the leaf water balance be improved.

In another example, increasing the cuticular wax of a plant may

only incidentally reduce water loss; a far more important effect could be a reduction in foliar leaching - a response that will be overlooked unless specifically searched for.

Resistance to foliar leaching as an adaptation to nutrient poor soils will probably be the most important factor to aim for in breeding programmes. This can be achieved by direct screening on poor soils and/or selecting plants with characters thought to be leaching resistant - that is, model 2 leaves.

The impression I have is that model 2 leaves are characteristic of climax vegetation - possibly because in climax vegetation a large part of the nutrients are locked up in the biomass. However, agricultural ecosystems are by definition not climax vegetation. There may therefore be a need for breeding crops with leaf features permitting foliar absorption, either to increase the availability of water to the plants, or, if we ever follow the 'eco-farmers' into the forest, to increase the foliar absorption of nutrients in the throughfall.

The CIAT mandate crops are at neither extreme of leaf type. Marginal teeth are very rare in legumes, so our beans and forage legumes do not have this very obvious feature. Cassava and beans have some water holding hairs, especially over the veins, where the leaf surface is channelled. An intermediate situation is a useful one, as then it is possible to push the leaf form in either direction.

I'll conclude with mentioning some puzzles I came across in looking at leaf form.

C₄ plants always seem to have stomata on both surfaces. Trees, in contrast, are almost entirely with stomata on the lower leaf surface only. This reminds me of an Andean genus Bomarea (Amaryllidaceae) which always has upside-down leaves.

Leaves with toothed margins tend to have long petioles (although I have no actual measurements for this).

Epidermal cells of model 1 leaves tend to have wavy margins in surface view, while in model 2 leaves the epidermal cells have more or less straight margins.

I'll leave you to speculate on these - I've done more than my share!

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