DRIPTIPS, TEETH AND PETIOLES AS LEAF MODIFIERS

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INTRODUCTION

Major geological periods from 100 to 15 Ma (million years ago) in New Zealand's complex geological history are represented by sedimentary deposits formed on land. Many of these sediments include assemblages of plant fossils, including leaves. Leaves are exposed to the weather, and use their DNA memory to form the most appropriate shape for particular parts of the leaf while undergoing cell division, a process known as *cladogensis.* Because of this, the opportunities that New Zealand provides for palaeobotanical studies also lead to information about past climates.

In the mid Cretaceous (100 Ma), New Zealand formed a coastal part of the southern mega-continent Gondwana, adjacent to the future Australian and Antarctic landmasses (Daniel 1989). New Zealand rifted first from Antarctica, and then from Australia in the late Cretaceous, as the Tasman Sea opened 80 to 60 Ma (McLaughlin 2001). Australia remained connected to Antarctica by the South Tasman Rise until approximately 55 Ma. The separation of these three landmasses by the end of the Eocene, and the subsequent opening of the Drake Passage between South America and the Antarctic Peninsula during the Oligocene (about 35-28 Ma) allowed the South Circumpolar Current (both ocean and wind) to develop. The Antarctic continent reached its present geographical isolation by the Pliocene, about 5 Ma (Hill et al. 1996). Prior to the break-up, the latitudinal ocean currents around Antarctica and Australia had mixed polar and tropical waters, thereby contributing to warmer conditions over a wider range of latitudes than at present. Today, these wind and water currents isolate Antarctica from New Zealand, and emphasise their respective continental and marine climates.

BROAD LAMINAS

Leaves achieve maximum light collection by expanding their surface without increasing their bulk. The extinct, arborescent seed fern *Glossopteris,* living at high latitudes during the Permian, already had an expanded lamina (leaf blade), but with only one order of anastomosing veins (i.e., veins that repeatedly divide and then rejoin). The dicots, however, developed a well-organised, ramifying (i.e., branching with free endings) complex of many orders of veins, thereby allowing the lamina to extend laterally without losing the close contact between conducting and supporting tissue and photosynthetic cells. This was achieved by increased activity of intercalary meristem (i. e., meristem that has been 'left behind' between zones of fully developed tissue) at the leaf edge, differentiating to give different kinds of tissue.

Esau (1977, p. 338) states that leaves expand laterally by anticlinal division (i.e., dividing along lines perpendicular to the leaf margin) of parallel layers of cells, called the "plate meristem", which constitute a major part of the intercalary growth by means of which the leaf reaches its mature size. Doyle & Hickey (1976), on the basis of their study of fossil leaves from the Potomac Group (Fredricksburg, Virginia, eastern U.S.A., of Barremian – Cenomanian age (i. e., mid Cretaceous), hypothesized a xeromorphic leaf (i.e., of a form characteristic of dry environments) intermediate in shape between the compound leaves of cycad-like gymnosperms and dicot leaves of simple outline, that had reduced activity in their marginal meristem. Thereafter, the marginal meristem became associated with progressive differentiation of second order veins. Secondary expansion by intercalary meristems was accompanied initially by progressive differentiation of ramifying third and higher order veins and ultimate veinlets, and later by simultaneous differentiation of percurrent (i.e., joining other third and higher order) veins to each other, and ultimate veinlets. Myrtaceae have an intramarginal vein joining the tips of secondary veins.

Isebrands & Larson (1980) showed that in *Populus deltoides* the midrib region of a developing leaf is a composite structure consisting of several discrete procambial bundles (i.e., precursors to the conducting strands) which differentiate progressively towards the leaf apex. The bundles are preceded by meristematic regions. Each bundle eventually diverges obliquely into the lamina giving rise to the secondary veins which develop sequentially downwards from the leaf tip. Subsequent differentiation and maturation of secondary veins occurs within the lamina. Both lamina elongation and expansion continue until the leaf is mature. Thus the basic framework of secondary veins that allows the lamina to extend laterally without becoming thicker is developed very early in the life of dicot leaves, through intercalary meristems.

In contrast, the monocots, which developed in equatorial and temperate latitudes of North Gondwana, have narrow leaves with parallel veins and cross-links; only occasionally are broader leaves with higher orders of venation developed, as in the Araceae, e. g., *Philodendron, Arum.*

APEX SHAPE

Acute apices typically dominate in wet cool climates, whereas rounded apices predominate in dry hot, and dry cool climates (Wolfe 1993). "Species" (defined according to their leaf shapes rather than their evolutionary relationships) with blunt or rounded apices (as opposed to acute to acuminate) are also more common in monsoon forests than in rainforests (Greenwood 1996). A high proportion of species with attenuated apices, including driptips, indicates high rainfall on a daily basis. Driptips tend to be a lowland tropical forest phenomenon, and occur especially on understorey plants (Fig. 1). However, some canopy trees without driptips may have saplings with them (Longman & Jeník 1974).

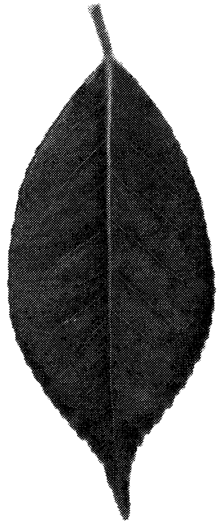

Fig 1: outline of leaf with drip tip.
Photo: P. E. Horn

Dean & Smith (1978) removed driptips from juvenile leaflets to test both thigmonasty (touch-sensitive movements) and nyctinasty (day/night movements) in relation to speed of moisture removal, especially under high rainfall. They showed that "drainage towards the acuminate leaf tips can significantly reduce both the amount of water retained on the upper surface, and the time required for complete drying".

Baker-Brosh & Peet (1997) showed that teeth (and some lobes) provide sites of precocious photosynthesis in temperate forest tree leaves of deciduous habit. They claim that "The adaptive significance of driptips, ...on leaves of tropical forest trees and lianas, ...has never been completely resolved". However, Raciborski (1900) & Ellenberg (1985) have described precocious driptip development also to be the norm, with "only a small proportion maturing with or after the primary leafblade". They go on to explain the different leaf parts as the result of differential leaf expansion, leading to "limiting the period of vulnerability to herbivory" of teeth and driptips.

Williamson (1981) suggests driptips may be an adaptation to minimise splash erosion, by reducing the size of drips. Big drips cause soil loss by sheet erosion, especially on soils with shallow litter layers, which is typical of tropical forests. I think this explanation is the best so far.

LEAF MARGIN

The most widely used physiognomic indicator of past climates, first developed by Bailey & Sinnott (1916), is the nature of the leaf margin. The percentage of leaf species with entire margins (i.e. margins without serrations) is believed to reflect both temperature and rainfall. Entire-margined leaves generally indicate moist tropical and sub-tropical environments, while non-entire margins predominate in cooler climates.

Teeth along the leaf margin create turbulent airflow and increase evaporation of water from the tips of the teeth (Mosbrugger & Roth 1996). Lobed leaves and those with toothed leaf margins are common among species colonising environments disturbed, for example, by storms or fire, and in strongly seasonal environments (Givnish 1984, 2002, Upchurch & Wolfe 1987). Summer droughts have a marked effect on leaf margin type. Where there is a need to conserve water, as in dry cool environments, not only are there fewer species with teeth, but the teeth are blunter, being compressed into the leaf margins, forming glands. These glands are interpreted as hydathodes (Lersten & Curtis 1982), which allow continued evaporation to maintain the transpiration stream when stomata are closed due to dry air. These marginal characters, together with broad-leaved evergreenness, suggest evaporation rates that are at least seasonally high (Wolfe 1993).

PETIOLATION

Of equal importance to lamina shape in achieving maximum light collection is the ability to adjust the orientation of the lamina with respect to the stem, in order to maintain it perpendicular to the incident light. This was achieved by development of a petiole.

Kaplan (1973) suggested that, in basal plan, the monocot leaf is of two parts, that furthest from the stem being unifacial (as in the cylindrical leaves of many rushes) and the proximal part being a bifacial sheath, i. e., the part adjoining the stem has upper and lower surfaces differing from each other. In monocot leaves that are more sharply jointed, the proximal section differentiates into a lamina and a "petiole" that sheaths the stem, while the distal section becomes rudimentary. He has shown, on the other hand, that the petiole of the dicot leaf develops from intercalary meristem between an upper (blade) zone and a lower (base) zone, either or both of which may be extended laterally. Isebrands & Larson (1980) showed that in the development of *Populus deltoides* leaves, of the eight secondary veins the three nearest the tip of the leaf begin to differentiate before the petiole begins to develop. This suggests that the petiole develops after and independently of the lateral expansion of the lamina.

Petioles that are rounded in cross-section and manoeuvrable are unique to dicots but absent in some e. g., *Dracophyllum.* In other plant groups a "pseudopetiole" may be developed by narrowing of the proximal part of the leaf, e. g., in *Agathis. Ginkgo biloba* has been described as having a distinct petiole (Sporne 1974), but actually it has a pseudopetiole produced by inrolling of the blade margins in the proximal part, while a more expanded lamina in the distal part is achieved only by greater dichotomy (branching) of the veins. Fossil *Ginkgoites* leaves from the Clarence deposits (Daniel 1989, 2004) lack a distinct petiole and have few or many dichotomies, the lamina width varying accordingly. Those from the Victorian Cretaceous (Douglas 1970) have distinct pseudopetioles and many vein dichotomies. Thus the degree of "petiolation" within *Ginkgoites* of similar geological age is variable. Flexible petioles allow leaves to flutter in gentle wind to resist tearing, and bend in strong wind to minimise drag (Vogel 1993).

The leaf base, proximal to the petiole, is swollen (especially in deciduous trees) and, with age or decreasing day length in autumn, a new intercalary meristem forms a cork cambium layer which retains phloem strands longer than xylem strands, thereby allowing resorption of nutrients, etc. As this zone thickens, it gradually becomes a zone of dehiscence progressing downwards.

CONCLUSIONS

Driptips serve to reduce soil sheet erosion, teeth serve to increase the speed of air flow over the hydathodes, and petioles have evolved to be able to adjust with best effect to incident light. Petioles are also a convenient place to form a layer of cork cambium to maximise retention of nutrients before dropping the leaf. Thus, modification of the leaf physiognomy to suit the environment increases the ability of the leaf to carry out its functions.

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