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Which common indices of sclerophylly best reflect differences in leaf structure?[1]

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Abstract: When describing the sclerophyllous nature of leaves, two indices are most commonly cited: fibre:protein ratio (FPR), better known as the Loveless sclerophylly index; and leaf mass per unit area (LMA), or its inverse, specific leaf area (SLA). Here, we assess the relative importance of these two indices in accounting for changes in leaf structure, the primary basis for variations in sclerophylly. FPR compares structural (*i.e.*, lignin and cellulose [crude fibre]) to non-structural (*i.e.*, protein ≈ protoplasm) leaf material, on the basis that increasing sclerophylly is associated with a greater contribution of crude fibre and smaller contribution of protein to total dry weight. However, raising the crude fibre content is just one way of increasing sclerophylly, and a decrease in the nitrogen content (*i.e.*, protein) does not contribute directly to the impression of leaf hardness. While FPR lacks a clear anatomical basis, it may provide a biochemical interpretation of sclerophylly. In contrast, LMA is the cross product of leaf thickness and leaf density, two (often independent) attributes that are linked to different components of a leaf's anatomical/structural attributes. We show that FPR and LMA are often poorly correlated and conclude that LMA is a more useful measure of sclerophylly, especially when thickness and density are known.

Keywords: sclerophylly, leaf mass per area, fibre:protein ratio, leaf structure.

Résumé : Deux indices sont souvent utilisés pour caractériser le degré de sclérophyllie des feuilles : le rapport fibres:protéines (RFP), mieux connu comme l'indice de sclérophyllie de Loveless, et la masse foliaire par unité de surface (MFS), ou son inverse la surface foliaire spécifique. Nous évaluons ici la capacité de ces deux indices à expliquer les changements de la structure foliaire à la base même des variations de sclérophyllie. Le RFP permet de comparer le matériel structural (lignine et cellulose) au matériel non structural (protéines) de la feuille, en présumant qu'une augmentation de la sclérophyllie est associée à une plus grande contribution des fibres et une plus faible contribution des protéines à la masse totale sèche. Cependant, accroître le contenu en fibres n'est qu'une des façons d'augmenter la sclérophyllie et une diminution du contenu en azote (en protéines) ne contribue pas directement à la résistance de la feuille. Bien que le RFP ne se réfère pas à une origine anatomique claire, il peut fournir une interprétation biochimique de la sclérophyllie. Par contre, le MFS est le produit de l'épaisseur de la feuille et de sa densité, deux caractéristiques souvent indépendantes et associées à des composantes différentes de l'anatomie et de la structure de la feuille. Nous démontrons que le RFP et le MFS sont souvent peu corrélés et concluons que le MFS est une mesure plus utile de la sclérophyllie, surtout lorsque l'épaisseur et la densité de la feuille sont connues.

Mots-clés : sclérophyllie, masse foliaire par unité de surface, rapport fibres : protéines, structure foliaire.

Introduction

Sclerophylly is a term used to describe leaves that are tough, stiff or leathery in texture (Schimper, 1903; Seddon, 1974). Literally meaning 'hard-leaved', sclerophylly was conceived as a purely descriptive term, requiring some measurable index for inter- or intraspecific comparisons of degree of sclerophylly. Clearly, a good index of a biological concept must accurately reflect the variable, be suitable for all material under study, and be relatively easy to measure. Various indices of sclerophylly have been proposed, including leaf moisture content (Loveless, 1961), dry matter content (Kalapos, 1994), leaf thickness (Mooney *et al.*, 1982), leaf fracture toughness (Lucas & Pereira, 1990), and anatomical measurements, such as relative palisade thickness (Grubb, 1986). However, the fibre:protein ratio (better known as the Loveless sclerophylly index) and leaf mass per area (LMA), or its inverse specific leaf area (SLA), are by far the most widely used. The assumption underlying these measures is that a change in their magnitude coincides with a matched change in the level of sclerophylly. But how accurate are these indices in quantifying sclerophylly? How well do they take into account variations in leaf structure, the primary basis for variations in sclerophylly? It is not the intention of this paper to review the background to all indices of sclerophylly cited in the literature, but rather to summarise the features of the fibre:protein ratio (FPR) and LMA (or SLA) that underlie their usage as measures of sclerophylly, and comment on their usefulness in interpreting the structural changes associated with sclerophylly.

Fibre: Protein ratio

This measure of sclerophylly was proposed by Loveless (1961) after he compared leaf chemistry data between species differing in leaf texture. Originally, he thought that crude fibre content (that part of dry matter insoluble in strong acid and alkali) would provide the most useful comparative measure of sclerophylly, which he actually believed was best represented by leaf dryness.

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However, when comparing a selection of 'mesophytic' and 'sclerophyllous' leaves, Loveless found that differences in fibre concentration of the two leaf types were not great, and could be partially explained by the fact that crude fibre per dry weight does not take into account other chemical components of the leaf. Assuming that fibre was an important component of sclerophylly, Loveless proposed that any estimate based on fibre should be compared with a non-structural component, either leaf fresh weight or some measure of leaf protoplasm. Leaf fresh weight was dismissed because it is unstable, depending on weather at time of harvest and subsequent treatment of the leaf. Crude protein content (calculated as nitrogen concentration multiplied by 6.25) was considered to reflect the part of dry leaf tissues that does not contain fibre. The ratio of crude fibre to crude protein content (FPR) was then used as the standard measure of sclerophylly by Loveless (1961; 1962). FPR has also been used as a measure of leaf palatability to herbivores (Waterman *et al.*, 1988; Choong *et al.*, 1992). However, the concepts of palatability, digestibility and sclerophylly should not be confused (Turner, 1994a).

Does fibre content adequately reflect differences in leaf properties as they affect sclerophylly? This might be true if cell wall thickening and the presence of sclerified tissues was the only means of increasing sclerophylly. But there are alternative ways of increasing sclerophylly that do not necessarily involve an increase in crude fibre or a decrease in protein. This can be achieved by decreasing the size of cells without changing cell wall density or cytoplasmic content, or by impregnating existing cells with extra cutin or crystals, in place of cellulose or lignin. Increasing the number or size of cells may change leaf dimensions, independent of their histochemistry. Such anatomical changes may be accompanied by a reduction (Groom, Lamont & Markey, 1997) or increase (Shipley, 1995) in leaf area, but more certainly by increases in leaf thickness and/or density. Independent of area or density, a thicker leaf will be tougher than a thin one.

Leaf mass per unit area

LMA (previously known as leaf specific mass) is calculated as leaf dry mass divided by projected leaf area. The inverse of this is SLA. We are not aware of the history of these indices, but Mooney *et al.* (1977) used LMA as an index of sclerophylly over 20 years ago. Both LMA and SLA may be considered the products of leaf density and thickness (Witkowski & Lamont, 1991), which are directly related to structural properties of the leaf. LMA has an advantage over SLA in that it is directly, rather than inversely, related to sclerophylly.

Witkowski & Lamont (1991) noted that variations in leaf density may be the result of differences in: (*i*) thickness and density of the cuticle and cell walls, (*ii*) inclusions in the cells (starch grains, crystals), and (*iii*) extent and abundance of air spaces, sclereids, fibre groups and vascular bundles. Variations in leaf thickness may be due to variations in leaf shape, number of layers and length of palisade cells, width of rest of mesophyll, epidermis, and hypodermis, and placement of veins. Thus, the two components of LMA represent different structural aspects of the leaf and should be independent. This is demonstrated in Figure 1: LMA values were not significantly different within leaf age classes for two co-occurring *Banksia* species, but the reasons were different. *B. petiolaris* has very thick leaves of relatively low density while *B. baueri* has thinner leaves of high density. Leaf density increased with age in both species while thickness remained static. Thus, for these two species, LMA, density, and thickness are not correlated.

Bulk density has been shown to account for variations in LMA for a number of species, with most studies conducted on grass species (Garnier & Laurent, 1994; van Arendonk & Poorter, 1994). Most studies that relate changes in LMA to leaf thickness failed to calculate density from the data (Abrams, 1994). Witkowksi & Lamont (1991) showed that for nine shrub species inhabiting a range of soil types, the

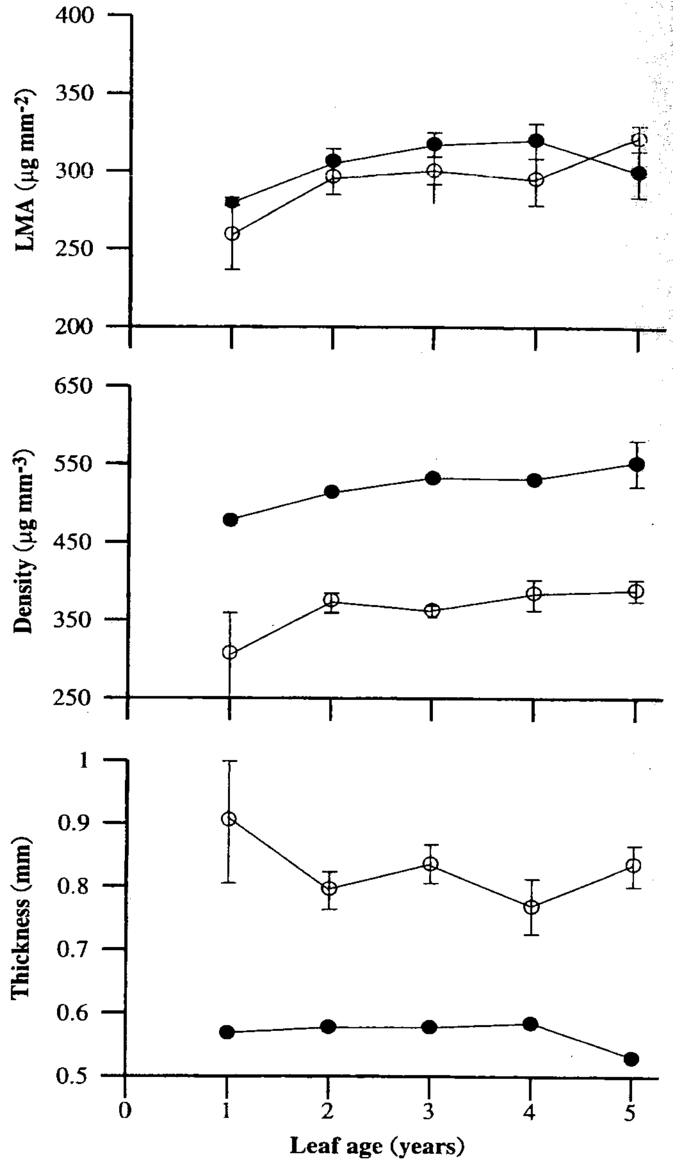

FIGURE 1. Variations in leaf mass per area (LMA) and its components, leaf thickness and density, in co-occurring *Banksia petiolaris* (open circles) and *B. baueri* (closed circles) in one- to five-year-old leaves. Bars are SE for 10 replicates (Witkowski *et al.*, 1992).

LMA of three species was linearly correlated with density, five with thickness, and one with both density and thickness.

Comparing the two indices

There are two issues to be considered: (*i*) whether FPR and LMA (or their components) are always correlated, and (*ii*) if they are not, which is a more valid index of sclerophylly? Omitting correlations between subsets of the data, there were no overall relationships between FPR and SLA or leaf thickness for monocots and dicots in southern Australia (Specht & Rundel, 1990). For a much larger data set from many parts of the world, there was no correlation between SLA and FPR or crude fibre, but there was between SLA and nitrogen (Turner, 1994b). For 42 tree species, Choong *et al.* (1992) showed that FPR was correlated with SLA and density but not with thickness, and that SLA was correlated with nitrogen but not with fibre. We conclude that FPR and LMA are poor indices of each other, especially when attempting to interpret the results in terms of their components.

Although Loveless (1961) proposed that protein content provided an independent basis for comparing fibre contents, this and subsequent work have usually shown a (negative) relationship between the two (Steubing & Albardi, 1973; Specht & Rundel, 1990). Where they are statistically independent, there is the problem that a high FPR could be due to a high fibre concentration (directly related to sclerophylly) or a low protein content (not directly related to sclerophylly). FPR may, however, provide us with a biochemical interpretation of sclerophylly. Highly sclerophyllous floras are usually associated with nutrient deficient soils, particularly those low in phosphorus and nitrogen (Beadle, 1966; Lamont, 1994). Because phosphorus and nitrogen are essential requirements for protein synthesis, carbon-rich metabolites which may have been used to form protein are therefore diverted to form other compounds, including cellulose and lignin. As a result, FPR may be viewed as more of a measure of metabolic efficiency than of sclerophylly. In addition, a nutritive interpretation is of little value if varying levels of sclerophylly are due to differences in light or water availability rather than nutrient availability (Oertli, Lips & Agami, 1990; Groom & Lamont, 1997).

LMA responds only to structural changes rather than to both structural and chemical changes. It is much more ecologically useful that nitrogen is correlated with the measure of sclerophylly (see above) rather than being a component of it, so that a common cause (low nutrients) is distinguished from its morphological effect. At best, FPR represents the density component of sclerophylly (as do the water/dry matter approaches) but ignores leaf (essentially mesophyll) thickness as an essential component of it. For example, it is generally agreed that adult and needle leaves are more sclerophyllous than conspecific seedling and broad leaves. Their LMA values support this impression, but the reason is that adult and needle leaves are thicker rather than denser than conspecific seedling and broad leaves (Groom, Lamont & Kupsky, 1994; Groom, Lamont & Markey, 1997).

The major drawback with LMA is that its measurement is based on leaf mass and area, and yet its interpretation as a measure of sclerophylly requires a knowledge of the two other components of mass: thickness and density (Witkowski & Lamont, 1991; Turner, 1994b). Conceptually, it assumes that these two pathways are of equal weight in influencing a change in the degree of sclerophylly. For example, the degree of sclerophylly may be doubled either by doubling density or thickness (or a combination of the two). In this regard, it is no different from FPR. Thickness is seldom determined (although it is simply done with vernier calipers or a spring-loaded screw gauge) and density almost never (although it is simply calculated as LMA/thickness).

There may be practical problems with flattening out broad leaves to obtain area, whereas ericoid leaves are best treated as cylinders and a correction factor applied (Witkowski & Lamont, 1991). When a prominent midrib is involved, the lamina should be used for all measurements, and judgement about leaf thickness may be needed when scattered protruding veins are involved. When shrinkage or drying is likely (*e.g.*, immature or succulent leaves) it is essential that thickness and area are measured on fresh (turgid) material before adequate drying. It is important that the density of such leaves be calculated on the original dimensions to ensure it is not overestimated. In this regard, thick leaves that collapse on drying cannot be considered very sclerophyllous, although the hydrostatic pressure associated with their turgidity may give the impression of reasonable hardness.

Generally, LMA and its components are simple to measure, may be measured on an individual leaf basis for all leaves, the methods are less destructive and expensive than other techniques, and replication and subsampling are easier. In addition, density and thickness may also be considered as (Charles-Edwards *et al.*, 1986) contributors to photosynthetic potential, as well as essential indices of palatability (Waller & Jones, 1991). In the absence of a thorough anatomical leaf analysis, we advocate leaf mass per unit area, together with a knowledge of its two components, thickness and density, as the best currently available measure of sclerophylly.

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