Oecologia (2000) 123:158–167

**Cheryl Edwards · Jennifer Read · Gordon Sanson**

# Characterising sclerophylly: some mechanical properties of leaves from heath and forest

Received: 4 March 1999 / Accepted: 22 November 1999

**Abstract** Although sclerophylly is widespread through the world and is often the dominant leaf-form in mediterranean climates, the mechanical properties of sclerophyllous leaves are poorly understood. The term "sclerophyllous" means hard-leaved, but biologists also use terms such as tough, stiff and leathery to describe sclerophyllous leaves. The latter term has no precise definition that allows quantification. However, each of the former terms is well-defined in materials engineering, although they may be difficult or sometimes inappropriate to measure in leaves because of their size, shape or composite and anisotropic nature. Two of the most appropriate and practically applicable mechanical properties of sclerophyllous leaves are "strength" and "toughness", which in this study were applied using punching, tearing and shearing tests to 19 species of tree and shrub at Wilson's Promontory, Australia. The results of these tests were compared with leaf specific mass (LSM) and a sclerophylly index derived from botanists' ranks. Principal components analysis was used to reduce the set of mechanical properties to major axes of variation. Component 1 correlated strongly with the botanists' ranks. Overall, leaves ranked as sclerophyllous by botanists were both tough and strong in terms of punching and tearing tests. In addition, tough and strong leaves typically had high toughness and strength per unit leaf thickness. There was also a significant correlation between component 1 and LSM. Although more detailed surveys are required, we argue that sclerophylly should be defined in terms of properties that have precise meanings and are measurable, such as toughness and strength, and that relate directly to mechanical properties as implicit in the term.

**Key words** Leaf specific mass · Biomechanics · Leaf strength · Leaf toughness · Sclerophylly

C. Edwards · J. Read (✉) · G. Sanson
Department of Biological Sciences, Monash University,
Clayton, Vic. 3168, Australia
e-mail: jenny.read@sci.monash.edu.au
Fax: +61-3-99055613

## Introduction

Sclerophyllous leaves have been described as hard, tough, stiff and leathery (Schimper 1903; Seddon 1974; Turner 1994a). The term "sclerophyll", meaning "hard leaf" (Greek *skleros* hard, *phullon* leaf), was initially coined by Schimper (1898, 1903) to distinguish xeromorphic plants with leathery leaves from those exhibiting succulence or leaflessness. Sclerophylly is particularly widespread in areas with a mediterranean climate, such as South Africa, central Chile, southern Australia, California and the Mediterranean region. The "heath" vegetation of these areas is typically a dense scrub dominated by woody evergreen sclerophyllous species (Mooney and Dunn 1970). However, sclerophyllous vegetation is also common on low-nutrient and ultramafic soils in other climate types, including regions of high rainfall from temperate to tropical latitudes (e.g. Jackson 1968; Jaffré 1980; Turner 1994b). Nor is sclerophylly limited to shrubs, with many forest and woodland trees having leathery or hard leaves.

The functional significance of sclerophylly remains controversial, with three main groups of hypotheses proposed to explain its adaptive significance. These centre around sclerophylly as (1) an adaptation to seasonal water deficits (e.g. Schimper 1903; Oertli et al. 1990), (2) an adaptation to, or consequence of, low-nutrient soils (e.g. Loveless 1961, 1962; Beadle 1966), and (3) enhancement of leaf longevity by leaf protection, thereby increasing leaf carbon gain per unit investment (e.g. Chabot and Hicks 1982; Grubb 1986; Turner 1994a). The last group of hypotheses includes those relating sclerophylly to anti-herbivore defence and is not necessarily mutually exclusive of the first two groups.

Despite sclerophylly being defined in terms of mechanical properties, little research has been undertaken on the mechanical properties of sclerophyllous leaves and on the characters contributing to these properties. Instead, sclerophylly has been most often measured indirectly as the ratio of crude fibre to crude protein (index of sclerophylly, Loveless 1961, 1962) and by leaf specific mass (LSM) (e.g. Witkowski and Lamont 1991). Sclerophyllous leaves commonly are thick, with thick cuticles and outer epidermal walls and with abundant sclerification, particularly of the vascular bundle sheaths (e.g. Schimper 1903; Beadle 1966; Grubb 1986). They have high bulk density and thickness as components of LSM (Witkowski and Lamont 1991). However, some of these characters are not restricted to hard-leaved plants, and not all hard-leaved plants possess all these characters. In addition, when sclerophyllous leaves have many of these characters, the extent to which each of these contributes to the mechanical properties is not clear.

However, the major problem is that no independent standard based on the mechanical properties that define, and are thought to characterise sclerophylly, has been erected, i.e. there is no currently accepted direct measure of sclerophylly. Most studies of leaf mechanical properties have not been directed at sclerophylly per se, and therefore have had relatively little influence on an understanding of this leaf form and its functional significance. Some mechanical properties of sclerophyllous leaves have been examined in the pioneering work of Choong et al. (1992) and Turner et al. (1993). The latter is the only work known to us that has examined leaf mechanical properties in any detail in plants from mediterranean-type climates where sclerophylly predominates. The paucity of studies may be partly attributed to the difficulty of measuring the mechanical properties of leaves. Such biological materials are commonly a complicated anisotropic, composite cellular matrix of various interfaces, with complex influences on mechanical properties (Atkins and Mai 1985; Vincent 1982, 1990; Niklas 1992).

Since sclerophylly means hard-leaved, hardness is an obvious property to measure. However, “hardness” can have different meanings in different fields of study. It can refer to resistance to penetration, wear, scratching or cutting and has also been used as a measure of flow stress (Mott 1956; Shaw 1973). The wide variety of hardness tests that are applied to surfaces may not reflect the properties of the sub-surface material. Moreover, this sense of hardness was probably never intended in the original coining of the term, particularly if “leathery” is a more precise translation of Schimper’s initial description of sclerophyllous leaves (Schimper 1903, p. 8), although he also referred to “stiffness” as a property of the thick, leathery leaves (Schimper 1903, e.g. p. 507). Mott (1956) suggests a more useful general definition of hardness (not specifically in the context of leaves) as a measure of the resistance to permanent deformation or damage and notes that “No method of measuring hardness is dependent on a single physical property but may involve both the elastic and plastic deformation characteristics of the material, so that the elastic limit, elastic modulus, yield point, tensile strength, brittleness etc., all play a part in the result obtained”.

Not all these properties can be measured easily in biomaterials. However, properties such as toughness, strength and stiffness have precise meanings in materials science and can be measured using instruments that measure applied force and displacement from which stress-strain curves may be generated (Gordon 1976; Vincent 1990). These properties can be used to characterise sclerophyllous leaves in terms of their structural integrity, such as the capacity of the whole structure to resist deformation and fracture, and are properties that are influenced by sub-surface as well as surface characteristics. “Strength” is the force needed to fracture the material per unit area over which the force is applied. “Stiffness”, or resistance to plastic deformation, can be derived from the initial slope of a force-displacement curve. “Toughness” is defined as the resistance to crack propagation (Gordon 1976) and can be derived from the area under the force-displacement curve (Atkins and Mai 1985).

Turner (1994a) describes sclerophylls as being tough, “and frequently also hard and stiff”. However, no studies of sclerophylly to our knowledge have measured stiffness, and even hardness has not been investigated in terms of the range of properties suggested by Mott (1956). The aims of this study were to (1) measure a range of mechanical properties in leaves of varying texture, (2) examine correlations of these mechanical properties to allow interpretation of character combinations, and (3) correlate these mechanical properties with one direct and one indirect index of sclerophylly to facilitate interpretation of the mechanical characters of sclerophyllous leaves. A later paper will discuss the chemical, morphological (including size and LSM) and anatomical properties of these leaves.

## Materials and methods

### Study locality and plant species

Leaves were collected in November 1995 from Lilly Pilly Gully at Wilson’s Promontory National Park in the far south-east of the Australian mainland (39°8’S, 145°25’E). The climate is relatively mild with few extremes of temperature and annual rainfall of *c*. 1000 mm (Ashton and Webb 1977). The rainfall is higher and more uniformly distributed through the year than in much of southern Australia, allowing close proximity of rainforest, eucalypt-dominated forest and heath. However, none of the species investigated is endemic to this area, most also occurring in areas with a more pronounced summer-dry rainfall regime.

The plants were sampled in three types of vegetation over a distance of *c*. 500 m: an open forest dominated by *Eucalyptus obliqua* with a shrub and tree understorey including rainforest species, a 1–2 m heath with occasional stunted *E. baxteri*, and an intermediate vegetation of open forest of *E. obliqua* and *E. baxteri* with a shrub and tree understorey. *Banksia marginata* occurred in both the forest understorey and the heath and was collected at both sites to investigate phenotypic variation. All plants occurred on sandy soils overlying granite. However, there is some variation in the structure and nutrient content of the soils underlying the different vegetation types, the forest soils being deeper, with more clay and organic matter, and higher levels of phosphorus (Parsons 1966).

### Sampling procedure

Nineteen species (Table 1) were selected on the basis of the following characteristics:

1. Species were represented by five or more individuals.
2. Each of the five plants had sunlit branches, about 1–2 m above the ground.
3. Leaves were flat rather than terete, the latter being unsuitable for application of some mechanical tests used in this study.

Since all suitable species in the sampling area were used, any bias in species choice is limited to the constraints above. Leaves varied in texture from soft to stiff and leathery.

**Table 1** The species investigated, their collection site, habit and canopy cover. The species' habit exhibited on the study site is given in *parentheses*, with additional forms recorded elsewhere (Costermans 1981) given in *braces* (*T* tree, *sT* small tree, *S* shrub). *Canopy cover* is the mean projected foliar cover above the five replicate plants, with s.e.m.

| Species and habit | Canopy cover (%) |
|---|---|
| Forest | |
| *Acmena smithii* Poirel. (Myrtaceae) (T) | 7±3 |
| *Banksia marginata* Cav. (Proteaceae) (S, sT) | 12±5 |
| *Bedfordia arborescens* Hochr. (Asteraceae) (sT) | 6±1 |
| *Goodenia ovata* Smith (Goodeniaceae) (S) | 19±5 |
| *Hedycarya angustifolia* Cunn. (Monimiaceae) (S, sT) | 17±8 |
| *Hibbertia aspera* D.C. (Dilleniaceae) (S) | 8±5 |
| *Olearia argophylla* Labill. (Asteraceae) (S, sT) | 13±3 |
| *Pimelea drupacea* Labill. (Thymeleaceae) (S) | 16±6 |
| *Pomaderris aspera* Sieber ex D.C. (Rhamnaceae) (S, sT) | 20±3 |
| *Zieria arborescens* Simms (Rutaceae) (S) | 11±5 |
| Intermediate | |
| *Acacia melanoxylon* R.Br. (Mimosaceae) (T) | 24±3 |
| *Eucalyptus obliqua* L'Her. (Myrtaceae) (T) | 12±3 |
| Heath | |
| *Acacia suaveolens* (Sm) Willd. (Mimosaceae) (S) | 8±3 |
| *B. marginata* (S, {sT}) | 0 |
| *Banksia spinulosa* Smith (Proteaceae) (S) | 12±8 |
| *Eucalyptus baxteri* Benth. (Myrtaceae) (sT {T}) | 3±2 |
| *Leptospermum laevigatum* Gaertner (Myrtaceae) (S {sT}) | 10±5 |
| *Melaleuca squarrosa* Labill. (Myrtaceae) (S {sT}) | 7±1 |
| *Monotoca scoparia* Smith. ex R.Br. (Epacridaceae) (S) | 19±4 |
| *Platylobium obtusangulum* Hook. (Fabaceae) (S) | 29±1 |

Five plants of each species were chosen haphazardly, the only criterion being item 2 in the list above, for reasons of consistency. Leaves that expanded during the previous growing season were collected from sunlit branches. The acacia foliage comprises phyllodes but these are referred to as leaves for simplicity. Ten leaves were sprayed with water and placed in a sealed plastic bag with moist tissue in an insulated container. They were kept as fully hydrated as possible since fracture properties are affected by changes in leaf turgidity (Atkins and Vincent 1984). The percentage cover from overhanging vegetation in a circular area of *c*. 10 m diameter centred over each plant was estimated by eye to provide an estimate of its light environment, since shade can affect leaf morphology, and therefore mechanical properties.

### Indices of sclerophylly

Seven botanists independently ranked the test species in order of increasing sclerophylly (by feel), to provide a direct assessment of sclerophylly, i.e. an index based on leaf texture. No direction was given to the botanists about the judgements they should employ. The leaves were stored overnight in moist tissue in plastic bags and the following day one leaf of each species was presented to each botanist, randomly positioned on a bench. The ranks were analysed using Friedman two-way analysis of variance to test the hypothesis that there is no significant difference among species in sclerophylly ranks (Friedman's test) and to test the agreement among botanists in their rankings (Kendall's coefficient of concordance, ranges between 0 and 1). The rank sums were used as an index of sclerophylly to examine the relationship between leaf mechanical properties and sclerophylly as recognised by botanists.

LSM (leaf dry mass per unit area) was measured on two leaves (petioles removed) chosen haphazardly from each of five replicate plants per species. Leaf area was measured by image analysis (Bioscan Image Analyser). The leaves were then dried at 40°C to constant weight and weighed.

### Leaf mechanical properties

Tests were undertaken within 48 h of collection on one of three haphazardly chosen leaves from each replicate plant of each species, including the two separate collections of *B. marginata*. A Universal Testing Machine (Chatillon Universal Tension and Compression Tester, model UTSE-2) was modified to produce a data output of 800 points per second to a personal computer. Punching, tearing and shearing tests were undertaken and the mechanical properties (Table 2) derived from force-displacement curves using software written by M. Logan (Monash University). Toughness was measured as the area under the force-displacement curve until complete fracture, which we term work to fracture.

**Table 2** Measured and derived mechanical parameters used in this study [*F* maximum force (N), *A* area of punch ($\mathrm{m^2}$), *T* thickness of leaf at position of test (m), *D* displacement of moving head of test machine (m), *C* cross-sectional area of tear ($\mathrm{m^2}$), *W* width of leaf in plane of shear (m)]

| Parameter | Calculation | Property being measured |
|---|---|---|
| Punch strength | $F/A$ ($\mathrm{N\ m^{-2}}$) | Absolute punch strength of the whole leaf at the point of testing. |
| Adjusted punch strength | $(F/A)/T$ ($\mathrm{N\ m^{-2}\ m^{-1}}$) | Punch strength per unit leaf thickness at the point of testing. |
| Work to punch | $(F/A)\times D$ ($\mathrm{J\ m^{-2}}$) | The absolute amount of work done to force the punch through the leaf which will be affected by the leaf thickness. |
| Adjusted work to punch | $[(F/A)\times D]/T$ ($\mathrm{J\ m^{-2}\ m^{-1}}$) | The amount of work done to force the punch through the leaf per unit leaf thickness. |
| Tear strength | $F/C$ ($\mathrm{N\ m^{-2}}$) | Tear strength of the leaf. |
| Work to tear | $F\times D$ (J) | The absolute amount of work done to tear the leaf which will be affected by the leaf cross-sectional area. |
| Adjusted work to tear | $F\times D/C$ ($\mathrm{J\ m^{-2}}$) | The amount of work done to tear the leaf per unit leaf thickness. |
| Work to shear | $(F\times D)/W$ ($\mathrm{J\ m^{-1}}$) | The absolute amount of work done to shear the leaf per unit leaf width. |
| Adjusted work to shear | $[(F\times D)/W]/T$ ($\mathrm{J\ m^{-2}}$) | Work to shear per unit leaf thickness. |

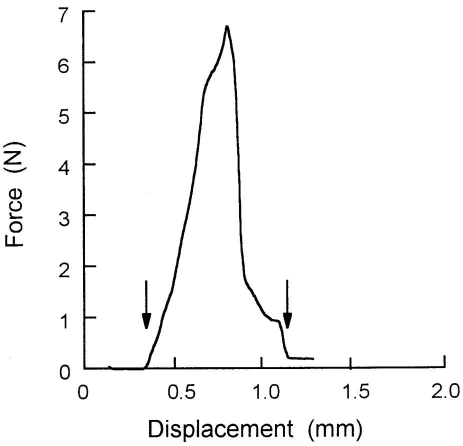


**Fig. 1** A force-displacement plot for *Banksia spinulosa* obtained from a punching test. The *displacement* is the distance travelled by the punch relative to the die. The *arrows* indicate the displacement over which the area of the curve is measured to estimate work to fracture. The derivations of the mechanical properties are given in Table 2

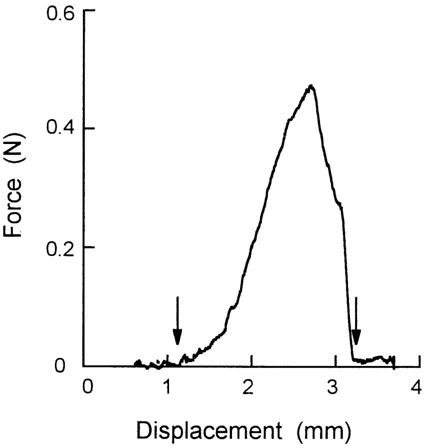


**Fig. 2** A force-displacement plot for *Goodenia ovata* obtained from a tearing test. The *displacement* is the distance the clamps moved apart. The *arrows* indicate the displacement over which the area of the curve is measured to estimate work to fracture. The derivations of the mechanical properties are given in Table 2

Some aspects of these tests have been evaluated more recently by Aranwela et al. (1999).

### Punch test

This test involves punching a hole through the leaf lamina. It has been commonly described as a test of compression properties, though Vincent (1992) suggested the resistance to penetration is a combination of shear and compressive strength and resistance to crack propagation. A die was mounted onto the moving head of the test machine so that it engaged a steel, flat-ended, sharp-edged cylindrical punch with 1.13 $mm^2$ area and a clearance of 0.068 mm. The displacement speed was set at 0.5 mm $s^{-1}$. Ideally, the mechanical properties of both the tissue between the main veins (midrib and 2° veins) and the vascular tissue should be investigated. However, time was a major constraint since leaves had to be tested as soon as possible after collection. Therefore, we standardised the punch position to the left-hand side of the leaves midway between leaf tip and base, between the midrib and the leaf margin, avoiding main veins where possible. A blank run was performed every 10–20 runs to measure background friction and was subtracted from the leaf force-displacement curves. Lamina thickness was measured in video-projected microscope images of fresh sections (the mean of three measures). Leaf strength and toughness were derived from the force-displacement curve (Fig. 1; Table 2).

### Tearing test

A longitudinal strip of lamina 32–40 mm long and 4–5 mm wide was cut from the middle of the left-hand side of each leaf, where large enough, such that the length was more than 8 times the width to counter the effects of necking (Vincent 1990; Lucas et al. 1991).

Test strips were clamped in the force-tester using pneumatic clamps set at 350 kPa. The clamped ends of the test strips were wrapped in damp absorbent tissue to reduce cell collapse that might lead to low force readings due to the lamina breaking at this point. The strips were inspected following the test to determine if slippage had occurred. Where it was detected the test was repeated on a fresh strip. The strips were notched on the left-hand side up to a known length of 2 mm, maintaining a constant ratio of notch to test strip width as far as possible. The notch directs the position of fracture so the test strip does not break at the clamps. However, this might cause a stress concentration at the notch, possibly leading to inaccurate estimation of fracture properties in notch-sensitive materials. To test for notch-sensitivity, tensile strength can be plotted against the relative length of the notch (expressed as a fraction of the strip width). A notch-insensitive material is indicated by a straight line (Vincent 1990; Lucas et al. 1991). However, we had insufficient time between collection and the time when it was considered testing should be completed to test notch sensitivity. In addition, the small leaves of many species prevented a sufficiently wide range of notch lengths being accurately applied to allow testing of notch sensitivity. There was no solution to this problem. Any effect was minimised by standardising the relative notch length as far as possible.

It was impossible to obtain the recommended aspect ratio from lamina tissue alone in the small- and narrow-leaved species (*Acacia suaveolens*, *Banksia* spp., *Platylobium obtusangulum*, *Hibbertia aspera*, *Leptospermum laevigatum* and *Monotoca scoparia*) and therefore the test strips of these species included the midrib and leaf margins. In *Melaleuca squarrosa* we could not maintain the aspect ratio and whole leaves were used.

The fracture length of the leaf was measured using callipers and lamina thickness was measured as for the punch test to estimate the cross-sectional area of the fractured leaf, corrected for the area of the initial notch. The head speed was set at 0.5 mm $s^{-1}$. Figure 2 illustrates a typical tearing force-displacement plot from which the tensile strength and toughness were derived (Table 2). The initial linear section of the slope could not be consistently detected. Therefore, measurement of stiffness was abandoned.

### Shearing test

Previous studies have used mounted scissors in shearing tests (Lucas and Pereira 1990; Lucas et al. 1991; Choong et al. 1992). In this method the approach angle is constantly changing, thereby altering the amount of tissue being sheared as the blades close and rendering the data more difficult to interpret. In the following tests a guillotine with silver-steel gauge plates was mounted onto the Chatillon Universal force-testing machine. The cutting edge was horizontal in the lower blade and 12° in the upper blade. This provided a constant approach angle of 12°. The widest part of each leaf was placed beneath the upper stationary blade and the bottom, horizontal blade moved at a displacement speed set at 0.5 mm $s^{-1}$, shearing the test leaf into two parts. Neither blade was raked but

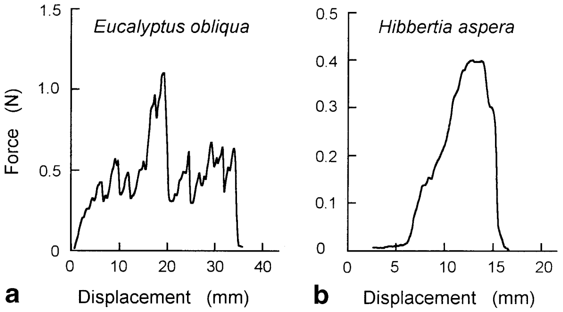


**Fig. 3a,b** Force-displacement plots obtained from shearing tests. The *displacement* is the distance travelled by the horizontal blade relative to the angled blade. **a** The peaks in the plot of *Eucalyptus obliqua* indicate the approximate positions of the midrib and secondary veins. **b** The major veins cannot be discriminated in the plot of *Hibbertia aspera*. The full *area under the curve* is used to estimate work to fracture. The derivations of the mechanical properties are given in Table 2

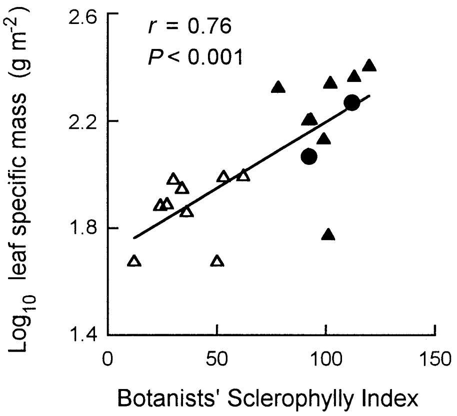


**Fig. 4** The correlation of leaf specific mass with the botanists' sclerophylly index (BSI) (*open triangles* forest species, *filled circles* intermediate species, *filled triangles* heath species). The *line of best fit* was derived by linear regression

the bottom blade had a relief angle of *c*. 5°. A blank run of the blades was undertaken before every 15–20 test runs to record background friction and was subtracted from the test force-displacement curves. The blade was started in exactly the same place each time to standardise background friction. A transverse cut was made across the leaf, midway between the base and tip, including the midrib. Initial trials indicated that the midrib and 2° veins could be distinguished from the intercostal lamina in a transverse cut, thereby allowing additional information about these components. However, the experimental force-displacement plots showed considerable variation among species in shape, and discrimination of veins (Fig. 3). The only consistent measurements that could be made were of work to fracture obtained from the full transverse cut. The cross-sectional area of the leaf at the shearing plane was estimated by measurement of leaf width by callipers and leaf thickness as in the punch test to allow work to be expressed per unit leaf width and thickness (Table 2).

### Statistical analyses

ANOVA was used to test for differences among species in each mechanical property. ANOVA assumptions were checked and $\log_{10}$ transformations used to normalise the data and to reduce heteroscedasticity of variances. Where outliers remained, the data were re-analysed without the outliers to see if conclusions were altered. In each case the conclusion was not altered and in the absence of a priori reasons for exclusion the outliers were retained. A critical value of $\alpha$=0.05 was used in hypothesis testing. Correlation analysis was used to examine relationships among leaf characters using $\log_{10}$-transformed data. Sequential Bonferroni adjustment of the experiment-wise error rate by the Holmes method was used in multiple comparisons. Principal components analysis (PCA) was used to reduce the set of nine mechanical parameters ($\log_{10}$-transformed) to major components. All analyses were undertaken using SYSTAT® 7.0 for windows®. No statistical tests were undertaken on species from different habitats, other than *B. marginata*, since this was not planned at the time of leaf collection, and consequently no a priori hypotheses were erected prior to sampling.

**Table 3** The sclerophyll rank (rank sum) of each species given by seven botanists at Monash University, calculated using a Friedman two-way analysis of variance. The 19 species are ranked in order of increasing sclerophylly. The rank sum is subsequently used as an index of sclerophylly termed the botanists' sclerophylly index (BSI). The habitat from which the plant was collected is given next to the species (*f* forest, *i* intermediate site, *h* heath)

| Species | Sclerophyll rank |
|---|---|
| *Goodenia ovata* (f) | 12 |
| *Zieria arborescens* (f) | 24 |
| *Pimelea drupacea* (f) | 27 |
| *Pomaderris aspera* (f) | 30 |
| *Bedfordia salicina* (f) | 34 |
| *Hibbertia aspera* (f) | 36 |
| *Hedycarya angustifolia* (f) | 50 |
| *Olearia argophylla* (f) | 53 |
| *Acmena smithii* (f) | 62 |
| *Platylobium obtusangulum* (h) | 78 |
| *Banksia spinulosa* (h) | 92 |
| *Acacia melanoxylon* (i) | 92 |
| *Leptospermum laevigatum* (h) | 93 |
| *Monotoca scoparia* (h) | 99 |
| *Melaleuca squarrosa* (h) | 101 |
| *Acacia suaveolens* (h) | 102 |
| *Eucalyptus obliqua* (i) | 112 |
| *Banksia marginata* (h) | 113 |
| *Eucalyptus baxteri* (h) | 120 |

## Results

### Indices of sclerophylly

Species varied significantly in their rankings of sclerophylly (Friedman statistic=102.18; $P$<0.001), with high agreement among botanists in their rankings (Kendall coefficient of concordance=0.81). *Eucalyptus baxteri* was judged the most sclerophyllous species, with the forest understorey shrub *Goodenia ovata* judged the least sclerophyllous (Table 3). Generally, forest species were judged less sclerophyllous than those from heathland and intermediate sites, and taller tree species judged more sclerophyllous than understorey species from the same habitat (Tables 1, 3).

LSM and BSI were positively correlated (Fig. 4). Less variation was recorded in LSM (47–98 g $m^{-2}$) among species with low BSI values (BSI<70), than among species with a high BSI (>70) (LSM values of 59–251 g $m^{-2}$). There was significant variation among

**Table 4** Results of leaf punching, tearing and shearing tests. The values given are means of five replicates with s.e.m. with *F*-ratios and *p*-values from ANOVA for each parameter (using $\log_{10}$-transformed data)

| Species | Punch tests | | | | Tear tests | | | Shearing tests | |
|---|---|---|---|---|---|---|---|---|---|
| | Strength (MN m$^{-2}$) | Adjusted strength (×10$^3$ MN m$^{-2}$ m$^{-1}$) | Work to punch (×10$^2$ J m$^{-2}$) | Adjusted work to punch (MJ m$^{-2}$ m$^{-1}$) | Strength (MN m$^{-2}$) | Work to tear (×10$^{-3}$ J) | Adjusted work to tear (kJ m$^{-2}$) | Work to shear (J m$^{-1}$) | Adjusted work to shear (kJ m$^{-2}$) |
| *Acacia suaveolens* | 2.23±0.24 | 5.08±0.68 | 3.39±0.32 | 0.77±0.11 | 5.12±0.65 | 12.66±3.43 | 4.48±1.08 | 2.69±0.45 | 6.04±0.99 |
| *A. melanoxylon* | 4.93±0.38 | 19.12±1.61 | 4.28±1.15 | 1.66±0.45 | 7.22±0.86 | 8.28±2.92 | 4.96±0.94 | 0.31±0.06 | 1.18±0.31 |
| *Acmena smithii* | 3.80±0.18 | 10.56±0.51 | 5.10±0.44 | 1.42±0.12 | 1.01±0.25 | 2.31±2.57 | 1.32±0.34 | 0.89±0.11 | 2.50±0.34 |
| *Banksia marginata* (heath) | 8.78±0.74 | 28.62±3.16 | 15.89±3.44 | 5.16±0.11 | 12.32±4.38 | 26.67±4.66 | 12.10±1.37 | 1.35±0.07 | 4.40±0.41 |
| *B. marginata* (forest) | 7.05±1.28 | 27.13±4.42 | 10.84±1.93 | 4.15±0.65 | 6.35±0.65 | 13.88±3.07 | 8.51±1.93 | 0.98±0.09 | 3.78±0.21 |
| *B. spinulosa* | 6.05±0.64 | 22.95±3.61 | 21.88±1.59 | 8.28±1.04 | 3.61±0.07 | 9.51±1.29 | 6.08±0.61 | 0.50±0.06 | 1.86±0.28 |
| *Bedfordia salicina* | 0.49±0.12 | 2.29±0.56 | 0.21±0.09 | 0.10±0.04 | 0.4±0.05 | 0.56±0.04 | 0.38±0.06 | 0.30±0.04 | 1.32±0.09 |
| *Eucalyptus baxteri* | 5.88±0.28 | 12.36±0.25 | 8.40±0.68 | 1.76±0.10 | 1.71±0.14 | 6.20±0.60 | 1.93±0.17 | 0.46±0.06 | 0.97±0.15 |
| *E. obliqua* | 5.05±0.12 | 12.58±0.39 | 5.38±0.19 | 1.34±0.07 | 1.64±0.29 | 3.67±0.85 | 1.24±0.32 | 0.35±0.02 | 0.86±0.06 |
| *Goodenia ovata* | 0.32±0.11 | 1.48±0.47 | 0.04±0.03 | 0.02±0.01 | 0.39±0.04 | 0.83±0.16 | 0.49±0.11 | 0.09±0.03 | 0.43±0.12 |
| *Hedycarya angustifolia* | 3.02±0.23 | 11.03±0.51 | 4.09±0.27 | 1.50±0.05 | 0.77±0.20 | 1.77±0.77 | 1.19±0.54 | 0.17±0.04 | 0.60±0.13 |
| *Hibbertia aspera* | 1.54±0.20 | 7.41±1.04 | 1.46±0.40 | 0.72±0.21 | 1.17±0.21 | 1.19±0.21 | 0.55±0.12 | 0.19±0.04 | 0.89±0.18 |
| *Leptospermum laevigatum* | 3.44±0.23 | 10.14±0.60 | 2.48±0.34 | 0.73±0.09 | 4.39±0.93 | 11.49±3.87 | 4.79±1.69 | 0.56±0.11 | 1.67±0.33 |
| *Melaleuca squarrosa* | 3.10±0.25 | 13.67±1.07 | 2.25±0.37 | 1.01±0.19 | 9.37±0.95 | 1.29±0.26 | 2.50±0.54 | 0.14±0.02 | 0.63±0.07 |
| *Monotoca scoparia* | 2.38±0.19 | 6.29±0.36 | 1.94±0.31 | 0.51±0.07 | 9.19±1.20 | 2.97±0.40 | 2.76±0.30 | 0.54±0.11 | 1.46±0.32 |
| *Olearia argophylla* | 2.52±0.18 | 11.20±0.78 | 3.17±0.75 | 1.40±0.30 | 1.03±0.08 | 1.31±0.13 | 0.86±0.22 | 0.39±0.05 | 1.74±0.22 |
| *Pimelea drupacea* | 1.95±0.30 | 7.36±0.94 | 2.71±0.56 | 1.01±0.19 | 0.53±0.02 | 1.49±0.15 | 0.83±0.09 | 0.24±0.06 | 0.99±0.30 |
| *Platylobium obtusangulum* | 2.49±0.50 | 11.17±2.66 | 2.91±0.57 | 1.27±0.23 | 14.38±3.88 | 8.74±1.34 | 9.13±2.41 | 0.32±0.04 | 1.41±0.15 |
| *Pomaderris aspera* | 1.45±0.09 | 11.11±0.30 | 2.10±0.07 | 1.62±0.10 | 0.50±0.08 | 0.93±0.28 | 0.64±0.18 | 0.08±0.00 | 0.63±0.07 |
| *Zieria arborescens* | 0.73±0.16 | 3.29±0.90 | 0.29±0.07 | 0.13±0.04 | 0.44±0.03 | 0.72±0.10 | 0.44±0.05 | 0.08±0.01 | 0.35±0.04 |
| *F*-ratio | 42.49 | 29.46 | 40.22 | 33.66 | 47.75 | 22.47 | 19.06 | 31.87 | 18.69 |
| *P* | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

**Table 5** Correlations among the mechanical properties across species. The data given are Pearson product-moment correlation coefficients (*r*) using log-transformed data. *Asterisks* indicate significant values of *r* following sequential Bonferroni adjustment of the experimentwise error rate for multiple planned comparisons (*PS* punch strength, *APS* adjusted punch strength, *WP* work to punch, *AWP* adjusted work to punch, *TS* tearing strength, *WT* work to tear, *AWT* adjusted work to tear, *WS* work to shear, *AWS* adjusted work to shear)

| | PS | APS | WP | AWP | TS | WT | AWT | WS |
|---|---|---|---|---|---|---|---|---|
| APS | 0.94* | | | | | | | |
| WP | 0.96* | 0.93* | | | | | | |
| AWP | 0.91* | 0.96* | 0.98* | | | | | |
| TS | 0.66* | 0.61 | 0.57 | 0.52 | | | | |
| WT | 0.78* | 0.66* | 0.72* | 0.64* | 0.79* | | | |
| AWT | 0.75* | 0.70* | 0.69* | 0.65* | 0.91* | 0.94* | | |
| WS | 0.59 | 0.39 | 0.59 | 0.47 | 0.56 | 0.77* | 0.67* | |
| AWS | 0.54 | 0.43 | 0.58 | 0.51 | 0.55 | 0.73* | 0.67* | 0.96* |

species in the percentage cover of overhanging vegetation (Table 1) ($F$=3.85; $P$<0.001; arcsine-square-root transformed data), but no significant correlation with BSI ($R$=–0.34; $P$=0.32) or LSM ($R$=–0.34; $P$=0.30).

Since BSI is a rank sum, it does not encompass magnitude of variation among species. Hence, spread of values would alter and relationships with other leaf characters would be altered in slope or curve shape if magnitude was incorporated into this index.

## Leaf mechanical properties

ANOVA indicated significant differences among species in all measured mechanical properties (Table 4). Some properties were more variable among species than others. For example, there was a 414-fold variation in adjusted work to punch, ranging from 0.02 MJ m$^{-2}$ m$^{-1}$ in *Goodenia ovata* to 8.28 MJ m$^{-2}$ m$^{-1}$ in *Banksia spinulosa*. In contrast, the variation among species in adjusted punch strength was 19-fold, ranging from 1.48×10$^3$ MN m$^{-2}$ m$^{-1}$ to 2.86×10$^4$ MN m$^{-2}$ m$^{-1}$ in *G. ovata* and *B. marginata* (heath) respectively.

Following $\log_{10}$-transformation, many of the mechanical parameters from the three tests (tearing, punching and shearing) showed positive linear correlations (Table 5). The exceptions were the shearing properties with the punching tests and tearing strength, and three of the punch tests with tearing strength (Table 5). Since some workers do not apply adjustments of probability levels for multiple comparisons it is important to note that in the absence of adjustment, all comparisons were significant at the 95% level except the two shearing tests with adjusted punch strength.

It is not clear how much of the variation in tearing properties was caused by the inclusion of midrib and margins on tearing test strips in some species. Although values of tearing parameters were high in these species (e.g. Fig. 5), most of the narrow-leaved and small-leaved species in which the margins and midrib were included would be predicted to have high strength and toughness from their BSI values. *H. aspera* showed a low adjusted work to tear value, consistent with other soft-leaved species (Fig. 5).

The first component derived by PCA explained 74% of the total variance, with 96% explained by the first three components (Table 6). Component loadings were all relatively high on the first axis, with punching and tearing properties contributing more than shearing properties, but the shearing properties contributed more to the second component than the punching and tearing parameters.

The plot of species' scores along components 1and 2 indicated a continuum but with separation along component 1 of the forest species from the heath and intermediate species, other than *Acmena smithii* which overlapped with the lower scores of the intermediate and heath species (*Melaleuca squarrosa*, *Monotoca scoparia* and *Eucalyptus obliqua*) (Fig. 6) and *B. marginata* collected from the forest positioned close to the heath collection of the same species. There was no separation of the three groups of species along component 2 (Fig. 6) or component 3, with the forest and heath species showing a similar range of scores.

**Table 6** Component loadings from the principal components analysis of the leaf mechanical properties

| Mechanical properties | Component 1 | 2 | 3 |
|---|---|---|---|
| Punch strength | 0.93 | –0.30 | 0.05 |
| Adjusted punch strength | 0.87 | –0.47 | –0.02 |
| Work to punch | 0.91 | –0.33 | 0.20 |
| Adjusted work to punch | 0.87 | –0.43 | 0.17 |
| Tearing strength | 0.80 | 0.20 | –0.51 |
| Work to tear | 0.91 | 0.24 | –0.15 |
| Adjusted work to tear | 0.90 | 0.19 | –0.35 |
| Work to shear | 0.76 | 0.54 | 0.33 |
| Adjusted work to shear | 0.76 | 0.52 | 0.34 |
| Percent of total variance explained | 74 | 14 | 8 |

Component 1 was strongly correlated with BSI (Fig. 7). However, this trend was only evident in comparisons of all species, and among species with a BSI of less than *c*. 95,

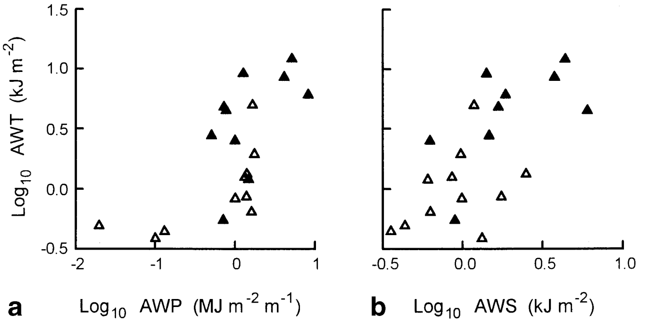


**Fig. 5** The relationship between adjusted work to tear and **a** adjusted work to punch and **b** adjusted work to shear (*filled triangles* species in which the midrib and leaf margins were included in the test strip, *open triangles* species measured using an excised test strip)

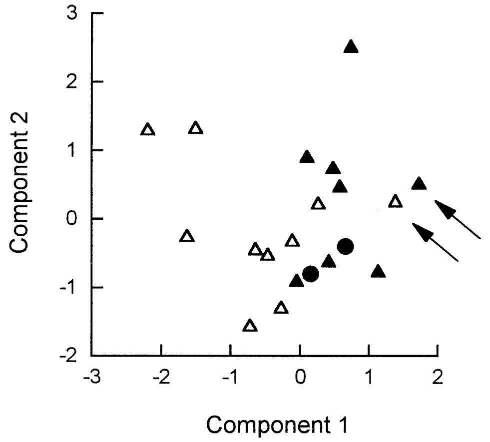
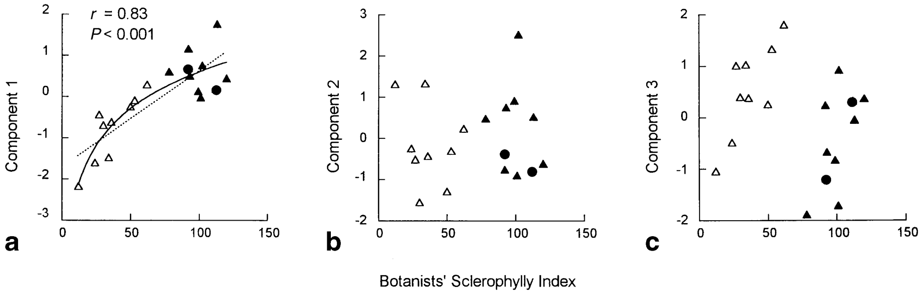


**Fig. 6** The plot of all species along the first two components derived by principal components analysis (PCA) (*open triangles* forest species, *filled circles* intermediate species, *filled triangles* heath species). The two collections of *Banksia marginata* are indicated by *arrows*

**Fig. 7a–c** The relationship between component scores from the PCA and the BSI (*open triangles* forest species, *filled circles* intermediate species, *filled triangles* heath species). The Pearson correlation coefficient and *P* value is given for untransformed data in each plot. The *bold line* in **a** is the line of best fit using linear regression of $\log_{10}$-transformed BSI ($r$=0.88; $P$<0.001)



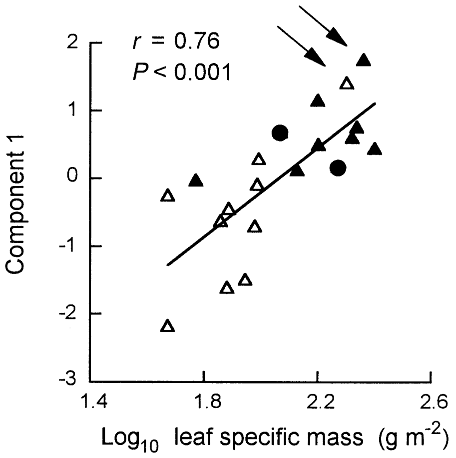


**Fig. 8** The relationship between Component 1 scores from the PCA and leaf specific mass (*open triangles* forest species, *filled circles* intermediate species, *filled triangles* heath species). The two collections of *Banksia marginata* are indicated by *arrows*

with no clear trend among species with BSI values above 95. There was no significant correlation of components 2 and 3 with BSI (Fig. 7). However, there was a roughly linear relationship within heath and intermediate species separately from forest species in the plot of component 3 against BSI (Fig. 7) which warrants further investigation. Correlations of individual mechanical properties with BSI (all $\log_{10}$-transformed) indicated that only punch strength correlated as highly with BSI ($R$=0.86; $P$<0.001) as component 1 ($R$=0.88). $R$-values for the other mechanical properties ranged from 0.58 to 0.81. Component 1 was also significantly correlated with LSM (Fig. 8).

*B. marginata* leaves collected from the heath had higher values for each test parameter than those from the forest, particularly in the tearing parameters (Table 4). However, statistically significant differences only occurred in work to shear ($t$=3.23, $P$=0.01).

## Discussion

### Methodological issues

Five main methodological issues arose in this study:

1. The punch test, using a penetrometer, is simple to apply and commonly used (see Choong et al. 1992) and “frequently yields results which can be correlated with ‘firmness’ (a quasi-parameter which is probably closely related to stiffness)” (Vincent 1992, p. 181). However, Vincent (1992) argues that resistance to penetration by a punch involves a combination of shear and compressive strength and resistance to crack propagation. In addition, damage is uncontrolled and spreads ahead of the punch. Vincent (1992, p. 81) further argues that, since most other mechanical tests are aimed at producing quantifiable parameters, “it is a waste of time....to use penetrometry, which cannot give a result that can either be modelled or translated to another size level in the structure of the plant” and concluded that the technique should be taken no further. However, the technique is relatively straightforward and uses less time than other tests. In addition it might be argued that since the test does involve a number of mechanical attributes of interest, even if they cannot be discriminated, the overall result is of significant interest in the understanding of whole-leaf properties. Even when the load is incrementally applied by loading the punch with ball bearings (rather than using a force tester that continuously loads at a constant velocity) the force to punch is significantly correlated with work to shear (Choong et al. 1992). Our study showed significant correlations among all of the punch parameters and between punch parameters and some of the tear parameters (Table 5) but not shear parameters. Furthermore, tests of tearing and shearing can be difficult to interpret in small or narrow leaves and comprehensive testing is time-consuming to undertake in a thorough manner. Irrespective of the limitations noted by Vincent (1992), the strong positive correlations in this study between parameters measured in punch tests and parameters measured from most of the tearing tests, together with its relationship with BSI, suggests that it might provide a useful estimate of sclerophylly. Portable force-testing machines that can undertake these punch and shear tests have been built (G. Sanson, unpublished work) and therefore the technology is not a limitation to field measurements. In addition, punch tests may be all that can be used in some small or narrow leaves to differentiate the properties of vascular versus non-vascular tissue.
2. In general, the punch was positioned to fracture the lamina between secondary veins. However, *Monotoca scoparia* and to a lesser degree *Acacia melanoxylon*, have closely-aligned longitudinal parallel secondary veins. Certainly in the former species, and possibly in the latter species, the punch would have passed through secondary vein(s). While closely spaced secondary veins may contribute significantly to sclerophylly there is a problem of scale inherent in these measurements. That is, the punch diameter must be chosen in relation to the scale of leaf venation, within the context of the biological question being investigated.
3. Tearing tests were undertaken without testing for notch sensitivity. The presence of a notch and small differences in relative notch length might lead to inaccurate estimations of tensile properties. We were unable to assess these potential effects. In addition, strips with the recommended aspect ratio could not be obtained from the smallest-leaved species.
4. In eight species, the midrib and margins were included in the tissue used in tearing tests. Therefore, higher forces may have been recorded than on lamina tissue alone.
5. In the shearing tests, leaves were cut through the midrib and through 2° veins. Veins can be 20–30 times tougher than the lamina matrix (Lucas et al. 1991;

Choong et al. 1992; Turner et al. 1993). However, these differences in magnitude between lamina and higher-order veins may vary among leaf types, probably more so in malacophylls than in sclerophylls. Although it is appropriate to include secondary vein characteristics in analyses of sclerophylly, it is preferable to obtain an understanding of the variability of mechanical properties across the leaf rather than only an inclusive measure derived from a leaf profile.

## Mechanical properties of sclerophyllous leaves

These methodological problems complicate interpretation of some properties of these leaves and some conclusions must remain tentative. Even so, the positive correlations among the mechanical parameters of a particular test indicate two main points. First, generally the species that are tough (high work to fracture) are also strong. Second, the correlations indicate that in general the leaves that are tough or strong also have high toughness and strength per unit tissue thickness. That is, leaf toughness and strength are influenced by properties of leaf tissue other than simply leaf thickness. Choong et al. (1992) found no significant correlation between leaf thickness and leaf mechanical properties expressed per unit leaf thickness, but a significant positive correlation with unadjusted force to punch. Choong et al. (1992) also recorded a significant correlation between specific leaf area (inverse of LSM) and each of mean fracture toughness and force to punch (probabilities unadjusted for multiple comparisons), but not with force to punch per unit leaf thickness.

The major difficulty in interpreting these results in the context of sclerophylly still lies in the absence of any strict reference for comparison, other than using something like a BSI. One of the two most widely used indices of sclerophylly is LSM. However, there is no reason to assume that the leaf mass per unit area is a good measure of sclerophylly since it ignores the fact that different materials and arrangements of materials in a composite can produce different mechanical properties. In addition, LSM is confounded by its two often independent components, leaf density and thickness, making interpretation of the results difficult where these have not been measured separately (Witkowski and Lamont 1991). Although positive correlations have been recorded between leaf mechanical properties and LSM, more detailed investigation is necessary to determine whether LSM is valuable for the detection of fine-scale patterns in sclerophylly. In this study mechanical properties correlated more strongly with BSI than LSM. The second widely used index, Loveless' index of sclerophylly was based on the assumption that sclerophylly could be defined by the amount of fibre per unit protoplasm, the latter estimated by crude protein content (Loveless 1961, 1962), rather than by any test of association with mechanical properties. Beadle (1966) noted that while this index may adequately define fibrosity, it does not provide a measure of sclerophylly imposed by effects of heavy cutinization or silicification. Despite these flaws, recent investigations have shown significant positive correlations of this index with fracture toughness, force to punch and force to punch per unit leaf thickness (Choong et al. 1992). However, it would be incautious to conclude from those results that sclerophyllous leaves are tough (in the materials science sense of the term) and require high forces to punch, since the Loveless index is essentially untested as an index of sclerophylly.

The use of the BSI has its own limitations. First, since it is derived from ranks, it cannot be used to indicate the absolute magnitude of sclerophylly, or to compare among studies without some type of standard. Second, error might be expected in estimating properties intended by the usage of the term “sclerophylly”. For example, botanists may be influenced inadvertently by features such as leaf size and knowledge of the species' ecology, unless a blind trial with leaf discs of equal size is used. Despite these limitations, we argue that this type of index is the best available for exploratory studies aimed at characterising more precisely the nature of the mechanical properties of sclerophyllous leaves, and allowing subsequent development of an improved definition of sclerophylly that allows quantification.

If the BSI provides a true ranking of sclerophylly, as the term was intended by Schimper (1903) and understood by subsequent biologists, then the results from this study suggest that sclerophyllous leaves are both strong and tough, in tension and shearing, at the level of whole leaf and generally per unit leaf thickness. No particular mechanical parameters are outstanding in their contribution to component 1 of the PCA. However, the shearing properties contribute least to component 1, possibly due to the inclusion of midrib effects which may neither contribute to nor correlate with sclerophylly. The poor fit of species with high BSI scores in the correlation with component 1 of the PCA (Fig. 7) may be caused by difficulties in estimating the degree of sclerophylly at this end of the range. Alternatively, it may be caused by a greater variation in the combinations of mechanical properties of these leaves, i.e. there may be a variety of ways to be highly sclerophyllous.

In the Introduction we questioned the usefulness of using hardness to quantitatively define sclerophyllous leaves since this property as defined in the narrowest sense by engineers is measured on surfaces and is difficult to relate to integrated composite materials such as leaves. While hardness in this sense may contribute to sclerophylly, it may not be as important as properties such as strength and toughness. Based on our data and those of Choong et al. (1992) and Turner et al. (1993) we suggest that the latter mechanical properties, which are components of the more general sense of hardness (Mott 1956), are more useful parameters on which to base definitions of sclerophylly. However, more detailed investigation of these properties is needed, and of other measurable properties such as stiffness, over a wide range of leaf textures.

### Differences between forest and heath species

To some extent the delineation of species as heath, forest and intermediate species is artificial in that it reflects the collection site, not necessarily the general habitat of the species. For example, *A. melanoxylon* was sampled from the forest-heath ecotone but also grows with rainforest species in the same region. Although the leaves of heath plants were generally stronger and tougher than those of forest species, the tough and strong leaves of *E. obliqua*, *A. melanoxylon* and *B. marginata* (forest collection) are contrary to these trends and indicate that any simple habitat relationship with sclerophylly is likely be confounded by other ecological and evolutionary influences.

The relative roles of genotype versus growing conditions in causing differences in tearing strength and work to shear of the two collections of *B. marginata* are unknown. The tougher and stronger leaves of the heath plants is not surprising given the higher light conditions and probable lower soil nutrient status of the heath. Leaves produced under these conditions have been reported to have higher LSM, density and thickness (Witkowski and Lamont 1991). These differences in growing conditions may have influenced the measured properties of the other species, as well as the observed differences between forest and heath species. However, the magnitude of the differences recorded in the punch parameters and adjusted work to shear between the two collections of *B. marginata* was small compared with that between heath and forest species in general. This suggests that the differences recorded in mechanical properties between heath and forest species reflect genetically based differences in leaf properties, rather than only differences in their growing environment.

**Acknowledgements** We thank P. Fell for writing the data collection software, M. Logan for writing the force-displacement analysis software, F. Clissold for assistance during leaf collection, R. Winders for assistance with measurements of the mechanical properties, D. Gaff, B. Gott, N. Hallam, K. Kevekordes, D. O'Dowd, G. Rayner and R. White for ranking leaves and N. Aranwela and F. Clissold for helpful comments on an early draft of the manuscript. We also thank reviewers for helpful comments.

## References

Aranwela N, Sanson G, Read J (1999) Methods of assessing leaf-fracture properties. New Phytol 144:369–383

Ashton DH, Webb RN (1977) The ecology of granite outcrops at Wilson's Promontory, Victoria. Aust J Ecol 2:269–296

Atkins AG, Mai Y-W (1985) Elastic and plastic fracture. Ellis Horwood, Chichester

Atkins AG, Vincent JFV (1984) An instrumented microtome for improved histological sections and the measurement of fracture toughness. J Mater Sci Lett 3:310–312

Beadle NCW (1966) Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47:992–1007

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Annu Rev Ecol Syst 13:229–259

Choong MF, Lucas PW, Ong JSY, Pereira B, Tan HTW, Turner IM (1992) Leaf fracture toughness and sclerophylly: their correlations and ecological implications. New Phytol 121:597–610

Costermans LF (1981) Native trees and shrubs of south-eastern Australia. Weldon, Sydney

Gordon JE (1976) The new science of strong materials, or why you don't fall through the floor, 2nd edn. Penguin, London

Grubb PJ (1986) Sclerophylls, pachyphylls and pycnophylls: the nature and significance of hard leaf surfaces. In: Juniper B, Southwood R (eds) Insects and the plant surface. Edward Arnold, London, pp 137–150

Jackson WD (1968) Fire, air, water and earth – an elemental ecology of Tasmania. Proc Ecol Soc Aust 3:9–16

Jaffré T (1980) Étude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle Calédonie (Travaux et Documents de l'ORSTOM 124). ORSTOM, Paris

Loveless AR (1961) A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophytic leaves. Ann Bot 25:168–184

Loveless AR (1962) Further evidence to support a nutritional interpretation of sclerophylly. Ann Bot 26:551–561

Lucas PW, Pereira B (1990) Estimation of the fracture toughness of leaves. Funct Ecol 4:819–822

Lucas PW, Choong MF, Tan HTW, Turner IM, Berrick AJ (1991) The fracture toughness of the leaf of the dicotyledon *Calophyllum inophyllum* L. (Guttiferae). Philos Trans R Soc Lond B 334:95–106

Mooney HA, Dunn EL (1970) Convergent evolution of mediterranean-climate evergreen sclerophyll shrubs. Evolution 24:292–303

Mott BW (1956) Micro-indentation hardness testing. Butterworths, London

Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago

Oertli JJ, Lips SH, Agami M (1990) The strength of sclerophyllous cells to resist collapse due to negative turgor pressure. Acta Oecol 11:281–289

Parsons RF (1966) The soils and vegetation at Tidal River, Wilson's Promontory. Proc R Soc Vict 79:319–355

Rundel PW (1988) Leaf structure and nutrition in mediterranean-climate sclerophylls. In: Specht RL (ed) Mediterranean-type ecosystems. Kluwer, Dordrecht, pp 157–167

Schimper AFW (1898) Pflanzengeographie auf physiologischen Grundlage. Fischer, Jena

Schimper AFW (1903) Plant-geography upon a physiological basis (translated by W.R. Fisher). Clarendon, Oxford

Seddon G (1974) Xerophytes, xeromorphs and sclerophylls: the history of some concepts in ecology. Biol J Linn Soc 6:65–87

Shaw MC (1973) The fundamental basis of the hardness test. In: Westbrook JH, Conrad H (eds) The science of hardness testing and its research applications. American Society for Metals, Metals Park, Ohio, pp 1–11

Turner IM (1994a) Sclerophylly: primarily protective? Funct Ecol 8:669–675

Turner IM (1994b) A quantitative analysis of leaf form in woody plants from the world's major broadleaved forest types. J Biogeogr 21:413–419

Turner IM, Choong MF, Tan HTW, Lucas PW (1993) How tough are sclerophylls? Ann Bot 71:343–345

Vincent JFV (1982) The mechanical design of grass. J Mater Sci 17:856–60

Vincent JFV (1990) Fracture properties of plants. Adv Bot Res 17:235–287

Vincent JFV (1992) Plants. In: Vincent JFV (ed) Biomechanics – materials. Oxford University Press, Oxford, pp 165–191

Witkowski ETF, Lamont BB (1991) Leaf specific mass confounds leaf density and thickness. Oecologia 88:486–493