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In Tropical Lowland Rain Forests Monocots have Tougher Leaves than Dicots, and Include a New Kind of Tough Leaf

NATHANIEL J. DOMINY[1,*], PETER J. GRUBB[2], ROBYN V. JACKSON[3], PETER W. LUCAS[4], DANIEL J. METCALFE[5], JENS-CHRISTIAN SVENNING[6] and IAN M. TURNER[7,†]

[1]*Department of Anthropology, University of California, 1156 High St, Santa Cruz, CA 95064, USA,* [2]*Plant Sciences Department, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK,* [3]*19 Cananga Close, Kamerunga, Qld 4870, Australia,* [4]*Department of Anthropology, George Washington University, 2110 G Street, NW, Washington, DC 20052, USA,* [5]*Commonwealth Scientific and Industrial Research Organization, Sustainable Ecosystems, Tropical Forest Research Centre, PO Box 780, Atherton, Queensland 4883, Australia,* [6]*Department of Biological Sciences, University of Aarhus, Ny Munkegade 1540, DK-8000, Aarhus C, Denmark and* [7]*Singapore Botanic Gardens, National Parks Board, 1 Cluny Road, Republic of Singapore 259569*

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• *Background and Aims* There has been little previous work on the toughness of the laminae of monocots in tropical lowland rain forest (TLRF) despite the potential importance of greater toughness in inhibiting herbivory by invertebrates. Of 15 monocot families with >100 species in TLRF, eight have notably high densities of fibres in the lamina so that high values for toughness are expected.
• *Methods* In north-eastern Australia punch strength was determined with a penetrometer for both immature leaves (approx. 30 % final area on average) and fully expanded, fully toughened leaves. In Singapore and Panama, fracture toughness was determined with an automated scissors apparatus using fully toughened leaves only.
• *Key Results* In Australia punch strength was, on average, 7× greater in shade-tolerant monocots than in neighbouring dicots at the immature stage, and 3× greater at the mature stage. In Singapore, shade-tolerant monocots had, on average, 1·3× higher values for fracture toughness than neighbouring dicots. In Panama, both shade-tolerant and gap-demanding monocots were tested; they did not differ in fracture toughness. The monocots had markedly higher values than the dicots whether shade-tolerant or gap-demanding species were considered.
• *Conclusions* It is predicted that monocots will be found to experience lower rates of herbivory by invertebrates than dicots. The tough monocot leaves include both stiff leaves containing relatively little water at saturation (e.g. palms), and leaves which lack stiffness, are rich in water at saturation and roll readily during dry weather or even in bright sun around midday (e.g. gingers, heliconias and marants). Monocot leaves also show that it is possible for leaves to be notably tough throughout the expansion phase of development, something never recorded for dicots. The need to broaden the botanist's mental picture of a 'tough leaf' is emphasized.

Key words: Dicots, fracture toughness, herbivory, leaves, monocots, punch strength, tropical rain forest.

INTRODUCTION

There is a long history of work on the 'toughness' of leaves as a protection against herbivory that stretches back to Williams (1954), and has been summarized by Wright and Vincent (1996), Lucas *et al.* (2000), Sanson *et al.* (2001), Read and Stokes (2006) and Sanson (2006). There have been two major approaches to measuring the 'toughness' of leaves (Lucas *et al.*, 2000; Read and Sanson, 2003). A 'penetrometer' measures punch strength, the force needed to pass a rod of given diameter through the lamina; this property involves not only the properties of the materials in the leaf but also their arrangement and amount. An apparatus based on scissors or a guillotine measures work to shear, from which it is possible to derive specific work to shear (fracture toughness) which is work to shear per unit thickness. Choong *et al.* (1992) found a significant positive correlation between punch strength and fracture toughness ($r^2 = 0{\cdot}420$; $P < 0{\cdot}01$) and not surprisingly a stronger one when punch strength was divided by lamina thickness ($r^2 = 0{\cdot}555$; $P < 0{\cdot}001$). The chief determinant of fracture toughness in leaves is generally the extent of development of fibres around the vascular bundles (Lucas *et al.*, 1995, 2000), though other tissues may be important in a minority of species (Read *et al.*, 2000). There is still uncertainty as to whether punch strength or fracture toughness has the closer correlation, in general, with inhibition of herbivory by invertebrates (Lucas *et al.*, 2000; Read and Stokes, 2006; Sanson, 2006). In this paper, following Read and Stokes (2006), we use the unqualified term 'toughness' to include measurements of both punch strength and fracture toughness.

There have been extensive studies of both punch strength and fracture toughness for dicots (eudicots and magnoliids) in tropical lowland rain forest (TLRF), but not for monocots. All of the earlier measurements were of punch strength, and made in the context of understanding the inhibition of herbivory, particularly by invertebrates (Coley and Barone, 1996; Coley and Kursar, 1996). More recently there has been a number of studies on the fracture toughness of dicots (Lucas *et al.*, 1991; Choong *et al.*, 1992; Turner *et al.*, 1993, 2000; Yamashita, 1996; Dominy *et al.*, 2003;

* For correspondence. E-mail njdominy@ucsc.edu
† Present address: Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK.

Iddles *et al.*, 2003; Read and Sanson, 2003; Read and Stokes, 2006; Read *et al.*, 2006; Eichhorn *et al.*, 2007). In contrast, we have traced no study of fracture toughness in monocots of TLRF, and only two studies of punch strength; both concern palms. Bernays (1991) found that the mean punch strength for eight unnamed palms was 1·6× the mean for 89 unnamed species of woody dicot species. Braker and Chazdon (1993) recorded mean punch strength for three understorey palms in Costa Rica. The lack of information on toughness of tropical monocots contrasts with the results of critical studies of temperate grasses obtained by Wright and Illius (1995) and Henry *et al.* (1996, 2000).

As pointed out by Edwards *et al.* (2000), botanists often make a subjective estimate of 'toughness' or 'sclerophylly' by testing stiffness (resistance to bending). By this approach most palm leaves seem 'tough' because they are stiff; also they do not change shape readily when they begin to dry. However, other monocots in TLRF have relatively closely set veins and a marked development of fibres along the vascular bundles, but lack stiffness and indeed may roll readily under drying conditions, e.g. aroids, gingers, heliconias and marants. Of the 15 families of monocots with >100 species in TLRF, eight have notably high densities of fibres in the laminae of most species (Table 1). Clearly there is a strong likelihood that the leaves of all these plants will have relatively high values for fracture toughness and punch strength. In the context of herbivory by invertebrates, particular interest attaches to the toughness of immature leaves. For dicots the losses to invertebrates are generally greater during the expansion phase than the mature phase (Coley and Barone, 1996; Coley and Kursar, 1996).

The study presented here sought to answer two questions. (1) In TLRF, do monocot leaves on average have higher or lower values than dicots for punch strength and fracture toughness? This question was addressed by working in three widely separated parts of the wet tropics (north-eastern Australia, Singapore and Panama) and making determinations for mature leaves of species in a wide range of monocot families, and for their neighbouring dicots. (2) Is the relative toughness of monocot and dicot leaves approximately the same when immature as when mature? This question was answered for species in north-eastern Australia.

In the Discussion, it is first emphasized that it is necessary to confine any comparison of monocots and dicots to either shade-tolerators or light-demanders, and that it is desirable to make phylogenetically controlled contrasts between shade-tolerant and light-demanding species within either monocots or dicots wherever possible. Secondly, the contrast between monocots and dicots in the development of toughness during and after leaf expansion is reviewed. Thirdly, the relationship between punch strength and fracture toughness, and the relative strengths of correlation between those two properties and the rate of loss of leaf area to invertebrate herbivores is considered. Fourthly, the range in toughness of mature monocot leaves, and the need to recognize that monocots in TLRF include a type of tough leaf quite different from that considered in the classical literature is emphasized. In this final section use is made of data on the water contents of leaves given in a companion paper on the extent of leaf area loss to invertebrate herbivores suffered by monocots and dicots at six different TLRF sites (Grubb *et al.*, 2008).

TABLE 1. *Families of monocots with 100 or more species in TLRF arranged firstly in decreasing order of degree of development of fibres in the lamina, and then alphabetically*

Family (order)	Extent of development of fibres*	Reference
Arecaceae (Arecales)	+++	Tomlinson (1961); Knapp-Zinn (1973)
Bromeliaceae (Poales)	+++	Tomlinson (1969)
Cyclanthaceae: Carludovicioideae (Pandanales)	+++	Tomlinson and Wilder (1984); Wilder (1985*a*, *b*)
Pandanaceae (Pandanales)	+++	North and Willis (1970, 1971); Tomlinson and Wilder (1984)
Cyclanthaceae: Cyclanthoideae (Pandanales)	++	Tomlinson and Wilder (1984); Roth (1990)
Cyperaceae (Poales)	++	Metcalfe (1971)
Marantaceae (Zingiberales)	++	Tomlinson (1969)
Poaceae (Poales)	++	Metcalfe (1960)
Zingiberaceae (Zingiberales)	++	Tomlinson (1969)
Araceae (Alismatales)	+	Solereder and Meyer (1928–33); Roth (1990)
Costaceae (Zingiberales)	+	Tomlinson (1969)
Heliconiaceae (Zingiberales)	+	Tomlinson (1969)
Orchidaceae (Asparagales)	+	Solereder and Meyer (1928–33)
Commelinaceae (Commelinales)	–	Tomlinson (1969)
Dioscoreaceae (Dioscoreales)	–	Ayensu (1972)
Smilacaceae (Liliales)	–	Solereder and Meyer (1928–33)

* Key to degrees of development of fibrous tissue: +++, substantial strands of fibres along vascular bundles, girders of fibres from vascular bundles to one or both of the epidermides, and strands of fibres not associated with vascular tissues running through the leaf, often under the epidermis; ++, substantial strands of fibres along vascular bundles, and girders of fibres from vascular bundles to one or both of the epidermides; +, most species with strands of fibres along vascular bundles, some without; –, most species with little or no development of fibre-strands along vascular bundles, a few with substantial strands.

MATERIALS AND METHODS

Study sites

The locations are set out in Table 2, together with rainfall data and the sources of species nomenclature. The families and orders recognized follow Stevens (2007).

Selection of species

All of the species chosen, both monocot and dicot, have wide-ranging distributions with respect to topography within the forests concerned. Thus our samples form an appropriate basis for comparing monocots and dicots in a given forest-type. However, it was long ago established for dicot trees in TLRF that punch strength is appreciably greater, on average, in shade-tolerant species than in species which need canopy gaps for establishment (Coley, 1983). Therefore, care is taken in this paper to confine the comparisons of monocots and dicots to shade-tolerant species at the sites where there were very few light-demanding monocots to sample. At the Panamanian site it was feasible to compare monocots and dicots using both shade-tolerant and light-demanding species.

Selection of material

Dominy *et al.* (2003) showed for dicot trees in the same forest as that studied by Coley (1983) that, on average, the fracture toughness is 1·7× greater in sun-exposed leaves than in highly shaded leaves, although they also found that species varied greatly so that the difference between exposed and shaded leaves ranged from a factor of ×3·7 to there being no significant difference. All of the monocot leaves sampled in the present study were collected within a few metres of the ground, and therefore values for shaded dicot leaves were used.

TABLE 2. *Characteristics of the sites at which leaves were sampled for determination of punch strength or fracture toughness, and the sources of species nomenclature*

Site	Latitude, longitude, altitude	Mean rainfall data*	Source of species nomenclature
Australian low-rainfall			
Wongabel State Forest	145°26'E, 17°18'S, approx. 750 m	1400 mm year^{-1}, 4 dry months	Bostock and Holland (2007)
Australian high-rainfall			
Wooroonooran National Park	145°43'E, 17°23'S, approx. 800 m	3500 mm No dry month	Bostock and Holland (2007)
Singaporean site			
Bukit Timah Nature Reserve	103°47'E, 1°21'N, approx. 100 m	2400 mm year^{-1}, no dry month	Turner (1995)
Panamanian site			
Barro Colorado Natural Monument	79°51'W, 9°9'N, approx. 50 m	2650 mm year^{-1}, 2 dry months	Henderson *et al.* (1995) for palms, otherwise Croat (1978) and updates in Condit *et al.* (1995)

* Number of dry months as defined by Walter (1971).

Measurements of punch strength for the Australian species

A penetrometer of the design of Sands and Brancatini (1991) was used, and in almost all cases three leaves (each from a different plant) were used per species at each stage of development studied. Measurements were made in January 1999 and August 2003. In 1999 measurements were made near the top, middle and bottom of the leaf blade, and the mean taken. At the low-rainfall site, *Castanospora alphandii* and *Hodgkinsonia frutescens* were, respectively, the commonest sapling and commonest shrub; at the high-rainfall site *Wilkiea angustifolia* was judged subjectively to be the toughest-leaved dicot in the forest. For most species, tests were made on both fully expanded but untoughened leaves, and on fully toughened leaves.

In August 2003, measurements were made on immature leaves that had expanded to varying extents depending on the species, and on the first fully expanded and toughened leaf on the same shoot. The immature leaves of the monocots and of the one dicot with relatively late-folded leaves (*Argyrodendron trifoliolatum*) were carefully unrolled or unfolded before measurements were made. The length (l) and breadth (b) were recorded for each leaf in millimetres, and the area of the immature leaf as a percentage of the area of the first fully expanded leaf was estimated from the respective values for lb; the mean value for this estimate was calculated for each species. By chance, immature leaves of monocots that were estimated to have 15–75 % of final lamina area and dicots with 1·6–67 % were found. The ultimate objective of the present study was to compare the leaves of monocots and dicots both when immature and when mature, and to do this in a way that was sensitive to any generalized difference there might be between the two groups in the relationship between punch strength and the extent of lamina expansion. To achieve this the following were investigated: (*a*) whether for dicots punch strength remained essentially constant during lamina expansion, as reported by Kursar and Coley (1992) for four of five dicots studied in TLRF on Panama; and (*b*) whether or not the same was true for monocots. All values for fully toughened leaves of *Freycinetia excelsa* in 1999 and *Pandanus monticola* in 2003 were beyond the limits of the apparatus (150 g cm^{-2} in 1999 and 155 g cm^{-2} in 2003), and were treated as 150 and 155 g cm^{-2}, respectively, for statistical analysis.

Measurements of fracture toughness for the Singaporean and Panamanian species

A portable universal tester of the design of Darvell *et al.* (1996) was used. Measurements were made in

August–October 2001 in Panama, and in August–September 2003 in Singapore. Only fully toughened leaves were tested. The mean fracture toughness for a species was calculated from four (sometimes three) mature leaves from an individual plant; each leaf was fractured with a single transverse cut perpendicular to the midrib equidistant between the base and apex.

RESULTS

Measurements of punch strength on leaves at different stages of development

In the initial study at two Australian sites, the punch strength of fully expanded leaves was markedly higher for monocots than dicots, both before and after they became fully toughened (Appendix 1). In that study, few dicots were tested, and the monocots were a mixture of shade-tolerant and gap-demanding species. However, the difference between monocots and dicots was confirmed in a second study of fully hardened leaves, which used only shade-tolerant species and in which the dicots were from a wide range of families ($t = 7{\cdot}99$, $P < 0{\cdot}001$; Appendix 2).

When, for dicots, all the individual values for percentage final punch strength are plotted against percentage final lamina area no trend toward increased punch strength in more expanded leaves is found (Fig. 1). There was relatively little variation in the extent to which punch strength increased between the immature and mature states: eight of 11 species increased by a factor of 3·6–5·4, the remaining three by factors of 1·5, 2·5 and 6·4 (cf. Appendix 2).

For monocots, there appears to be a decrease in the percentage final punch strength with increase in percentage final lamina area (Fig. 1). However, this result is an artefact which arises from the finding, by chance, of relatively smaller leaves on the species which have higher values for percentage final punch strength when immature. An analysis of variance shows that there is no effect of percentage final lamina area on percentage final punch strength, only an effect of species [F (percentage final lamina area) $= 0{\cdot}27$, $P = 0{\cdot}61$; F (species) $= 24{\cdot}18$, $P < 0{\cdot}0001$]. Figure 1 shows that there is no consistent trend for a reduction in punch strength with increasing lamina area for single species. The factors by which punch strength increased between immature and mature leaves were much lower than for dicots; they ranged from 1·1–1·9 for the one Zingiberaceae, three pandans and *Flagellaria*, to 2·8 for the one Araceae. In the 1999 study, similar increases in punch strength were found between the fully expanded but not yet fully toughened leaves and the fully mature leaves: 1·3–1·6 for four Zingiberaceae, a palm and a pandan, and 2·0–3·1 for two Araceae and *Cordyline* – based on data in Appendix 1.

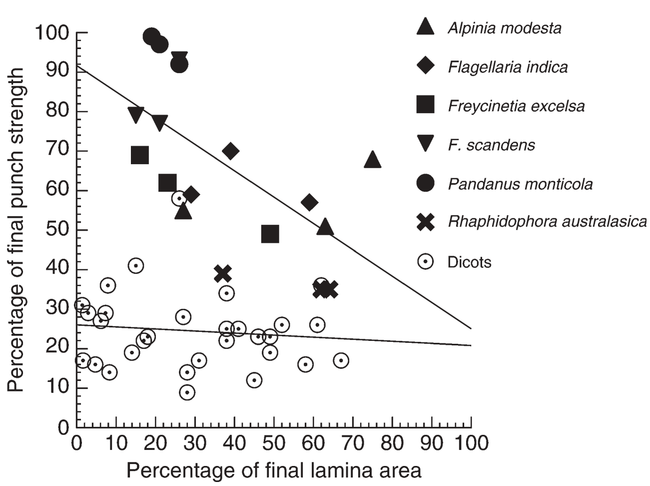

FIG. 1. Percentage final punch strength as a function of percentage final lamina area for individual leaves of ten species of dicots (open circles) and six species of monocots (different symbol for each species) at the Australian high-rainfall site. The regressions are $y = 90{\cdot}6 - 0{\cdot}664x$ ($r = 0{\cdot}629$), and $y = 26{\cdot}0 - 0{\cdot}052x$ ($r = 0{\cdot}105$).

If it is concluded that the stage in expansion when punch strength is measured is immaterial for dicots, and probably so for monocots, then it is reasonable to use all the results for immature leaves to compare monocots and dicots. In that case the monocots had 7·1× greater punch strength than dicots while still expanding, and only 2·8× greater when fully expanded and toughened.

Measurements of fracture toughness on fully expanded and fully toughened leaves

In Singapore the dicots, considered without respect to phylogeny, showed significantly and markedly higher fracture toughness in the shade-tolerators than in the light-demanders: 605 ± 28 vs. 322 ± 36 J m^{-2} ($t = 8{\cdot}93$, $P < 0{\cdot}0001$; Fig. 2 and Appendix 3). In phylogenetic contrasts, comparing genera within one family (or within two very closely related families) the shade-tolerators had higher values in five out of seven cases and there was one tie (Table 3); in one comparison among species within a genus (*Clerodendrum*) the shade-tolerator had a higher value, and in another (*Ficus*) the shade-tolerators did not have a higher value. All of the monocots tested were shade-tolerant; they had significantly higher fracture toughness than the shade-tolerant dicots: 798 ± 105 vs. 605 ± 28 J m^{-2} ($t = 7{\cdot}60$, $P < 0{\cdot}0001$; Fig. 2 and Appendix 3). Metcalfe and Grubb (1995) noted that there is a dearth of light-demanding species – whether monocot or dicot – among the herbs, shrubs, climbers and tall trees (as opposed to short and mid-height trees) at the Singaporean site; it was not practicable to make a comparison of shade-tolerant and light-demanding monocots.

In Panama, the dicots, considered without respect to phylogeny, again showed significantly higher fracture toughness in the shade-tolerators than in the light-demanders, but the difference was not as marked as in Singapore: 572 ± 37 vs. 418 ± 41 J m^{-2} ($t = 10{\cdot}21$, $P < 0{\cdot}0001$; Fig. 2 and Appendix 3). In phylogenetic contrasts, comparing genera within one family, the shade-tolerators had higher values in five out of seven cases and there was one tie (Table 3); for the 13 species of *Psychotria* tested (nine shade-tolerant and four gap-demanding) there was a tie. Only in Panama was it possible to make a useful comparison between shade-tolerant and light-demanding monocots, and this did not involve any phylogenetically

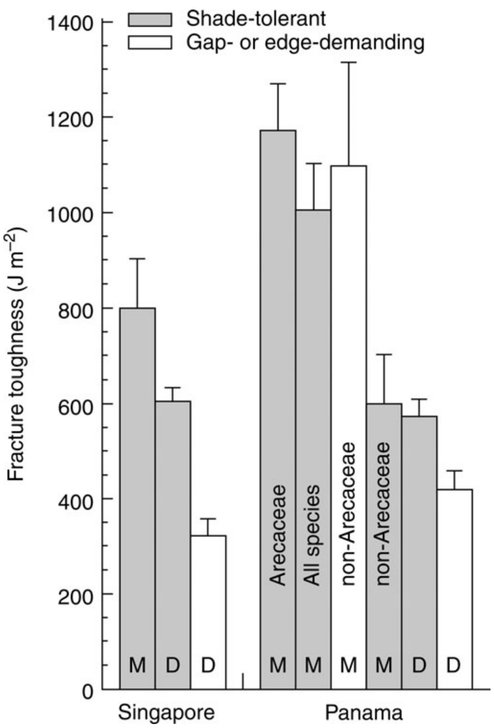

FIG. 2. Mean values (±s.e.) for fracture toughness of the lamina of fully expanded and toughened leaves: Singapore – nine shade-tolerant monocots, 46 shade-tolerant dicots and 16 light-demanding monocots; Panama – 15 Arecaceae (all shade-tolerant, excluding four introduced species), 21 shade-tolerant monocots (15 Arecaceae and 6 non-Arecaceae), eight light-demanding non-Arecaceae, six shade-tolerant non-Arecaceae, 46 shade-tolerant dicots and 21 light-demanding dicots; original data in Appendix 3. M, Monocot; D, dicot.

controlled comparison. There was no significant difference: shade-tolerators 1006 ± 96 vs. gap-demanders 1097 ± 218 J m^{-2} ($t = 0{\cdot}45$, $P = 0{\cdot}66$; Fig. 2 and Appendix 3); for this comparison the four palm species marked ‡ in Appendix 3 were omitted. For both shade-tolerant and light-demanding species the monocots had much greater mean values for fracture toughness than the dicots: 1006 ± 96 vs. 572 ± 37 ($t = 10{\cdot}51$, $P < 0{\cdot}0001$), and 1097 ± 218 vs. 418 ± 41 J m^{-2} ($t = 5{\cdot}04$, $P < 0{\cdot}002$), respectively (Fig. 2).

Although palms, as a whole, had the highest fracture toughness values, it is notable that at both the Singaporean and Panamanian sites members of the Marantaceae had much higher values than some accompanying palms (Appendix 3). Other members of the Zingiberales also had notably high values: *Elatteriopsis curtisii* (Zingiberaceae) in Singapore and *Heliconia catheta* and *H. mariae* (Heliconiaceae) in Panama (Appendix 3).

TABLE 3. *Phylogenetically controlled contrasts in fracture toughness of leaf laminae between shade-tolerant (ST) and light-demanding (LD) trees – the value given is the quotient of the logarithmic mean for the ST species over that for the LD species*

SINGAPORE	
Cannabaceae	
Gironniera (1)/*Trema* (2)	1·28
Fabaceae	
Albizia (1) + *Milletia* (1) + *Parkia* (1) + *Sinodora* (1)/ *Archidendron* (1)	1·15
Loganiaceae	
Strychnos (1)/*Fagraea* (1)	0·949
Melastomataceae	
Pternandra (1)/*Melastoma* (1)	1·00
Moraceae	
Artocarpus (2) + *Ficus* (2)/*Ficus* (1)	1·04*
Phyllanthaceae + Euphorbiaceae	
Aporusa (2) + *Baccaurea* (1)/*Endospermum* (1) + *Macaranga* (3) + *Sapium* (1)	1·16
Verbenaceae	
Clerodendrum (1)/*Clerodendrum* (1)	1·14
PANAMA	
Anacardiaceae	
Astronium (1)/*Anacardium* (1) + *Spondias* (2)	0·937
Annonaceae	
Guatteria (1) + *Unonopsis* (1) + *Xylopia* (1)/*Annona* (1)	1·01
Burseraceae	
Protium (2) + *Tetragastris* (1)/*Trattinickia* (1)	1·14
Malvaceae	
Quararibea (1) + *Sterculia* (1)/*Apeiba* (1) + *Guazuma* (1) + *Luehea* (1) + *Pseudobombax* (1)	1·12
Moraceae	
Brosimum (1) + *Perebea* (1) + *Poulsenia* (1)/*Ficus* (1)	1·16
Rubiaceae	
Genipa (1) + *Psychotria* (9)/*Psychotria* (4)	0·992†
Urticaceae	
Pourouma (1)/*Cecropia* (2)	1·30

The number in parenthesis after the generic name is the number of species for which values are available – the original data are in Appendix 3.

* 0·999 if only the *Ficus* species are considered.

† 0·994 if only the *Psychotria* species are considered.

DISCUSSION

Comparison of monocot and dicot leaves when fully expanded and fully toughened

Any satisfactory comparison must allow for the marked difference in toughness generally found within dicots between shade-tolerant and light-demanding species. However, the matter is more complicated than has been appreciated until now. The present results show that this widely recognized difference is not always found within genera. For the 13 *Psychotria* species studied in Panama the fracture toughness values for the four light-demanders are embedded within the range found for the shade-tolerators (Appendix 3). A similar result was found in *Ficus* in Singapore where only three species were studied (Appendix 3). The situation is reminiscent of that found by Grubb and Metcalfe (1996) in TLRF in NE Queensland in respect of seed dry mass; it was generally higher in shade-tolerators than in light-demanders if genera were compared within families, but not when species were compared within genera. Clearly new research is needed to see if the pattern found in *Psychotria* is widespread within genera that have considerable numbers of species in both shade-tolerant and light-demanding categories. It has long been known that there are wide, overlapping ranges of punch strength among both shade-tolerators and light-demanders in TLRF (Coley, 1983), but there has been no study of the significance of the range in each category, just as the wide range of foliar nitrogen concentration has been largely ignored (cf. Grubb, 2002). Valladares *et al.* (2000) reported on the morphological and physiological responses to shade of 16 *Psychotria* species in the Panamanian forest studied. They gave mean values for leaf longevity of nine of the species for which fracture toughness is available. The longevity values are positively correlated with fracture toughness values for three light-demanding species ($r = 0{\cdot}912$), and at a given fracture toughness the longevity values for four shade-tolerant species are much higher than for the one relevant light-demander (approx. 650–900 d vs. approx. 200 d). The longevity values for the two shade-tolerators with relatively high values for fracture toughness are surprisingly low, and fall on the line for the light-demanders, so that for the shade-tolerators there is a negative correlation overall ($r = -0{\cdot}661$). The explanation is not at all obvious.

The present results for dicots in Panama show that a satisfying comparison of shade-tolerant and light-demanding monocots in respect of fracture toughness must involve both intergeneric and intrageneric tests. In a comparison made without respect to phylogeny it was found that, on average, there was no difference within the monocots between shade-tolerators and light-demanders (Fig. 2 and Appendix 3). However, the value of the comparison is limited. Palms made up a large majority of the shade-tolerators, palms were not represented among the gap-demanders, and palms, on average, had significantly greater fracture toughness than other monocots (1270 ± 99 vs. 883 ± 145 J m^{-2}; $t = 12{\cdot}81$, $P < 0{\cdot}0001$). For the non-palm monocots in the present sample, it was found that the shade-tolerators had markedly lower fracture toughness than the gap-demanders: 598 ± 104 vs. 1097 ± 218 J m^{-2} (Wilcoxon Signed-Rank test, $t = 10{\cdot}5$, $P = 0{\cdot}03$). The value of this comparison is limited by the over-representation of the Poaceae in the shade-tolerant sample. Clearly new comparisons of shade-tolerators and gap-demanders within such families as Marantaceae and Zingiberaceae are needed.

This section concludes by emphasizing that, when only shade-tolerant species are used, it is consistently found that the monocots have tougher leaves on average than the dicots. That is true for punch strength in the Australian high-rainfall forest, and for fracture toughness in the Singaporean and Panamanian forests.

Difference between monocot and dicot leaves when still expanding

The conclusion for shade-tolerant dicots in TLRF that there is no appreciable increase in punch strength during the expansion phase agrees with the findings of Kursar and Coley (1992) for three of the four shade-tolerant species they studied in Panama. Their fourth species seemed to show a small but significant increase in the 10 d before expansion ceased, and that may well happen in some Australian species; by chance the present study did not include any dicot species with leaves having >67 % of final leaf area. Brunt *et al.* (2006) found evidence that toughness began to increase before expansion was complete in *Nothofagus moorei*, a tree of Australian subtropical montane rain forest. The limited data in the present study suggest that in monocots too the punch strength of the lamina does not change appreciably during expansion, but further work is needed to test that conclusion. Monocots differ from dicots through having absolutely greater punch strength while expanding; they differed by a factor of about 7 in the present study of shade-tolerant species, but the factor would probably be greater if light-demanding species were studied because it is certain for dicots that the punch strength of light-demanders is appreciably lower than that of shade-tolerators, while for monocots the limited evidence suggests only a small difference between light-demanders and shade-tolerators (see above).

It seems most likely that the difference between monocots and dicots arises from the early development of fibres along the vascular bundles, and from the vascular bundles being relatively close. For both monocot and dicot leaves there is a need for new research on the changes during and after expansion in biomechanical properties, and in the major chemical fractions of the cell walls, along the lines of the classic study by Taylor (1971*a*, *b*) on leaves of mango.

The relationship between punch strength and fracture toughness

Choong *et al.* (1992) found a close relationship between fracture toughness and punch strength only after correcting for lamina thickness. The authors do not have values for both variables at any of the sites, but for the Panamanian forest the values for punch strength published by Coley (1983) and the present values for fracture toughness can

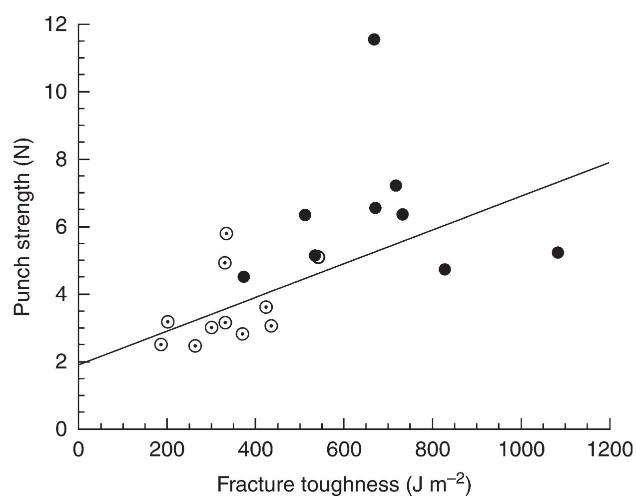

FIG. 3. The relationship between punch strength determined by Coley (1983) and fracture toughness (values from Appendix 3) for mature leaves of 20 dicot tree species: 11 light-demanding (open circles) and nine shade-tolerant (closed circles); the regression line ($y = 2{\cdot}44 + 0{\cdot}0042x$, $r = 0{\cdot}634$) is for the two groups of species together, omitting the outlier (*Calophyllum longifolium*).

be compared (Fig. 3). There is no significant relationship between the two variables if only the nine shade-tolerant species are considered ($r = 0{\cdot}007$; $P = 0{\cdot}99$), and a weak correlation if only the 11 light-demanding species are considered ($r = 0{\cdot}460$; $P = 0{\cdot}15$), but there is a significant and marked correlation if all species are considered together ($r = 0{\cdot}560$; $P = 0{\cdot}01$). The correlation becomes appreciably stronger if one shade-tolerant species (*Calophyllum longifolium*) is omitted ($r = 0{\cdot}639$; $P = 0{\cdot}003$). This finding parallels that of Coley (1988) who obtained significant positive correlations between leaf life span and the concentrations of tannins and fibres when using a data set comprising both strongly shade-tolerant and light-demanding species, but no significant correlation within either group when considered alone even though there were 21 species in the first group and 20 in the second.

As punch strength is not simply related to fracture toughness in dicots, it is not expected that the difference in fracture toughness between monocots and dicots during expansion will necessarily parallel closely the difference in punch strength.

Relevance to extent of herbivory

Leaf properties can only ever be a partial explanation of the extent of loss to invertebrate herbivores. Once an animal has evolved the ability to attack a certain type of leaf, the extent of damage is largely a function of how far the herbivore's population is kept down by predators, parasitoids and disease (Strong *et al.*, 1984). This is well shown by the way in which certain palms become badly damaged when in plantations rather than scattered in the forest (Cock *et al.*, 1987). A leaf property such as toughness can be effective in two ways: in making evolution of a specialist herbivore difficult, and in reducing attack by generalists. The latter seems more likely to be important in TLRF, as generalists have been found to dominate the herbivorous insect community (Novotny and Basset, 2005).

It is a fact that almost all those who have considered extent or rate of loss of area to invertebrate herbivores in relation to leaf 'toughness' in both tropical and temperate vegetation have used what we now call punch strength as their measure of 'toughness' (Williams, 1954; Tanton, 1962; Feeny, 1970; Coley, 1983; Lowman and Box, 1983; Raupp, 1985; Aide and Londoño, 1989; Ernest, 1989; Nichols-Orians and Schulz, 1990; Sagers, 1992; Braker and Chazdon, 1993; Feller, 1995; Filip *et al.*, 1995; Jackson, 1995; Coley and Barone, 1996; Coley and Kursar, 1996; Jackson *et al.*, 1999; Blundell and Peart, 1998; Howlett and Davidson, 2001; Marquis *et al.*, 2001; Spiller and Agrawal, 2003; Xiang and Chen, 2004). In contrast, those authors reporting critical, wider-ranging studies on the mechanical properties of leaves, in particular fracture toughness, have not also recorded rates of loss of leaf area in their study species, although the papers by Choong (1996), Iddles *et al.* (2003), Clissold *et al.* (2006) and Eichhorn *et al.* (2007) are exceptions. Peeters *et al.* (2007) recorded toughness measurements and related them to the densities of herbivorous insect guilds.

For the forest in Panama, it is possible to compare the correlations between log rate of loss of area from mature leaves with (*a*) punch strength and (*b*) fracture toughness. Coley (1983) provided the data for (*a*) and the authors have the data for (*b*). Of course, it would be better to have data on (*a*) and (*b*) from the same leaves, but a preliminary comparison is worthwhile. The correlation is tighter for punch strength than for fracture toughness ($r = 0{\cdot}727$ vs. $0{\cdot}660$; $P = 0{\cdot}0003$ vs. $0{\cdot}0021$; Fig. 4). *Calophyllum longifolium* which had zero loss to herbivores and a heavily biasing influence was left out of this analysis; if it were retained and the rate treated as 0·01 % per day, the difference between the two correlations would be even greater (punch strength: $r = 0{\cdot}796$, $P < 0{\cdot}0001$; fracture toughness: $r = 0{\cdot}655$, $P = 0{\cdot}0017$). In the present study, Coley (1983) has been followed in using the log rate of herbivory, but arguably the relationship between the rate of

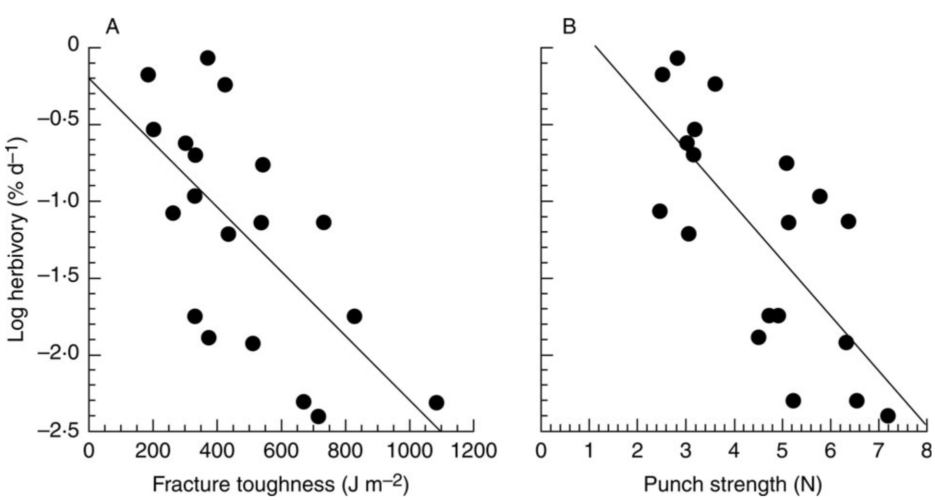

FIG. 4. The relationship between log rate of loss of leaf area to herbivores (y, determined by Coley, 1983) and (A) fracture toughness (x_1, Appendix 3), and (B) punch strength (x_2, Coley 1983). Regressions are: $y = 0{\cdot}455 - 0{\cdot}00482x_1$ ($r = 0{\cdot}660$), and $y = 0{\cdot}848 - 0{\cdot}812x_2$ ($r = 0{\cdot}727$).

herbivory and punch strength found in her classic study is not well characterized by a regression. Rather punch strength sets an upper limit to the probable rate of herbivory; the actual rate varies greatly at low values of punch strength, often being far below the limit set by punch strength (fig. 3 of Grubb *et al.*, 2008).

In a number of more recent studies on dicots in the wet and seasonally dry tropics there has been no evidence of lower rates of loss from tougher leaves. Eichhorn *et al.* (2007) measured the rate of loss over 6 months from seedlings of five species of Dipterocarpaceae in TLRF in Sabah, and found a negative correlation with the concentration of phenolics but a positive correlation with fracture toughness. Blundell and Peart (1998) had earlier found no relationship between herbivory and toughness in four species of Dipterocarpaceae, and Howlett and Davidson (2001) in two species of the same family, likewise Braker and Chazdon (1993) with three species of palms. Filip *et al.* (1995) found no significant correlation between toughness and the rate of herbivory in a tropical dry forest. Two studies based on intraspecific comparisons yielded no significant correlation between toughness and extent or rate of herbivory: those of Ernest (1989) and Feller (1995). These results have to be balanced against the positive correlations between greater toughness and less extensive herbivory reported from intraspecific comparisons by Aide and Londoño (1989), Nichols-Orians and Schulz (1990), Sagers (1992), Jackson (1995) and Spiller and Agrawal (2003), and from the comparison of four species of *Ficus* by Xiang and Chen (2004). The only study to yield a positive correlation between toughness and extent of herbivory based on comparisons of a large number of species (25) is that of Marquis *et al.* (2001) for a cerrado (savanna) site in Brazil. Here toughness and herbivory increased in the order herbs < shrubs < trees. Such a result might depend on a parallel trend in the number of herbivorous species, as is found in other vegetation-types (Strong *et al.*, 1984). There is no correlation between toughness and herbivory among the ten tree species studied by Marquis *et al.* (2001).

Notwithstanding the results of Eichhorn *et al.* (2007) and some other authors, we hypothesize that in TLRF the greater toughness of the leaves of monocots, especially the much greater toughness at the immature stage, is associated with smaller losses of leaf area to insects. This hypothesis is tested in a companion paper (Grubb *et al.*, 2008), which also considers the independent hypothesis that the much greater incidence in monocots of tight folding or rolling of leaves to a late stage in development will deter herbivorous invertebrates (Grubb and Jackson, 2007).

The range in toughness of fully mature leaves of monocots

In the light of work with dicots (Lucas *et al.*, 1995, 2000), the range in toughness among monocots would be expected to parallel the degree of development of fibres in the leaves. To an extent that appears to be the case, even when the crude categorizations for fibre-richness given in Table 1 are used. Most of the Arecaceae, Cyclanthaceae and Pandanaceae (all given a rating of +++ in Table 1) have relatively high values for fracture toughness or punch strength, while the Araceae (rated +) and Dioscoreaceae (rated –) have relatively low values (Appendices 1–3). However, some of the highest values for fracture toughness are for species of Marantaceae and Zingiberaceae (both rated ++) and Heliconiaceae (+). Clearly more sophisticated studies are needed to test the correlation between fracture toughness and development of fibres in the monocots of TLRF.

A new kind of tough leaf

The 'sclerophyll', which is characteristic of trees and tall shrubs in all five regions of the world with a Mediterranean type of climate, has been regarded by botanists since around 1900 as the type of leaf that is especially tough as well as hard and stiff. From the 1930s it came to be realized that scleromorphic leaves are also characteristic of forest and scrub communities of the wet tropics on exceptionally nutrient-poor soils (Grubb, 1986). In the last 15 years it has become clear that the Mediterranean-type sclerophylls, on average, do not have especially high fracture toughness when compared with leaves of trees of TLRF on average soils (Turner *et al.*, 1993) or even when compared with some mesomorphic evergreen leaves of the transition between Mediterranean-climate forest and warm temperate rain forest (Edwards *et al.*, 2000). The botanists' idea of sclerophylly is now known to correlate best with high values for dry mass per unit leaf area, leaf thickness and stiffness (Edwards *et al.*, 2000; Read and Sanson, 2003; Read *et al.*, 2006). Among the sclerophylls, those with a marked development of fibres along the vascular bundles have higher fracture toughness than those with minimal development of such fibres, e.g. among species of the Mediterranean Basin *Laurus nobilis* and *Quercus ilex* versus *Arbutus andrachne* and *A. unedo* (Turner *et al.*, 1993). A properly revised perspective of the 'tough leaf' among dicots is that it can be found among evergreen species in the whole gamut of vegetation-types from TLRF on both average soils and very poor soils through to Mediterranean-climate forests (Turner *et al.*, 1993, 2000; Edwards *et al.*, 2000; Read *et al.*, 2005, 2006).

Among the monocots of TLRF with high values for punch strength and fracture toughness, the Heliconiaceae, Marantaceae and Zingiberaceae (all Zingiberales) possess a new kind of tough leaf. They differ in five ways from those scleromorphic dicots with genuinely tough leaves found in the same kind of forest: they are typically much larger, have a greater incidence of water-storage tissue under the epidermides, higher saturated water concentrations, a lack of stiffness and a tendency to wilt readily under drying conditions.

The majority of the leaves of dicot trees in TLRF fall into the mesophyll size-class of Raunkiaer, as amended by Webb (1959), i.e. 4500–18 225 mm^2. In contrast, a high proportion of the Zingiberales have leaves in the macrophyll and megaphyll classes (18 225–164 025 and >164 025 mm^2). The families of TLRF in the Zingiberales with the largest leaf laminae are the Musaceae (up to at least 4000 × 1000 mm in *Ensete ventricosum*; Palgrave, 1983) and Strelitziaceae (up to at least 4000 mm long in *Ravenala madagascariensis*; Brickell, 2003). There are no measurement of lamina toughness for these families but, on the basis of their anatomy (Tomlinson, 1961), they would be expected to comply with the present findings for large-leaved Heliconiaceae.

Among dicots in TLRF the incidence of a colourless hypodermis is modest, 25 % or less of the species (Grubb *et al.*, 1975; Choong *et al.*, 1992), but it is very general in the Zingiberales, and such tissue generally occupies 20–45 % of the lamina thickness (Solereder and Meyer, 1928–33; Tomlinson, 1969; Roth, 1990). No data have been found on the saturated water concentrations of the leaves of the TLRF dicots shown by Turner *et al.* (1993, 2000) to have the highest recorded values for fracture toughness. However, among the dicots in high-rainfall forest in Australia, the five species found to have the greatest punch strength at maturity (45–54 g cm^{-2}; Appendix 2) are known to have saturated water concentrations of 1·1–1·9 g g^{-1} dry mass (Appendix 2 of Grubb *et al.*, 2008). In contrast, the ten species of Zingiberales for which toughness measurements are given in Appendices 1–3 had saturated water concentrations in the range 2·3–5·1 g g^{-1} (mean 3·8 ± 0·82 g g^{-1} s.e.; appendix 2 of Grubb *et al.*, 2008). Sclerophylls in general do not change shape easily when partially dried out (Grubb, 1986), and that statement certainly applies to those that are genuinely tough. In contrast, leaves of most Zingiberales do not combine toughness with stiffness, and many roll up readily under drying conditions. This behaviour has been seen at various sites in TLRF during rainless spells, and even in bright sunshine around midday in large canopy gaps and at forest edges when the soil has not dried out.

The palms of TLRF are much closer in form and behaviour to the tough dicots in the same forest, despite the typically large size of their leaves. These have only weakly developed colourless water-storage tissue or none (Tomlinson, 1961), and the saturated water concentration is in the same range as that of the tough dicots in TLRF (1·5–1·7 g g^{-1} dry mass, $n = 4$; appendix 2 of Grubb *et al.*, 2008). The leaves are mostly stiff and do not change shape readily as they dry out. The Cyclanthaceae and the Pandanaceae (both in the Pandanales) are intermediate between palms and the Zingiberales through being rich in fibres (Table 1) and relatively stiff, but rich in water: 3·1–3·7 g g^{-1} ($n = 3$; Grubb *et al.*, 2008).

The tough leaves of such monocots in TLRF as those of Zingiberales and Pandanales are new in kind in a further sense. Coley and Barone (1996, p. 319) wrote that 'toughness is not compatible with leaf expansion', but the monocots in question show that that is not true. The present results from Australian TLRF show that in leaves of Zingiberales and Pandanales with only 15–60 % of final lamina area the punch strength was already greater (by a factor of 2·1 on average) than in the fully expanded and fully toughened leaves of the neighbouring shade-tolerant dicots (cf. Appendix 2).

Turner *et al.* (1993) and Edwards *et al.* (2000) revised the botanist's concept of the tough leaf by showing that among dicots rain forest trees commonly have leaves that are as tough as, or indeed tougher than, sclerophylls of the Mediterranean-climate regions. Now, we suggest that botanists and ecologists should pay more attention to monocots in this context, and make a further adjustment to their concept of the 'tough leaf'.

CONCLUSIONS

As forecast on the basis of the abundance of fibres in their leaves, monocots in TLRF do indeed have greater punch strength and fracture toughness than the dicots with which they live. Many of the very tough monocot leaves are quite unlike the tough dicot sclerophylls of TLRF in being rich in water, and changing shape easily. Further work is needed to establish: (*a*) whether or not there is in monocots as in dicots, on average, greater toughness in shade-tolerators than in light-demanders, and (*b*) the anatomical and biochemical basis of the variation in fracture toughness and punch strength among the monocots. We forecast that the greater toughness of the monocots will be associated with smaller losses of leaf area to herbivorous invertebrates.

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APPENDIX 1

TABLE A1. Mean toughness (punch strength) values determined with a penetrometer for fully expanded leaves at two sites in Australian TLRF; species are ordered by the mean value for fully toughened leaves

	Family	Toughness of fully expanded but not fully toughened leaves (g cm^{-2})	Toughness of fully toughened leaves (g cm^{-2})
LOW-RAINFALL SITE			
Monocots			
Pothos longipes	Araceae	52	106
Pleuranthodium racemigerum	Zingiberaceae	79	109
Alpinia caerulea	Zingiberaceae	88	110
Alpinia modesta	Zingiberaceae	80	111
Alocasia brisbanensis	Araceae	39	122
Calamus caryotoides	Arecaceae	83	130
Mean (s.e.m.)		70 (8·1)	115 (3·8)
Dicots			
Hodgkinsonia frutescens	Rubiaceae	18	33
Castanospora alphandii	Sapindaceae	25	40
Mean (s.e.m.)		22 (3·5)	37 (3·5)
HIGH-RAINFALL SITE			
Monocots			
Alpinia arctiflora	Zingiberaceae	50	72
Cordyline cannifolia	Laxmanniaceae	48	95
Calamus australis	Arecaceae	ND	127
Freycinetia excelsa	Pandanaceae	101	>150
Mean (s.e.m.)		66 (17)	111 (17)
Dicots			
Cryptocarya pleurosperma	Lauraceae	24	48
Wilkiea angustifolia	Atherospermataceae		87
Mean (s.e.m.)		ND	68 (20)

Note: *Alpinia arctiflora, A. caerulea* and *Pleuranthodium racemigerum* all need tree-fall gaps or forest edges for establishment; the other species are shade-tolerant at establishment.

ND, not determined.

APPENDIX 2

TABLE A2. Mean toughness (punch strength) values determined with a penetrometer for immature leaves and for fully expanded and toughened leaves at the Australian high-rainfall site

Plant species	Family	Immature lamina area as % of mature lamina area (mean)	Mean toughness when immature (g cm^{-2})	Mean toughness when mature (g cm^{-2})
Monocots				
Rhaphidophora australasica	Araceae	50	26	73
Freycinetia scandens	Pandanaceae	21	66	80
Alpinia modesta	Zingiberaceae	55	58	109
Flagellaria indica	Flagellariaceae	42	86	138
Freycinetia excelsa	Pandanaceae	29	92	153
Pandanus monticola	Pandanaceae	22	142	>155
Mean		37	78	118
s.e.m.		5·9	16	15
Dicots				
Prunus turneriana	Rosaceae	16	7	29
Atractocarpus hirtus	Rubiaceae	22	20	29
Cupaniopsis flagelliformis	Sapindaceae	26	7	32
Pouteria castanosperma	Sapotaceae	20	15	38
Ardisia bifaria	Myrsinaceae	55	10	39
Opisthiolepis heterophylla	Proteaceae	20	12	43
Neolitsea dealbata	Lauraceae	17	7	45
Beilschmiedia tooram	Lauraceae	19	10	46
Cryptocarya mackinnoniana	Lauraceae	45	12	51
Franciscodendron laurifolium	Malvaceae	36	13	52
Argyrodendron trifoliolatum	Malvaceae	43	10	54
Mean		29	11	42
s.e.m.		4·1	1·2	2·7

All species can become established in the shade. The leaves of the monocots and the *Argyrodendron* were unrolled or unfolded before measurements were made – the leaves of the other dicots were neither rolled nor folded at the stage when measurements were made.

APPENDIX 3

TABLE A3. Mean fracture toughness values of the lamina determined for species in various functional groups in Singapore and Panama

	Family	Fracture toughness of the lamina (J m^{-2})
SINGAPORE		
Monocots (all shade-tolerant)		
Schismatoglottis wallichii	Araceae	308
Molineria latifolia	Hypoxidaceae	475
Tacca integrifolia	Dioscoreaceae	568
Calamus oxleyanus	Arecaceae	750
Amischotolype gracilis	Commelinaceae	782
Elettariopsis curtisii	Zingiberaceae	908
Caryota mitis	Arecaceae	1030
Hanguana malayana	Hanguanaceae	1052
Stachyphrynium griffithii	Marantaceae	1311
Mean (s.e.m.)		798 (105)
Gap- or edge-demanding dicots		
*Sapium discolor**	Euphorbiaceae	81
*Trema cannabina**	Cannabaceae	122
Clerodendrum villosum	Verbenaceae	211
Archidendron clypearia	Fabaceae	229
*Trema tomentosa**	Cannabaceae	266
*Dillenia suffruticosa**	Dilleniaceae	283
*Macaranga heynei**	Euphorbiaceae	285
*Ploiarium alternifolium**	Pentaphylaceae	307

Continued

TABLE A3. *Continued*

	Family	Fracture toughness of the lamina (J m^{-2})
Adinandra dumosa	Pentaphylaceae	339
*Macaranga gigantea**	Euphorbiaceae	343
Melastoma malabathricum	Melastomataceae	357
Macaranga conifera	Euphorbiaceae	359
Ficus aurantiaca	Moraceae	368
Endospermum diadenum	Euphorbiaceae	378
Fagraea fragrans	Loganiaceae	528
*Myrica esculenta**	Myricaceae	689
Mean (s.e.m.)		322 (36)
Shade-tolerant dicots		
Parkia speciosa	Fabaceae	234
Pellacalyx saccardianus	Rhizophoraceae	253
Strombosia javanica	Olacaceae	289
Ficus grossularioides	Moraceae	303
Pternandra echinata	Melastomataceae	357
Dysoxylum cauliflorum	Meliaceae	380
Strychnos axillaris	Loganiaceae	384
Garcinia parvifolia	Clusiaceae	403
Prunus polystachya	Rosaceae	404
Milletia atropurpurea	Fabaceae	439
Ficus fistulosa	Moraceae	443
Clerodendrum laevifolium	Verbenaceae	457
Gynotroches axillaris	Rhizophoraceae	458
Aporusa frutescens	Phyllanthaceae	539
Palaquium microcarpum	Sapotaceae	549
Artocarpus elasticus	Moraceae	550
Bhesa paniculata	Celastraceae	561
Calophyllum pulcherrimum	Clusiaceae	566
Xylopia malayana	Annonaceae	573
Timonius wallichianus	Rubiaceae	581
Santiria apiculata	Burseraceae	585
Ochnastachys amentacea	Olacaceae	597
Baccaurea parviflora	Phyllanthaceae	599
Artocarpus integer	Moraceae	609
Diospyros buxifolia	Ebenaceae	633
Elaeocarpus ferrugineus	Elaeocarpaceae	641
Palaquium gutta	Sapotaceae	654
Castanopsis lucida	Fagaceae	660
Albizia splendens	Fabaceae	662
Rhodamnia cinerea	Myrtaceae	663
Streblus elongatus	Moraceae	668
Aporusa benthamiana	Phyllanthaceae	690
Lithocarpus conocarpus	Fagaceae	700
Eugenia grandis	Myrtaceae	706
Buchanania arborea	Anacardiaceae	713
Dacryodes buxifolia	Burseraceae	713
Garcinia griffithii	Clusiaceae	732
Campnosperma auriculatum	Anacardiaceae	759
Anisophyllea disticha	Anisophylleaceae	771
Gironniera parvifolia	Cannabaceae	788
Nephelium lappaceum	Sapindaceae	791
Durio zibethinus	Malvaceae	805
Mangifera indica	Anacardiaceae	862
Sindora wallichiana	Fabaceae	1005
Xanthophyllum maingayi	Polygalaceae	1025
Fibraurea tinctoria	Menispermaceae	1061
Mean (s.e.m.)		605 (28)
PANAMA		
Gap- or edge-demanding non-palm monocots		
Costus laevis	Costaceae	370
Costus guinaiensis	Costaceae	510
Heliconia latispatha	Heliconiaceae	618
Heliconia mariae	Heliconiaceae	995
Calathea lutea	Marantaceae	1119
Heliconia catheta	Heliconiaceae	1307

Continued

TABLE A3. *Continued*

	Family	Fracture toughness of the lamina (J m^{-2})
Carludovica palmata	Cyclanthaceae	1695
Pleiostachya pruinosa	Marantaceae	2164
Mean (s.e.m.)		1097 (218)
Shade-tolerant non-palm monocots		
Philodendron pterotum	Araceae	151
Chusquea simpliciflora	Poaceae	479
Streptochaeta spicata	Poaceae	652
Streptochaeta sodiroana	Poaceae	662
Pharus latifolius	Poaceae	795
Streptogyne americana	Poaceae	850
Mean (s.e.m.)		598 (104)
Palms (all shade-tolerant)		
Desmoncus orthocanthos	Arecaceae	572
Chamaedorea tepejilote	Arecaceae	590
Geonoma interrupta	Arecaceae	673
Synecanthus warscewiczianus	Arecaceae	869
Bactris barronis	Arecaceae	928
Bactris coloradonis	Arecaceae	1022
Socratea exorrhiza	Arecaceae	1033
Attalea butyracea	Arecaceae	1175
Wettinia panamensis[‡]	Arecaceae	1265
Bactris major	Arecaceae	1329
Chamaedorea warscewiczii[‡]	Arecaceae	1345
Cryosophila warscewiczii	Arecaceae	1422
Oenocarpus mapora	Arecaceae	1501
Bactris coloniata	Arecaceae	1506
Elaeis oleifera	Arecaceae	1562
Astrocaryum standleyanum	Arecaceae	1573
Geonoma cuneata	Arecaceae	1776
Phytelephas seemannii[‡]	Arecaceae	1868
Euterpe precatoria[‡]	Arecaceae	2116
Mean (s.e.m.)		1270 (99)
Gap- or edge-demanding dicots		
Trema micrantha[§]	Cannabaceae	186
Cordia alliodora[†,§]	Boraginaceae	201
Psychotria pubescens	Rubiaceae	234
Terminalia amazonica	Combretaceae	241
Trattinnickia aspera[†,§]	Burseraceae	263
Guazuma ulmifolia	Malvaceae	280
Ficus insipida[†]	Moraceae	290
Luehea seemannii[†,§]	Malvaceae	301
Apeiba tibourbou[§]	Malvaceae	331
Sapium aucuparium[§]	Euphorbiaceae	332
Cecropia insignis[†,§]	Urticaceae	333
Cecropia obtusifolia[†,§]	Urticaceae	370
Spondias radlkoferi[†,§]	Anacardiaceae	424
Zanthoxylum belizense[§]	Rutaceae	435
Annona spraguei[§]	Annonaceae	545
Psychotria brachiata	Rubiaceae	585
Psychotria racemosa	Rubiaceae	596
Anacardium excelsum[†]	Anacardiaceae	628
Pseudobombax septenatum	Malvaceae	682
Psychotria poeppigiana	Rubiaceae	686
Spondias mombin[†]	Anacardiaceae	841
Mean (s.e.m.)		418 (41)
Shade-tolerant dicots		
Platypodium elegans	Fabaceae	202
Psychotria horizontalis	Rubiaceae	206
Psychotria chagrensis	Rubiaceae	217
Psychotria limonensis	Rubiaceae	240
Psychotria marginata	Rubiaceae	311
Lacmellea panamensis[†]	Apocynaceae	340
Serjania mexicana[†]	Sapindaceae	362
Virola surinamensis[†]	Myristicaceae	364

Continued

TABLE A3. *Continued*

	Family	Fracture toughness of the lamina (J m^{-2})
Virola sebifera[†,§]	Myristicaceae	373
Virola multiflora[†]	Myristicaceae	376
Tabernaemontana arborea	Apocynaceae	378
Unonopsis pittieri	Annonaceae	381
Symphonia globulifera[†]	Clusiaceae	397
Astronium graveolens[†]	Anacardiaceae	405
Pourouma bicolor[†]	Urticaceae	410
Genipa americana	Rubiaceae	413
Dendropanax arboreus[†]	Araliaceae	432
Psychotria graciliflora	Rubiaceae	450
Tachigalia versicolor[†]	Fabaceae	461
Garcinia intermedia	Clusiaceae	463
Hasseltia floribunda	Salicaceae	495
Xylopia macrantha	Annonaceae	506
Protium panamense[†]	Burseraceae	509
Protium tenuifolium	Burseraceae	512
Trichilia tuberculata	Meliaceae	521
Aspidosperma cruenta[†]	Apocynaceae	535
Hirtella triandra[§]	Chrysobalanaceae	537
Piper reticulatum[†]	Piperaceae	545
Brosimum alicastrum	Moraceae	609
Calophyllum longifolium[†,§]	Clusiaceae	669
Guarea grandiflora[§]	Meliaceae	669
Psychotria psychotrifolia	Rubiaceae	678
Sterculia apetala	Malvaceae	704
Cupania rufescens	Sapindaceae	712
Poulsenia armata[†,§]	Moraceae	717
Tetragastris panamensis[§]	Burseraceae	732
Chrysophyllum cainito[†]	Sapotaceae	740
Chrysophyllum argenteum[†]	Sapotaceae	758
Psychotria brachybotrya	Rubiaceae	819
Quararibea asterolepis[§]	Malvaceae	829
Perebea xanthochyma[†]	Moraceae	837
Beilschmiedia pendula	Lauraceae	925
Guatteria dumetorum[†,§]	Annonaceae	1085
Psychotria capitata	Rubiaceae	1129
Psychotria deflexa	Rubiaceae	1144
Dipteryx panamensis	Fabaceae	1232
Mean (s.e.m.)		572 (37)

Values for the fracture toughness of the veins and midrib are available from Dr N. J. Dominy. All values are original unless otherwise stated.
* Values taken from Choong *et al.* (1992); these are not used in Fig. 2.
[†] Values taken from Dominy *et al.* (2003).
[‡] Species not present in Barro Colorado Natural Monument.
[§] Species used by Coley (1983) in her comparison of 'toughness' values in 'pioneer' and 'persistent' species.