Monocot Leaves are Eaten Less than Dicot Leaves in Tropical Lowland Rain Forests: Correlations with Toughness and Leaf Presentation

PETER J. GRUBB[1,*], ROBYN V. JACKSON[2], IGNACIO M. BARBERIS[1,†], JENNIE N. BEE[1,‡],
DAVID A. COOMES[1], NATHANIEL J. DOMINY[3], MARIE ANN S. DE LA FUENTE[4],
PETER W. LUCAS[5], DANIEL J. METCALFE[6], JENS-CHRISTIAN SVENNING[7], IAN M. TURNER[8,§]
and ORLANDO VARGAS[9]

[1]*Plant Sciences Department, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK,* [2]*19 Cananga Close, Kamerunga, Qld 4870, Australia,* [3]*Department of Anthropology, University of California, 1156 High St, Santa Cruz, CA 95064, USA,* [4]*Reserva Ecológica Bijagual, Apto. 353069, Puerto Viejo, Sarapiquí, Costa Rica,* [5]*Department of Anthropology, George Washington University, 2110 G Street, NW, Washington, DC 20052, USA,* [6]*Commonwealth Scientific and Industrial Research Organization, Sustainable Ecosystems, Tropical Forest Research Centre, PO Box 780, Atherton, Queensland 4883, Australia,* [7]*Department of Biological Sciences, University of Aarhus, Ny Munkegade 1540, DK-8000, Aarhus C, Denmark,* [8]*Singapore Botanic Gardens, National Parks Board, 1 Cluny Road, Republic of Singapore 259569 and* [9]*Organización para Estudios Tropicales, Estación Biológica La Selva, Aptdo 676 2050 San Pedro, Costa Rica*

• *Background and Aims* In tropical lowland rain forest (TLRF) the leaves of most monocots differ from those of most dicots in two ways that may reduce attack by herbivores. Firstly, they are tougher. Secondly, the immature leaves are tightly folded or rolled until 50–100 % of their final length. It was hypothesized that (*a*) losses of leaf area to herbivorous invertebrates are generally greatest during leaf expansion and smaller for monocots than for dicots, and (*b*) where losses after expansion are appreciable any difference between monocots and dicots then is smaller than that found during expansion.

• *Methods* At six sites on four continents, estimates were made of lamina area loss from the four most recently mature leaves of focal monocots and of the nearest dicot shoot. Measurements of leaf mass per unit area, and the concentrations of water and nitrogen were made for many of the species. In Panama, the losses from monocots (palms) and dicots were also measured after placing fully expanded palm leaflets and whole dicot leaves on trails of leaf-cutter ants.

• *Key Results* At five of six sites monocots experienced significantly smaller leaf area loss than dicots. The results were not explicable in terms of leaf mass per unit area, or concentrations of water or nitrogen. At only one site was the increase in loss from first to fourth mature leaf significant (also large and the same in monocots and dicots), but the losses sustained during expansion were much smaller in the monocots. In the leaf-cutter ant experiment, losses were much smaller for palms than for dicots.

• *Conclusions* The relationship between toughness and herbivory is complex; despite the negative findings of some recent authors for dicots we hypothesize that either greater toughness or late folding can protect monocot leaves against herbivorous insects in tropical lowland rain forest, and that the relative importance varies widely with species. The difficulties of establishing unequivocally the roles of leaf toughness and leaf folding or rolling in a given case are discussed.

Key words: anti-herbivore defences, dicots, herbivory, leaf folding, leaf rolling, leaf toughness, monocots, palms, tropical rain forest.

INTRODUCTION

In tropical lowland rain forest (TLRF) the leaves of monocots differ from those of dicots (eudicots and magnoliids) in two ways that are likely to reduce losses to herbivores. In general they are tougher, and a majority of them have the leaves tightly folded or rolled until a late stage of development. Dominy *et al.* (2008) found in a study of mature leaves spread across three rain forest regions that toughness (either punch strength or fracture toughness) was greater in monocots. The same authors showed for Australian rain forest that the difference in punch strength between monocots and dicots was relatively greater for immature leaves (with about 30 % mature area on average) than for fully expanded and fully toughened leaves. Critical studies on the fracture toughness of dicot leaves have shown that the chief determinant 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). Among monocots in TLRF greater toughness is characteristic of not only stiff-leaved plants, such as many

palms, but also monocots with water-rich leaves that readily roll up under drying conditions, such as many gingers.

For dicots in TLRF the classic study of Coley (1983) found that greater toughness (punch strength) was strongly negatively correlated with the rate of leaf area loss, and several later authors have found the same correlation, although some others have found no correlation (reviewed by Dominy *et al.*, 2008). Notwithstanding the negative findings of some recent authors, we hypothesize that in TLRF monocots will be found to suffer, on average, less extensive loss of leaf area than dicots.

Grubb and Jackson (2007, tables 1 and 2) reported that, when TLRF on all continents is considered, species with the leaves tightly folded or rolled until >50 % of mature length are found in 56 % of families of monocots, but in only 3·3 % of families of dicots. At the species level the difference is even greater as in the majority of major monocot families the leaves of every species are tightly folded or rolled to a late stage, while in the majority of the dicot families involved only a minority of species has the leaves folded or rolled until >50 % of mature length. Authoritative reviews of invertebrate herbivory and plant defence in TLRF have failed to mention the possibility that tight folding or rolling of leaves to a late stage of development could be an effective defence against herbivores (Coley and Barone, 1996; Coley and Kursar, 1996). However, it has been shown for both tropical and temperate plants that, although most losses to herbivorous insects occur while the leaf is expanding, the losses are very small when the young leaf is still folded or rolled (Jackson, 1995; Jackson *et al.*, 1999). Grubb and Jackson (2007) hypothesized that the late folding and rolling of the leaves of monocots in TLRF, while possibly of value in increasing structural stiffness as suggested by King *et al.* (1996), is of equal or greater importance in reducing attack by invertebrate herbivores.

In this paper, tests of two hypotheses are presented.

(1) Most of the loss of lamina area to herbivorous invertebrates occurs during leaf expansion, and the proportion lost is smaller for monocots than for nearest-neighbour dicots.
(2) At any site where there is appreciable loss of lamina area to herbivorous invertebrates after leaf expansion, the difference between monocots and nearest-neighbour dicots in the proportion lost to herbivorous invertebrates during expansion (i.e. when the laminae are rolled or folded to a late stage) is greater than any difference found once the laminae are fully expanded.

In the interpretation of the results, the measurements of punch strength and fracture toughness reported by Dominy *et al.* (2008) and original data on leaf mass per unit area and the concentrations of nitrogen and water were used. Also reported are the relative losses from palm leaflets and dicot leaves left on trails of leaf-cutter ants. In the Discussion, the problems of demonstrating that any reduction in leaf-area loss from monocots during expansion is a result of the folding or rolling is considered.

MATERIALS AND METHODS

Study sites

Details of four of our six sites are shown in table 1 of Dominy *et al.* (2008): the Australian low-rainfall and high-rainfall sites and the Singaporean and Panamanian sites.

The Ugandan site was in Kibale Forest National Park (30°21′E, 0°34′N; altitude approx. 1500 m), where the mean annual rainfall is 1500 mm, and there is one dry month *sensu* Walter (1971). Species nomenclature for this site follows the *Flora of Tropical East Africa* except that *Leptaspis zeylanica* Nees ex Steud., not *L. urceolata* R. Br., is recognized From families not yet covered by the *Flora*, *Dracaena fragrans* (L.) Ker Gawl, *D. laxissima* Engl., *Palisota mannii* C.B. Cl. and *Pollia condensata* C.B. Cl. were used

The Costa Rican site was at La Selva Biological Station (84°00′W, 10°26′N; altitude approx. 100 m), where the mean annual rainfall is 4000 mm, and there is no 'dry month'. Species nomenclature for this site follows the La Selva Florula (www.ots.ac.cr/local/florula2005). The families and orders recognized follow Stevens (2007).

Sampling leaves and recording percentage area lost

Observers walked along a path through the forest, or on a bearing within the understorey, making records for one individual of each species of monocot tested using the first individual encountered within 2 m of the centre of the path (or the bearing) until all had been covered. Records were then made for the next individual of each species encountered regardless of order until all species had been sampled for a second time. This procedure was followed until ten individuals of each study species had been recorded. For each individual monocot the following records were made. The percentage of lamina area missing was estimated separately for each of the first four fully expanded and fully toughened leaves on the scale: 0, <1, 1–5, 5–10, 10–15, 15–25, 25–50, 50–75, 75–100. The same was done for the dicot shoot nearest to the main axis of the monocot. For each of the leaves recorded, the actual value for area missing was assumed to be the geometric mean of the upper and lower limits of the interval concerned, i.e. 0, 0·32, 2·24, 7·1, 12·2, 19·4, 35·4, 61·2 and 86·6. A variant of this procedure was used at the two Australian sites; the percentage area missing from each of the four leaves per plant was estimated to one digit rather than in classes. In almost all cases the area recorded as 'missing' was wholly missing, but in a very few cases (notably *Calathea latifolia* in Panama) it was missing only on one side as a result of scraping by an invertebrate.

The data were arcsine square-root transformed, and subjected to a nested generalized linear model (leaves within species within sites). The significance of differences between specific classes of leaves was determined using a two-tailed *t*-test on the response variable (proportion of lamina area lost by one class of leaf minus the proportion lost by another class).

Sites used within the forests and numbers of species studied

All the species used are listed in Appendix 1. At the two Australian sites and the Singaporean site, records were made in January 1999. At the Australian low-rainfall site six monocot species were studied (two light-demanding and four shade-tolerant). They were sampled along a path in tall forest; the extent of opening of the canopy was often sufficiently great to allow the establishment of the light-demanding species. At the Australian high-rainfall site, five monocot species were studied: one light-demanding species at the forest edge, and four shade-tolerant species on a bearing in the understorey of tall forest. At the Singaporean site five shade-tolerant monocot species were studied, all sampled on narrow paths through the understorey of tall forest.

At the Ugandan site, records were made in September 2001. Ten monocot species were studied (two light-demanding and eight shade-tolerant). They were sampled in tall forest beside narrow paths; in places the extent of opening of the canopy was sufficient to allow the establishment of the light-demanding species.

At the Costa Rican site, records were made in January 2000; eight shade-tolerant monocot species were studied, all sampled along a narrow path through tall forest. At the Panamanian site, records were made in January 2000 for three species (the light-demanding *Calathea* and *Heliconia metallica*, and the shade-tolerant *Desmoncus*; $n = 5$) and April–May 2001 for the other five species (two light-demanding and three shade-tolerant; $n = 10$–15). These species were studied in tall forest along paths of varying width; in places the extent of opening of the canopy was sufficient to allow the establishment of the light-demanding species.

An important feature of the sampling method is that all of the monocots studied occurred widely through the forest; monocots confined to specialized habitats within the forest landscape such as *Pandanus ugandensis* and *Phoenix reclinata*, which occur in the study area in Uganda but are confined to swamps or river-edges, were not included. The Australian low-rainfall site and Costa Rican site have only gentle slopes, and the study species occur right across them. The Australian high-rainfall site and the Singaporean and Panamanian sites have more marked topography, and a sophisticated study would probably show that some of the monocots are more common at uphill or downhill sites, but all of them were seen to be widely distributed from ridges to lower slopes. The Ugandan site is the only one where the monocots are all confined to part of the area inhabited by the dicots in the study. The monocots are certainly not plants of the valley-floor swamps, but are confined to lower-slope sites; the dicots that occur on these sites also extend to upper slope sites and were not studied there.

Measurements of dry mass per unit area of lamina and the concentrations of nitrogen and water

In order to see how far, if at all, differences in the losses from the laminae of monocots and dicots might be explained by leaf properties other than toughness, leaf dry mass per unit fresh area (LMA) and the concentrations of water and nitrogen were measured. For all three variables, fully expanded and toughened leaves were used; those used for LMA and N determinations were put into an oven for about 24 h within about 6 h of collection from the parent plant. LMA was calculated using leaf areas determined with a Delta-T leaf area meter and cut-out outlines of leaves (Australia) or a LICOR area meter with either fresh leaves (Costa Rica) or cut-out outlines of leaves (Panama), or by weighing cut-out outlines against a standard area (Uganda). The total nitrogen concentration was determined using an automated Kjeldahl method in Cambridge, UK; as a check samples of a well-mixed leaf powder for which Dr E. V. J. Tanner had obtained analyses from a number of laboratories were included in the analyses. Water concentration at saturation was determined on leaves left to hydrate overnight in a saturated atmosphere with their bases in liquid water. In each case, three replicates were used to obtain a mean value unless indicated otherwise.

For the Australian low-rainfall site, all the monocot species shown in Appendix 1 were compared with the two overwhelmingly most abundant dicots (*Castanospora alphandii* and *Hodgkinsonia frutescens*) and six other dicots common at the site and characteristic of the forest-type ($n = 2$ for all species). For the Australian high-rainfall site, four of the monocot species in Appendix 1 (not *Pothos*) were compared with 41 shade-tolerators ($n = 2$ or 3).

At the Singaporean site all the monocot species were shade-tolerant, and all the species in Appendix 1 were compared with the 14 shade-tolerant dicot species analysed by Grubb *et al.* (1994); $n = 3$ in all cases. Note that *Ficus fistulosa* and *F. grossularioides* were categorized as light-demanding by Grubb *et al.* (1994) but found to be shade-tolerant at establishment by Metcalfe *et al.* (1998). For the Ugandan site, analyses were made in 2001 of nitrogen ($n = 1$) for six out of ten monocots in Appendix 1 (one light-demanding and five shade-tolerant) and compared with 18 of the most abundant dicots in the understorey ($n = 1$ for all species). All but one of these species were analysed for leaf dry mass per unit area and water concentration ($n = 3$) in 1998.

For the Costa Rican site, all the monocot species were shade-tolerant; all of those in Appendix 1 ($n = 3$) were compared with 17 of the nearest-neighbour dicot species ($n = 1$ mostly, in some cases 2–5). For the Panamanian site, analyses of water concentration and leaf dry mass per unit area were made for five out of eight monocots in Appendix 1 ($n = 3$; two light-demanding and three shade-tolerant) and for 15 unidentified nearest-neighbour dicots of the five species ($n = 3$).

Comparison of losses from dicots and palms to leaf-cutter ants

On 12 days in October–November 2001, eight fully expanded leaves (or leaflets in the case of palms with divided leaves), in healthy, undamaged condition, of two palm and two dicot tree or shrub species were placed alternately at 15-cm intervals on one of two neighbouring active

trails of *Atta colombica* at Gamboa, Panama. The mean areas ($\pm$ s.e.) of the palm leaflets and dicot leaves put out were not significantly different: 173 ± 20 cm^2 and 144 ± 24 cm^2. Percentage loss of leaf area was estimated visually for each leaf after 24–25 h. On each day a new set of plant species was used, except that two palm species (*Chamaedorea tepejilote* and *Bactris coloniata*) had to be used twice. Both native and exotic palms were used to increase the number of palm species tested. Dicots were selected to sample a broad range of life histories among common native trees and shrubs. In all, 21 palm species and 24 dicots were used. The hypothesis that palms experienced a smaller percentage area loss than dicots using the one-tailed sign test was tested, comparing the mean value for palms with that for dicots for each experiment ($n = 12$).

RESULTS

Incidence of lamina area loss relative to leaf development

At five of the six sites (not the one in Uganda) the apparent slight increases in area lost from the lamina between the first mature leaf and the fourth are not significant for either monocots or dicots. This result is consistent with the first part of our first hypothesis: that the losses of leaf area occur mostly before leaf expansion is complete.

Proportion of lamina lost by monocots and by nearest-neighbour dicots

At five of the six sites the second part of our first hypothesis was upheld; the estimated percentage area missing from monocots was significantly and markedly smaller than that missing from dicots (Fig. 1; $P < 0.01$ for four sites, and $P < 0.05$ for that in Panama). At the Costa Rican site monocots also tended to lose less lamina area, but the difference was not significant ($P > 0.05$); invertebrates removed as high a proportion of leaf area from three of the study species as from nearest-neighbour dicots, or even a greater proportion (Appendix 1). The only analogous cases were found in the Panamanian sample.

Relationship between lamina properties and area lost

There is no evidence that higher values for dry mass per unit leaf area, or lower values for nitrogen or water concentration, can explain the differences in extent of herbivory between monocots and dicots in the Old World. The present data on these variables for fully expanded and toughened leaves (Table 1) show few significant differences between monocots and dicots at a given site. In both cases where the difference is significant, the monocots would be expected to be more palatable (lower LMA at the Australian high-rainfall site and at the Ugandan site). Of the New World sites only the one in Costa Rica yielded a significant difference; the monocots had a significantly lower nitrogen concentration, but there was no significant difference between monocots and dicots in the extent of leaf area loss (Fig. 1).

Losses from monocots and dicots during expansion where there are significant losses after expansion

At the Ugandan site there were significant and marked increases in estimated percentage of lamina area missing between the first and fourth leaves for both monocots and dicots (Fig. 2). It was thus possible at this site to test the second hypothesis: that the difference between monocots
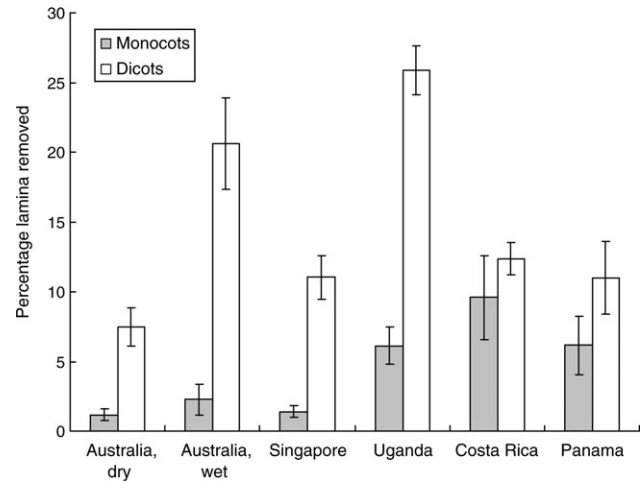

FIG. 1. The estimated mean percentage ($\pm$ s.e.) of lamina area missing from the first four fully expanded and toughened leaves of focal monocot species and their nearest-neighbour dicots at four sites in the Old World and two in the New World. For original data see Appendix 1.

TABLE 1. *Summary of mean values ($\pm$ s.e.) for characteristics of mature leaves of monocots and dicots at various sites*

	Dry mass per unit leaf area (mg cm^{-2})	Nitrogen concentration (mg g^{-1} dry mass)	Water concentration (g g^{-1} dry mass)
Australia: low-rainfall site			
Monocots	6.70 ± 2.15	23.9 ± 3.59	4.0 ± 1.1
Dicots	5.17 ± 0.50	28.2 ± 4.78	3.0 ± 0.5
Australia: high-rainfall site			
Monocots	5.35 ± 0.19***	18.3 ± 0.90	3.3 ± 0.6
Dicots	7.0 ± 0.31	19.1 ± 1.1	2.1 ± 0.1
Singapore			
Monocots	ND	25.7 ± 3.03	ND
Dicots	ND	17.9 ± 1.18	ND
Uganda			
Monocots	3.88 ± 0.28*	26.3 ± 2.01	4.2 ± 1.1
Dicots	5.18 ± 0.37	26.1 ± 1.35	2.4 ± 0.25
Costa Rica			
Monocots	4.86 ± 0.53	19.5 ± 2.36*	3.4 ± 0.43
Dicots	3.78 ± 0.23	27.2 ± 1.9	3.2 ± 0.37
Panama			
Monocots	4.34 ± 0.35	ND	1.8 ± 0.48
Dicots	5.16 ± 0.49	ND	2.4 ± 0.45

Primary data are given in Appendix 2.

The cases where monocots and dicots at a site were statistically different (two-tailed *t*-test) are indicated: *$P < 0.05$; ***$P < 0.001$.
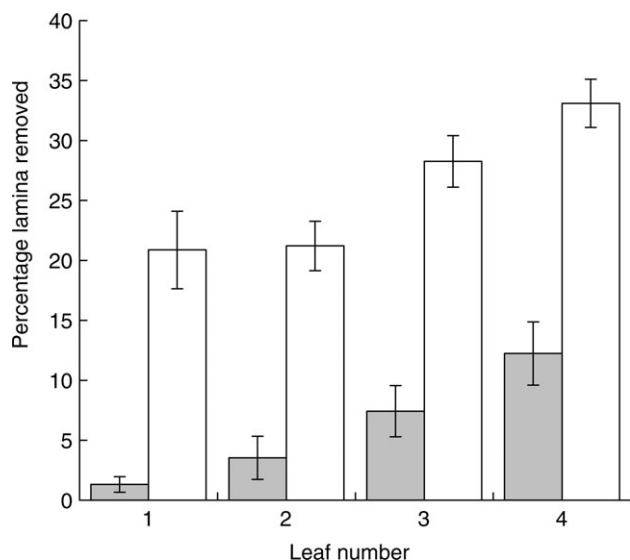
ND, not determined.

Fig. 2. The estimated mean percentage ($\pm$ s.e.) of lamina area missing from the first four fully expanded and toughened leaves of monocots and nearest-neighbour dicots at the Ugandan site. Leaf 1 is the most recent to become fully toughened.

and nearest-neighbour dicots in the proportion of leaf area lost to herbivorous invertebrates during expansion (i.e. when the laminae are rolled or folded to a late stage) is greater than any difference found once the laminae are fully expanded. Our hypothesis is supported; the losses from the first fully mature leaves were very much smaller for monocots than for dicots (Fig. 2; $P < 0.05$), while the mean increases between the first and fourth mature leaves (10·5 % monocots, 11·2 % dicots) were not significantly different ($P > 0.05$).

Losses from palm leaflets and dicot leaves placed on trails of leaf-cutter ants

The mean percentage losses were much smaller for palm leaflets (3·0 $\pm$ 1·8 %, s.e.) than for dicot leaves (61 $\pm$ 8·0 %; $P = 0.00024$).

DISCUSSION

Losses of leaf area from monocots and dicots

The hypothesis that monocots would be found to have smaller losses of leaf area than dicots proved to be correct at five out of six study sites. The same trend was found at the sixth site (in Costa Rica), but the difference was not significant. At the Panamanian site, the difference between monocots and dicots was less than at the four Old World sites. Possibly there is a higher incidence in the New World tropics of invertebrates able to overcome the defences of monocots. Certainly significant damage by invertebrates on palms and other monocots has been recorded at our Costa Rican site (Strong, 1977; Braker, 1991; Braker and Chazdon, 1993). However, some cases of severe damage to monocot leaves by invertebrates have been recorded from the Old World tropics too (Cock

et al., 1987), and further sampling is needed to test whether or not there is a consistent difference between the Old and New World tropics.

Losses from leaves before and after expansion

The finding that at the majority of sites most losses of lamina area from both monocots and dicots occurred during the expansion phase agrees with the results of earlier work (Coley, 1983; Lowman, 1985; Coley and Barone, 1996; Coley and Kursar, 1996). At the one site where there were appreciable losses after expansion (in Uganda), a useful test of the difference between monocots and dicots in loss of leaf area could be made both during and after expansion. There was no difference after expansion, but a huge difference during the expanding phase (Fig. 2). This result provides a *prima facie* case for the value of late rolling in protection against herbivorous invertebrates, but other interpretations are possible as is emphasized below.

Interpreting relative losses from monocots and dicots

There was no case that the smaller losses from monocots might be a result of larger amounts of dry mass per unit area, or smaller amounts of water or nitrogen per unit dry mass. On the other hand, recent research has shown that insect attack may be related to the balance between nitrogen and other key nutrients in leaves rather than to the concentration of nitrogen as such (cf. Clissold *et al.*, 2006), and new studies of this issue are needed for plants and insects in TLRF. Although some monocots in TLRF undoubtedly contain significant quantities of secondary metabolites that may deter herbivores, the general trend seems to be for a less marked development in monocots than in dicots (Hegnauer, 1963–86). Thus, there is a strong case for considering the impacts of leaf toughness and leaf rolling or folding.

The much smaller losses from mature palm leaflets than from mature dicot leaves placed on trails of leaf-cutter ants at our Panamanian site is consistent with the palm laminae having greater fracture toughness (appendix 3 in Dominy *et al.*, 2008). On the other hand the fact that at the Ugandan site mature leaves of monocots and dicots suffered the same losses of leaf area raises a problem. If at that site the monocot leaves are tougher than those of the dicots, as found for all four sites where Dominy *et al.* (2008) made tests (two in Australia and one each Singapore and Panama), then the evidence is against the importance of toughness. There was no palm or pandan at the Ugandan study site, and possibly the monocot leaves were not tougher than the dicot leaves (cf. dicots and non-palm monocots among the shade-tolerators in Panama; fig. 2 in Dominy *et al.* 2008). If so, the evidence would support the importance of leaf rolling as a protection.

Inspection of the relationship between the rate of loss of leaf area from mature leaves of dicot trees and their punch strength found by Coley (1983) shows that it is one where punch strength appears to set an upper limit. Many species with low punch strength suffer rates of loss far
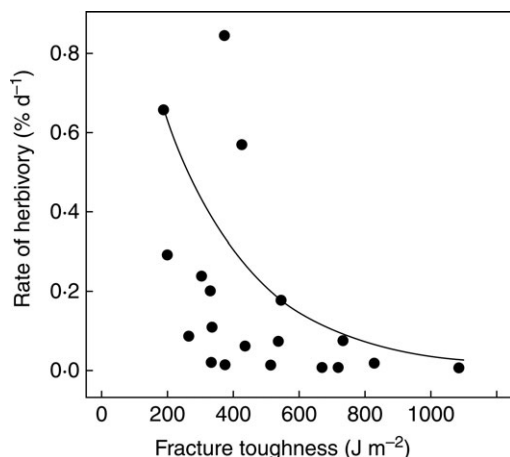
Fig. 3. The relationship between rate of loss of area to invertebrate herbivores and fracture toughness for mature leaves of 19 species of dicot trees in Panama; the line shows the upper 80 % quantile fitted by quantile regression implemented in R. Data on herbivory from Coley (1983) and on fracture toughness from Dominy *et al.* (2008).

below the limit, presumably because other defences (physical and/or chemical) are effective, or because the populations of the relevant herbivores are kept low by predators, parasitoids, disease or physical factors. Essentially the same relationship is found between rate of loss and fracture toughness, with the maximum rate of loss at $600 \, \text{J m}^{-2}$ reduced to about an order of magnitude lower than the maximum at $200 \, \text{J m}^{-2}$ (Fig. 3). Our working hypothesis for monocots is that values for fracture toughness above about $600 \, \text{J m}^{-2}$ are a strong disincentive to herbivores, and that late-rolling or -folding is likely to have the greater inhibitory effect at values $<600 \, \text{J m}^{-2}$. Almost all the palms we tested had fracture toughness values $>600 \, \text{J m}^{-2}$ (Appendix 3 of Dominy *et al.* 2008). We suggest that the late folding of palms and cyclanths is of value in reducing damage by at least some of the invertebrates which have evolved an ability to attack very tough unfolded laminae, e.g. caterpillars of the Limacodidae on palms (Cock *et al.*, 1987).

It is difficult to disentangle the parts played by toughness and rolling or folding of leaves. The fact that, at the Ugandan site, there was a big difference in loss of leaf area during leaf expansion but not after expansion suggests the importance of leaf rolling. However, at the Australian site the mean difference in punch strength between the monocots and dicots was much greater during the expansion phase than after full expansion and full toughening: $7\times$ versus $3\times$ (Dominy *et al.*, 2008). If that is also true at the Ugandan site, then the case for the importance of leaf rolling is weakened. It remains possible, though we think unlikely, that changes in concentrations of deterrent chemicals between the expanding and mature stages are dominant in controlling the extent of leaf loss. Only experiments, in which leaves are exposed unrolled at the immature stage, can give conclusive evidence on the importance of rolling. Experiments with chemical extracts in materials of known toughness are required to establish

the relative importance of chemical and physical defences of leaves that have been prematurely unrolled.

CONCLUSIONS

Our hypothesis that monocot leaves would be found to lose less leaf area to herbivores than immediately neighbouring dicots was supported unequivocally at four old World sites, but the difference was less marked at one of two New World sites, and not significant at the other. However, in the leaf-cutter ant experiment in Panama losses were markedly smaller for palms than for dicots. Only new work can determine whether or not there is a general difference between Old and New World TLRF in the relative losses from monocots and dicots. It is difficult to determine how far the generally lower losses of leaf area from monocots can be explained by (*a*) greater toughness and (*b*) later-lasting folding or rolling, and certainly the problem needs to be approached experimentally. It seems likely that some monocots receive much more protection from folding or rolling than from greater toughness, while the reverse is true of others, and some species receive significant protection from both. Studies on losses to herbivores at all stages of the life cycle of monocots and dicots are needed to follow up the implication that in at least some TLRF lower levels of herbivory on leaves might help to explain the high abundance of monocots relative to dicots in the understorey and among the climbers and epiphytes.

ACKNOWLEDGEMENTS

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APPENDIX 1

TABLE A1. Mean estimated percentages of leaf area missing from the first four fully expanded and toughened leaves of focal mono-cots and nearest-neighbour dicots at six sites in TLRF

Site and species	Family	Life form	Mean estimated percentage of leaf area missing from monocot	Mean estimated percentage of leaf area missing from nearest-neighbour dicots
AUSTRALIA: LOW-RAINFALL SITE				
Pothos longipes	Araceae	C	0	4·7
Alpinia modesta	Zingiberaceae	H	0·25	3·5
*Pleuranthodium racemigerum**	Zingiberaceae	TH	0·50	11·2
Alocasia brisbanensis	Araceae	TH	2·0	5·1
*Alpinia caerulea**	Zingiberaceae	TH	2·1	10·0
Calamus caryotoides	Arecaceae	TC	2·2	10·3
Mean (s.e.m.)			1·2 (0·4)	7·5 (1·4)
AUSTRALIA: HIGH-RAINFALL SITE				
Freycinetia excelsa	Pandanaceae	TC	0	14·7
Calamus australis	Arecaceae	TC	1·2	32·4
Cordyline cannifolia	Laxmanniaceae	S	1·5	18·9
*Alpinia arctiflora**	Zingiberaceae	TH	2·1	14·5
Pothos longipes	Araceae	C	6·6	22·6
Mean (s.e.m.)			2·3 (0·9)	20·6 (3·3)
SINGAPORE				
Hanguana malayana	Hanguanaceae	H	0·51	6·9
Stachyphrynium griffithii	Marantaceae	TH	1·0	11·0
Schismatoglottis wallichii	Araceae	H	1·1	9·6
Molinieria latifolia	Hypoxidaceae	H	1·5	11·2
Tacca integrifolia	Dioscoreaceae	H	2·9	16·6
Mean (s.e.m.)			1·4 (0·4)	11·1 (1·6)
UGANDA				
*Marantochloa leucantha**	Marantaceae	S	0·29	18·8
Aframomum cf. *angustifolium*	Zingiberaceae	TH	2·5	28·5
Aframomum mildbraedii	Zingiberaceae	H	3·4	19·3
Palisota mannii	Commelinaceae	H	3·7	20·1
Leptaspis zeylanica	Poaceae	H	4·2	26·2

Continued

TABLE A1.   *Continued*

Site and species	Family	Life form	Mean estimated percentage of leaf area missing from monocot	Mean estimated percentage of leaf area missing from nearest-neighbour dicots
Dracaena fragrans	Ruscaceae	S	5·1	34·7
Dracaena laxissima	Ruscaceae	S	8·7	27·8
Costus sp.*	Costaceae	TH	9·2	23·7
Culcasia falcifolia	Araceae	C	9·7	33·8
Pollia condensata	Commelinaceae	H	14·5	25·7
Mean (s.e.m.)			6·1 (0·7)	25·9 (1·8)
Costa Rica				
Calathea cleistantha	Marantaceae	H	2·6	6·8
Renealmia pluriplicata	Zingiberaceae	H	3·1	13·9
Welfia regia	Arecaceae	T	3·5	10·8
Asplundia uncinata	Cyclanthaceae	H (+C)	3·5	13·9
Heliconia irrasa	Heliconiaceae	H	6·5	17·8
Geonoma congesta	Arecaceae	S	13·4	12·8
Spathiphyllum fulvovirens	Cyclanthaceae	H	22·1	12·9
Cyclanthus bipartitus	Araceae	TH	22·2	10·2
Mean (s.e.m.)			9·6 (3·0)	12·4 (1·1)
Panama				
Rhipidocladium racemiflorum	Poaceae	SCR	0·14	6·3
*Pleiostachya pruinosa**	Marantaceae	TH	0·76	0·88
Chusquea simpliciflora	Poaceae	SCR	1·8	7·2
*Heliconia metallica**	Heliconiaceae	H	2·8	18·7
Pharus latifolius	Poaceae	H	6·1	19·2
*Heliconia catheta**	Heliconiaceae	H	8·2	3·5
*Calathea latifolia**	Marantaceae	TH	12·7	15·7
Desmoncus orthocanthos	Arecaceae	C	16·7	16·4
Mean (s.e.m.)			6·2 (2·1)	11·0 (2·6)

Life forms: T, tree; S, shrub; TC, tall climber (>20 m); C, climber; SCR, scrambler; TH, tall herb (2–4 m); H, herb (<2 m, generally 1·5 m or shorter).

All species are shade-tolerant except those marked with an asterisk, which need either a single-treefall gap or a greater increase in illumination.

APPENDIX 2

TABLE A2. Primary data for leaf dry mass per unit area, nitrogen concentration and water concentration

	Family	Dry mass per unit leaf area (mg cm^{-2})	Nitrogen concentration per unit dry mass (mg g^{-1})	Water concentration per unit dry mass (g g^{-1})
AUSTRALIA: LOW RAINFALL SITE				
Monocots				
Alocasia brisbanensis	Araceae	2·63	41·4	8·6
Alpinia caerulea	Zingiberaceae	4·35	21·1	4·0
Alpinia modesta	Zingiberaceae	4·00	20·6	3·2
Calamus caryotoides	Arecaceae	16·70	16·9	1·5
Pothos longipes	Araceae	8·33	22·6	1·9
Pleuranthodium racemigerum	Zingiberaceae	4·17	20·7	4·8
Mean (s.e.)		6·70 (2·15)	23·9 (3·6)	4·0 (1·1)
Dicots				
Aglaia sapindina	Meliaceae	5·56		1·9
Castanospora alphandii	Sapindaceae	7·14	23·0	1·5
Codiaeum variegatum	Euphorbiaceae	4·17	20·0	4·1
Dichapetalum papuanum	Dichapetalaceae	5·88	20·0	1·8
Hodgkinsonia frutescens	Rubiaceae	3·23	51·0	5·8
Neisosperma poweri	Apocynaceae	5·00		3·3
Phaleria octandra	Thymelaeaceae	6·67	26·0	2·4
Sauropus macranthus	Phyllanthaceae	3·70	29·0	2·9
Mean (s.e.)		5·17 (0·50)	28·2 (4·8)	3·0 (0·5)
AUSTRALIA: LOW RAINFALL SITE				
Monocots				
Alpinia arctiflora	Zingiberaceae	5·00	19·9	4·0
Calamus australis	Arecaceae	5·88	19·8	1·5
Cordyline cannifolia	Laxmanniaceae	5·26	16·9	4·1
Freycinetia excelsa	Pandanaceae	5·26	16·6	3·4
Mean (s.e.)		5·35 (0·19)	18·3 (0·9)	3·3 (0·6)
Dicots				
Aglaia australiensis	Meliaceae	8·3	26	2·6
Aglaia tomentosa	Meliaceae	5·0	32	2·2
Apodytes brevistylis	Icacinaceae	5·0	18	3·5
Argyrodendron peralatum	Malvaceae	11·1	18	1·1
Argyrodendron trifoliolatum	Malvaceae	8·6	17	1·3
Austromuellera trinervia	Proteaceae	6·8	11	1·4
Beilschmiedia brunnea	Lauraceae	5·7	27	2·2
Beilschmiedia tooram	Lauraceae	10·3	14	1·2
Bubbia semecarpoides	Winteraceae	10·3	17	2·5
Cardwellia sublimis	Proteaceae	6·7	9·2	2·0
Castanospora alphandii	Sapindaceae	6·9	20	1·7
Cryptocarya angulata	Lauraceae	6·2	18	1·5
Cryptocarya grandis	Lauraceae	5·8	18	1·8
Cryptocarya mackinnoniana	Lauraceae	8·5	14	1·4
Cryptocarya melanocarpa	Lauraceae	4·9	20	1·5
Cryptocarya pleurosperma	Lauraceae	7·9	14	1·9
Cupaniopsis flagelliformis	Sapindaceae	5·7	24	1·4
Daphnandra repandula	Atherospermataceae	4·4	32	3·4
Darlingia ferruginea	Proteaceae	6·3	13	2·5
Diploglottis bracteata	Sapindaceae	6·8	17	1·7
Doryphora aromatica	Atherospermataceae	5·7	28	2·5
Endiandra bessaphila	Lauraceae	7·4	16	2·2
Endiandra monothyra	Lauraceae	8·3	19	1·3
Flindersia bourjotiana	Rutaceae	11·6	9·4	1·8
Franciscodendron laurifolium	Malvaceae	6·3	14	1·9
Garcinia gibbsiae	Clusiaceae	9·2	13	2·8
Gillbeea adenopetala	Cunoniaceae	6·0	14	2·3
Goniothalamus australis	Annonaceae	4·8	25	2·5
Guioa lasioneura	Sapindaceae	7·0	16	1·4
Hypsophila dielsiana	Celastraceae	9·7	20	3·0
Litsea leefeana	Lauraceae	6·0	16	2·2
Melicope vitiflora	Rutaceae	3·2	42	6·4
Myristica globosa ssp. *muelleri*	Myristicaceae	6·4	17	2·6
Neolitsea dealbata	Lauraceae	5·9	15	1·1
Opisthiolepis heterophylla	Proteaceae	7·8	15	2·3

TABLE A2. *Continued*

	Family	Dry mass per unit leaf area (mg cm^{-2})	Nitrogen concentration per unit dry mass (mg g^{-1})	Water concentration per unit dry mass (g g^{-1})
Pouteria castanosperma	Sapotaceae	4·5	37	2·3
Prunus turneriana	Rosaceae	5·5	16	1·5
Sloanea australis	Elaeocarpaceae	5·9	21	1·8
Synima macrophylla	Sapindaceae	9·7	22	1·7
Syzygium cormiflorum	Myrtaceae	8·5	13	1·6
Syzygium cryptophlebium	Myrtaceae	4·8	15	1·4
Mean (s.e.)		7·0 (0·31)	19·1 (1·1)	2·1 (0·14)
SINGAPORE				
Monocots				
Hanguana malayana	Hanguanaceae		16·0	
Moliniera latifolia	Hypoxidaceae		22·1	
Schismatoglottis wallichii	Araceae		32·3	
Stachyphrynium griffithii	Marantaceae		31·3	
Tacca integrifolia	Dioscoreaceae		26·8	
Mean (s.e.)			25·7 (3·0)	
Dicots				
Baccaurea parviflora	Phyllanthaceae		12·6	
Calophyllum ferrugineum	Clusiaceae		11·3	
Canarium patentinervium	Burseraceae		15·2	
Cinnamomum iners	Lauraceae		20·9	
Cyathocalyx ridleyi	Annonaceae		21·2	
Diospyros buxifolia	Ebenaceae		18·2	
Ficus fistulosa	Moraceae		22·0	
Ficus grossularioides	Moraceae		23·2	
Gluta wallichii	Anacardiaceae		18·2	
Hopea griffithii	Dipterocarpaceae		16·8	
Knema communis	Myristicaceae		16·7	
Pternandra echinata	Melastomataceae		15·4	
Rhodamnia cinerea	Myrtaceae		12·6	
Shorea curtisii	Dipterocarpaceae		17·2	
Urophyllum hirsutum	Rubiaceae		26·4	
Mean (s.e.)			17·9 (1·2)	
UGANDA				
Monocots				
Aframomum angustifolium	Zingiberaceae	3·33	20·4	3·1
Dracaena laxissima	Ruscaceae	4·50	27·7	3·2
Leptaspis zeylanica	Poaceae	3·50	22·6	1·7
Marantochloa leucantha	Marantaceae		24·8	
Palisota mannii	Commelinaceae	4·61	34·5	8·3
Pollia condensata	Commelinaceae	3·44	27·6	4·6
Mean (s.e.)		3·88 (0·28)	26·3 (2·0)	4·2 (1·1)
Dicots				
Aningeria altissima	Sapotaceae	4·85	23·2	1·6
Cassipourea ruwenzorensis	Rhizophoraceae	6·54	27·2	1·5
Chrysophyllum gorungosanum	Sapotaceae	4·85	23·5	1·6
Citropsis articulata	Rutaceae	8·85	22·8	1·7
Clausena anisata	Rutaceae	3·24	22·3	2·5
Diospyros abyssinica	Ebenaceae	6·99	26·7	1·3
Ficus asperifolia	Moraceae	4·65	27·2	2·2
Monodora myristica	Annonaceae	3·83	20·9	2·8
Myrianthus arboreus	Urticaceae	4·98	25·1	2·4
Newtonia buchananii	Fabaceae	3·37	29·8	1·5
Piper capense	Piperaceae	2·92	37·0	5·4
Psychotria lauracea	Rubiaceae	5·21	23·5	4·0
Symphonia globulifera	Clusiaceae	5·10	15·6	2·7
Tabernaemontana pachysiphon	Apocynaceae	4·59	37·9	3·9
Tarenna pavettoides	Rubiaceae	4·41	32·6	2·9
Teclea nobilis	Rutaceae	7·75	28·9	1·5
Trichilia dregeana	Meliaceae	5·99	19·1	2·2
Uvariopsis congolana	Annonaceae	5·03	27·2	2·3
Mean (s.e.)		5·18 (0·37)	26·1 (1·4)	2·4 (0·25)
COSTA RICA				
Monocots				

TABLE A2. *Continued*

	Family	Dry mass per unit leaf area (mg cm^{-2})	Nitrogen concentration per unit dry mass (mg g^{-1})	Water concentration per unit dry mass (g g^{-1})
Asplundia uncinata	Cyclanthaceae	5·92	15·3	3·7
Calathea cleistantha	Marantaceae	2·65	24·8	5·1
Cyclanthus bipartitus	Cyclanthaceae	4·88	22·7	3·1
Geonoma congesta	Arecaceae	7·09	12·7	1·7
Heliconia irrasa	Heliconiaceae	3·60	20·1	3·7
Renealmia pluriplicata	Zingiberaceae	3·82	15·2	4·0
Spathiphyllum fulvovirens	Araceae	4·69	31·8	4·1
Welfia regia	Arecaceae	6·21	13·2	1·6
Mean (s.e.)		4·86 (0·53)	19·5 (2·4)	3·4 (0·43)
Dicots				
Anaxagorea crassipetala	Annonaceae	4·10	20·7	3·1
Aphelandra storkii	Acanthaceae	2·49	25·2	4·4
Dichapetalum axillare	Dichapetalaceae	3·88	18·0	2·4
Dichapetalum nervatum	Dichapetalaceae	6·25	27·9	2·1
Forsteronia myriantha	Apocynaceae	3·23	19·9	3·2
Ocotea cernua	Lauraceae	4·90	30·9	1·9
Paullinia grandifolia	Sapindaceae	4·81	26·5	2·0
Pentaclethra macroloba	Fabaceae	3·82	25·3	1·7
Perebea angustifolia	Moraceae	3·46	20·0	2·6
Piper holdridgeianum	Piperaceae	2·40	39·0	6·9
Piper trigonum	Piperaceae	2·82	39·3	6·1
Psychotria buchtienii	Rubiaceae	3·73	31·7	2·7
Psychotria surensis	Rubiaceae	3·61	27·9	2·7
Siparuna thecaphora	Siparunaceae	2·99	34·8	5·3
Swartzia sp. A	Fabaceae	3·66	38·6	2·9
Trophis involucrata	Moraceae	4·63	21·7	1·8
Virola sebifera	Myristicaceae	3·44	14·6	3·2
Mean (s.e.)		3·78 (0·23)	27·2 (1·9)	3·2 (0·37)
PANAMA				
Monocots				
Chusquea simpliciflora	Poaceae	4·74		1·2
Heliconia catheta	Heliconiaceae	3·51		3·5
Pharus latifolius	Poaceae	5·18		1·1
Pleiostachya pruinosa	Marantaceae	4·76		2·3
Rhipidocladium racemiflorum	Poaceae	3·50		1·0
Mean (s.e.)		4·34 (0·35)		1·8 (0·48)
Dicots				
Unidentified nearest-neighbour dicots (*n* = 15), mean (s.e.)		5·16 (0·49)		2·4 (0·45)