Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage?

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Leaves are most vulnerable to herbivory during expansion. We hypothesised that one factor favouring small leaves could be that smaller-leaved species have shorter expansion times and are therefore exposed to high levels of herbivory for a shorter period than large leaves. In order to test this hypothesis, leaf expansion time and leaf area loss were measured for 51 species from Sydney, Australia. Strong positive correlations were found between leaf length and area and leaf expansion time, confirming that small leaves do expand in a shorter time than large leaves. The amount of leaf area lost was highly variable (from 0.5 to 90% of total leaf area), but was significantly related to both leaf expansion time and log leaf area. The amount of leaf area lost was not significantly correlated with specific leaf area nor with the presence of distasteful substances in the leaves, but was lower on species with hairy expanding leaves.

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Leaf size varies widely among species, with leaf area ranging over 4–7 orders of magnitude in most floras. For example, there are at least 4 orders of magnitude in leaf area in Estonian species (Niinemets and Kull 1994); 6 orders of magnitude in British species (Grime et al. 1988); 6 orders of magnitude in New Zealand species (Halloy and Mark 1996); 5 orders of magnitude among species in Western New South Wales, Australia, and 7 orders of magnitude among species in Sydney, Australia (Leishman et al. 1995). Leaf size has been found to be correlated with photosynthetic productivity, herbivory, and size of stems and inflorescences, and has implications for thermal regulation, self-shading and water relations (Niinemets and Kull 1994, Ribeiro et al. 1994, Ackerly and Donoghue 1998, Stenberg 1998). These factors must affect the ecological advantage of having leaves of a certain size.

Herbivory is a major determinant of leaf mortality rates, and has been shown to affect plant fitness by decreasing reproductive output (Louda 1984, Marquis 1984). Herbivory tends to be concentrated during the leaf expansion phase, with young, expanding leaves usually experiencing higher levels of herbivory than mature leaves (Feeny 1970, Milton 1979, Coley 1983, Lowman and Box 1983, Bogacheva 1994, Coley and Kursar 1996, Kudo 1996, Wait et al. 1998). This is thought to be because expanding leaves are generally less sclerified, often contain lower levels of secondary metabolites such as tannins, monoterpenoids and phenols, and have greater specific leaf areas and higher concentrations of nitrogen and water than do mature leaves of the same species (Feeny 1970, Milton 1979, Lowman and Box 1983, Aide and Londoño 1989, Ribeiro et al. 1994, Folgarait and Davidson 1995, Goralka et al. 1996). It seems likely that reducing the time spent in this vulnerable state during the expansion phase would confer some selective advantage to a plant by reducing herbivore damage (Aide and Londoño 1989, Kursar and Coley 1991, Aide 1993, Coley and Kursar 1996).

Individual leaves are produced by a number of dividing cells, which may divide faster or slower, and over a

shorter or longer duration, giving rise to various total numbers of cells before the leaf finishes expanding (Dale and Milthorpe 1983). The eventual size of the leaf is also affected by the size to which each cell expands, and the duration over which individual cells expand might influence the duration of the whole leaf's expansion (Dale and Milthorpe 1983, Milford et al. 1985, Biemond 1995). In principle, the time over which a leaf is still expanding (and perhaps more vulnerable to herbivory) might be reduced through evolutionary time either by accelerating expansion rates (for example, through faster cell division rates or a larger proportion of cells dividing) or by reducing the final size of the leaf. In this study our interest is in the potential role of variation between species in final leaf size. We tested whether species with small leaves take less time to expand their leaves than do species with large leaves, and whether a shorter leaf expansion phase is associated with reduced damage incurred from herbivores. Some other relevant traits (leaf size, hairiness and bitterness) were measured directly, and their cross-correlations with leaf expansion time were assessed. We also considered the phylogenetic distribution of the results with a view to suggesting other, unmeasured traits that might be cross-correlated.

Methods

Three study sites were located in Ku-ring-gai Chase National Park in Sydney, Australia. Sites were chosen to include a variety of soil moisture and soil nutrient levels, in order to maximise species diversity. The first site (diatreme) was located on volcanic soils (33°33′53″S; 151°17′35″E), the second (heath) was on a sandstone ridge top (33°39′40″S; 151°13′59″E), and the third (terrace) was near a stream in a sandstone gully (33°39′50″S; 151°14′45″E). The diatreme site had the highest levels of phosphorus and nitrogen (646 μg g^{-1} total phosphorus; 0.41% nitrogen), and the terrace and heath sites had low levels of both nutrients (terrace: 144 μg g^{-1} total phosphorus; 0.08% nitrogen; heath: 79 μg g^{-1} total phosphorus; 0.05% nitrogen). To obtain soil nutrient data, an even profile of the top 10 cm of soil was taken from the top 10 cm of soil from five locations at each site. These subsamples were bulked, crushed and sent away to the laboratories of the Plant Industry Division, CSIRO, Canberra where XRF analysis was used to determine P concentration and combustion and mass spectrometry were used to determine N concentration.

All woody dicotyledonous species at each site that had at least 25 leaves beginning to expand in late August or early September 1998, and were represented by more than four individuals were included in this study (Appendix 1). A total of 51 species from 17

families were sampled. Only three species occurred at two sites, and values for these were averaged between sites in analyses where data from all sites were pooled. Five branches on five plants of each species were tagged. A water-based paint marker was used to mark each branch as close to the apex as possible. The number of leaves present between the mark and the growing tip was recorded, and the sample leaf was the youngest leaf visible at the time of marking. Species whose leaves were imbricate in bud were necessarily excluded from this study. The adult form of leaf was measured for all heteroblastic species. Leaf length was measured to 0.1 mm accuracy using vernier callipers. Leaves were considered to have ceased expansion when their length and width had remained unchanged for three successive days. Where species had compound leaves, entire leaves were measured.

Leaf area was determined by scanning 25 fully expanded leaves from each species, and analysing the images using Delta-T scan (Delta-T, Cambridge, UK). Leaf length data were taken from measurements of tagged leaves. SLA (specific leaf area) was determined from a sample of 25 leaves that had recently completed expansion for each species by dividing leaf area by dry weight. Taste and hairiness were assessed on expanding leaves. Leaves were considered hairy if any trichomes were visible to the naked eye, and distasteful if they caused a burning sensation or tasted bitter to the investigator when bitten.

The amount of leaf area lost was assessed for a total of 7126 leaves that had expanded between August 1998 and January 1999. The average number of leaves produced during this time was estimated for each species by counting the number of fully expanded leaves present above the marks on the stems used in the leaf expansion part of the study. Between 42 and 360 leaves were used for each species. These leaves were located on at least three branches of at least four plants. Wherever possible, plants used for leaf expansion measurements were not used for assessment of the amount of leaf area lost. The number of leaves missing from the sample was determined by counts of leaf scars on the stems. These leaves were recorded as having 100% of their area missing. Partially damaged leaves were scanned, and remaining leaf area was analysed using Delta-T Scan software (Delta-T, Cambridge, UK). In cases where a high proportion of the leaf lamina had been removed, the proportion of the leaf area lost was estimated by subtracting the remaining area of the damaged leaf from the average entire leaf area for that species. In cases where damage was less severe, a more accurate estimate was obtained by calculating the difference in area between the scanned image of the damaged leaf and the same image edited in Adobe Photoshop to approximate the area of the full, undamaged leaf.

Two measures of the amount of leaf area lost were used: 1) Loss of expanded leaf area$_{(total)}$, which includes

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instances where an entire branch and associated leaves had been removed 2) Loss of expanded leaf area$_{(excl)}$, in which instances where the entire branch and associated leaves had been removed were excluded from calculations. It is acknowledged that only herbivore damage that resulted in lamina loss (leaf removal, chewing, or mining) was accounted for. Herbivory by sap-sucking animals or on other plant parts was not assessed, and we are unable to discriminate between leaf area loss due to herbivory and that due to other processes.

Where necessary, data were log10 transformed before analyses, and loss of expanded leaf area data were arcsine transformed (Zar 1984). Following transformation, all data were approximately normally distributed. Analysis of covariance (ANCOVA) was used to determine whether regression lines for the three sites were significantly different for each of the relationships assessed (Appendix 2). None of these ANCOVAs showed significant differences in slope between sites (although it should be noted that the statistical power of this test was low due to the small number of degrees of freedom available). Some of the ANCOVAs showed significant differences in elevation: these relationships were described through a two factor model (variables added to the models in a single step) fitting parallel lines for the three sites. Otherwise relationships were described through a single regression pooled across sites. A three-factor linear model for the variables site, log expansion time and log leaf area was used to determine whether leaf area and leaf expansion time were separately important predictors of loss of expanded leaf area $_{(excl)}$ (variables added to all models in a single step).

Families or other clades were plotted with different symbols on the main correlation graphs. Phylogenetic regressions (Grafen 1989) were performed on the relationships between loss of expanded leaf area$_{(excl)}$ (arcsine transformed) and leaf expansion time and leaf area (log transformed) using phylogeny from Angiosperm Phylogeny Group (APG 1998), which indicated 35 higher nodes in the tree underlying the study species. These phylogenetic regressions were performed using a generalised linear interactive modelling program (phylo.glm version 1.03). Path segment lengths for the phylogenetic tree were calculated by assigning a height to each node that was one less than the number of species below or at that node in the tree (Grafen 1989).

Results

Median leaf expansion time ranged from 19 to 201 days (Appendix 1). There was a significant ($R^2 = 0.60$; $P < 0.001$) positive relationship between log leaf expansion time and log leaf area, pooled across all sites (Fig. 1). The strength of the correlation was approximately the same for leaf length ($R^2 = 0.60$; $P < 0.001$; pooled

across sites) as for leaf area. Thus, larger leaves did tend to have longer leaf expansion times than did small leaves.

There was a negative relationship between SLA and log expansion time (model with site as a factor, $F = 9.44$; df = 3, 51; $P < 0.001$; $R^2 = 0.38$). Expansion time for any given SLA was greatest at the diatreme site and least at the heath site. However, SLA did not explain much of the variation in expansion time remaining after log leaf area and site (R^2 only increased from 0.60 to 0.64 with the inclusion of SLA in the model).

Loss of expanded leaf area was highly variable among species, with between 0 and 100% of leaves having some area removed. Loss of expanded leaf area$_{(total)}$ ranged from 0.5 to 90% (mean = 28%; median = 25%), and loss of expanded leaf area$_{(excl)}$ was between 0 and 51% (mean = 10%; median = 6%). Loss of expanded leaf area $_{(total)}$ was not significantly related to log leaf expansion time (site taken into account; $F = 2.10$; df = 3, 51; $P = 0.75$). However, loss of expanded leaf area$_{(excl)}$ was significantly related to log leaf expansion time in both the cross-species regression (site included in model; $R^2 = 0.31$; $F = 7.08$; df = 3, 51; $P = 0.001$; Fig. 2) and the phylogenetic regression (also controlling for site; $F = 9.28$; df = 1, 31; $P = 0.005$). The proportion of leaf area loss due to whole branch loss was not related to leaf area ($R^2 = 0.02$; $P = 0.29$).

The strength of the correlation between loss of expanded leaf area$_{(excl)}$ and leaf area in both the cross-species regression ($R^2 = 0.31$; $P < 0.001$; Fig. 3), and the phylogenetic regression ($F = 9.43$; df = 1, 31; $P = 0.004$) was similar to the strength of the correlation between loss of expanded leaf area$_{(excl)}$ and leaf expansion time. Neither leaf area ($F = 2.47$; df = 1, 51; $P = 0.14$) nor leaf expansion time ($F = 0.27$; df = 1, 51; $P = 0.60$) added significant predictive power for loss of
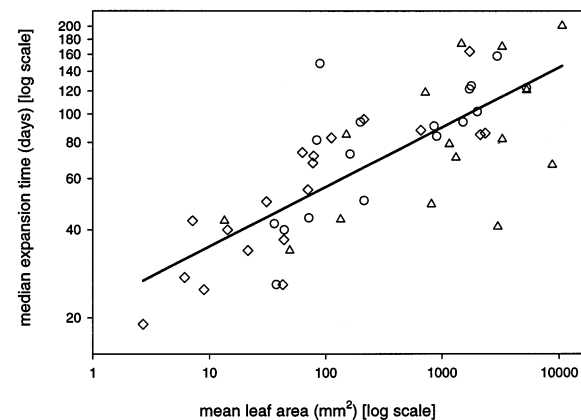

Fig. 1. Median expansion time in relation to mean leaf area at maturity for 51 species from Sydney, Australia. Species were from three sites: a heath ($\diamond$), a terrace ($\bigcirc$) and a diatreme ($\triangle$). The solid line is the regression line for all sites combined (linear regression: $P < 0.001$; $R^2 = 0.60$; $y = 0.20\ x + 1.34$).
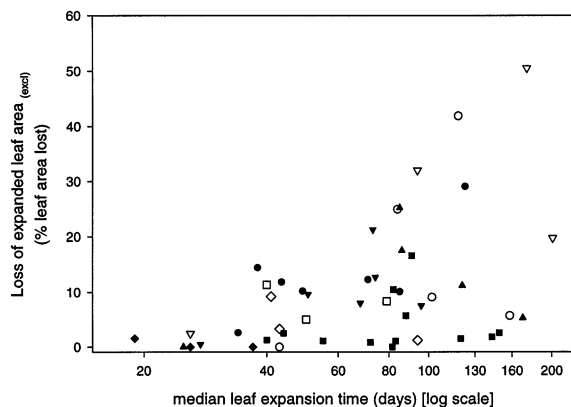
Fig. 2. Loss of expanded leaf area$_{(excl)}$ (% leaf area lost) in relation to median expansion time across 48 species from Sydney, Australia. Species were grouped taxonomically into the following categories according to the phylogeny of the Angiosperm Phylogeny Group (APG 1998): Proteaceae (■); Fabaceae (●); other rosids 1 (○); Myrtaceae (▲); Rutaceae (▼); other rosids 2 (▽); Epacridaceae (◆); other asterids (◇), and other higher eudicots (□).

expanded leaf area$_{(excl)}$ when added in to a cross-species model including site after the other. In summary, final leaf size and leaf expansion time were strongly correlated, and they had almost completely overlapping predictive power for loss of expanded leaf area$_{(excl)}$.

The phylogenetic regression examines evolutionary divergences for traits, in contrast to the cross-species regression which examines trait values in present-day species. Each radiation or node in the phylogenetic tree leading to the present-day species contributes one case to a phylogenetic regression. The question asked is whether divergence for trait A is consistently correlated with divergence for trait B, across multiple radiations.
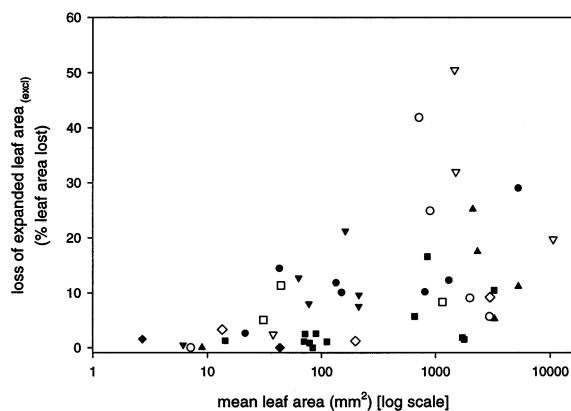

Fig. 3. Loss of expanded leaf area$_{(excl)}$ in relation to mean leaf area at maturity across 48 species from Sydney, Australia. Species were grouped taxonomically into the following categories: Proteaceae (■); Fabaceae (●); other rosids 1 (○); Myrtaceae (▲); Rutaceae (▼); other rosids 2 (▽); Epacridaceae (◆); other asterids (◇), and other higher eudicots (□).
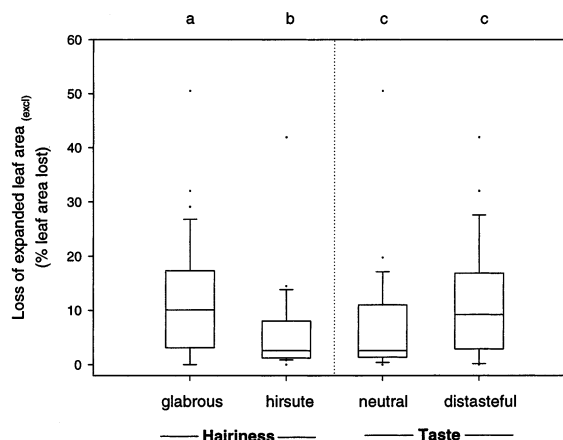

Fig. 4. Loss of expanded leaf area$_{(excl)}$ in relation to hairiness and taste of leaves for 48 species from Sydney, Australia. The boxes span from the 25th percentile to the 75th percentile. The line inside the box represents the sample median. Whiskers indicate the 10th and 90th percentiles. Outliers are shown as dots. Letters above boxes show the results of t-tests for significant differences between categories.

Situations can arise where an ecological correlation, across species successfully surviving in the present day, is highly statistically significant, but the correlation of evolutionary divergences is not significant. This might happen if only one or a few phylogenetic divergences, deep in the tree, have generated most of the range of variation in the traits or outcomes being correlated. In the present study phylogenetic regressions were very similar to cross-species regressions, as summarized in the preceding paragraphs. Consequently the complexities of interpretation are not discussed further.

Loss of expanded leaf area$_{(excl)}$ was not significantly related to SLA (site included in model: $F = 4.51$; df = 3, 51; $P = 0.07$). SLA did not explain a significant proportion of the variance remaining after loss of expanded leaf area$_{(excl)}$ was regressed on final leaf area (multiple regression; $R^2 = 0.07$; $P = 0.07$). Species with hairs on their leaves had lower levels of loss of expanded leaf area$_{(excl)}$ (one tailed t-test for data with unequal variances; $P = 0.04$; Fig. 4), but the possession of distasteful leaves (as judged by humans) was not significantly associated with low levels of loss of expanded leaf area$_{(excl)}$ (one-tailed t-test; $P = 0.20$). The relationship between hairiness and loss of expanded leaf area$_{(excl)}$ became stronger when small leaves were excluded (one-tailed t-test for data with unequal variances; $P = 0.03$), presumably because small leaves had low loss of expanded leaf area$_{(excl)}$ irrespective of hairiness. The relationship between taste and loss of expanded leaf area$_{(excl)}$ remained non-significant when small leaves (< 100 mm^2) were excluded from analyses ($P = 0.49$), as did the relationship between SLA and loss of expanded leaf area$_{(excl)}$ (linear regression; $R^2 = 0.03$; $P = 0.41$).

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Cross-correlations were not significant between log expansion time and taste (one-tailed t-test; $P = 0.23$); pubescence and taste ($\chi^2 = 1.03$; df = 1; $P = 0.31$), or SLA and taste (one-tailed t-test for data with unequal variances; $P = 0.11$).

Phylogeny did not suggest any particular further variables that might be cross-correlated with leaf size, expansion time and loss of expanded leaf area$_{(excl)}$. In Figs 2 and 3, no particular evolutionary divergence suggests itself as mainly responsible for the cross-species correlations. All the Epacridaceae included lay towards the lower left of the graphs. Several species towards upper right were from Rosid 1 or Rosid 2 clades. The correlation pattern was positive within each of Proteaceae, Fabaceae and Myrtaceae, but not so clearly as to be convincing within each family considered in isolation.

Discussion

Leaf expansion

Our prediction, that large leaves would take longer to expand than would small leaves, was confirmed. However, the slope of the graph of log expansion time vs log final leaf area was considerably less than 1. In other words, the expansion time of larger leaves was shorter than it would have been if they had increased in area at the same rate as smaller leaves. However, it is still the case that any given point on a leaf is expanding, and hence vulnerable to herbivory, for a shorter period of time if it occurs on a plant with small leaves than if it occurs on a plant with large leaves.

Herbivore damage

The average loss of expanded leaf area$_{(total)}$ was 28%, and the average loss of expanded leaf area$_{(excl)}$ was 10%. These figures are within the range of values given by other studies on herbivory, including those on 32 species in Panamanian rainforest (6 to 61%, mean = 24%, Aide (1993)), four species of Australian rainforest trees (4.8 to 32.5%, mean = 21.8%, Lowman and Box (1983)), four species in the southern Appalachians (4.5–9.6%; Reynolds and Crossley (1997)) and studies from 23 forest communities (average annual herbivore damage = 10.3% in tropical forests, and 7.5% in temperate forests; reviewed by Coley and Aide (1991)).

There was a significant positive relationship between leaf area and leaf expansion time and loss of expanded leaf area$_{(excl)}$. However, the relationship between loss of expanded leaf area$_{(total)}$ and log leaf expansion time was not significant. This was probably because herbivores that remove entire branches from plants are less affected by traits such as expansion time and leaf size

than are herbivores that select individual leaves and feed on them one at a time. It is possible that the inclusion of whole branch level herbivore damage was responsible for the lack of a significant correlation between expansion time and leaf area loss reported by Aide (1993).

Comparative data of the type collected in this study can only show whether traits are correlated with one another, they do not give evidence for direct causation. However, correlation strengths and overlaps can indicate the plausibility of alternative pathways of causation. In this study, final leaf area and leaf expansion time were strongly correlated, and behaved as a single compound variable. Each had considerable predictive power for loss of expanded leaf area$_{(excl)}$, but neither added further predictive power when added to the model after the other. Thus the correlative data are equally consistent with final leaf area, or leaf expansion time, or some third unconsidered but correlated variable, being the direct influence on the amount of leaf area a species lost.

There are some potential mechanisms through which final leaf area might influence herbivore damage. 1) Herbivore feeding decisions can be influenced by leaf size. For example, Ribeiro et al. (1994) showed that grasshoppers preferred to eat large mature leaves than small mature leaves of *Tabebuia ochracea* in laboratory trials. 2) Insect searching behaviour might lead them to large leaves more easily than to small leaves (Feeny 1976). 3) Small-leaved species would be exposed to a narrower spectrum of species that complete their larval development on an individual leaf than would large-leaved species. The current literature tends to the view that leaf developmental stage should be more important than leaf size in determining insect feeding preferences (Coley 1983, Kursar and Coley 1991), due to changes in leaf nutritional value, palatability and defence levels as leaves reach maturity (Feeny 1970, Milton 1979, Lowman and Box 1983, Aide and Londoño 1989, Ribeiro et al. 1994, Folgarait and Davidson 1995, Goralka et al. 1996). We examined the correlation graphs (Figs 2 and 3) for phylogenetic pattern, but there was little clear pattern either within or among families or other major clades. Hence phylogeny did not suggest any further unmeasured traits that might be the true cause of variation in loss of expanded leaf area$_{(excl)}$ and cross-correlated with leaf expansion time and final leaf size. On balance, we believe the likeliest interpretation of our results is that leaf expansion time directly influences loss of expanded leaf area$_{(excl)}$, and final leaf size is correlated via leaf expansion time.

The scattergrams for loss of expanded leaf area$_{(excl)}$ vs leaf size (Fig. 2) and expansion rate (Fig. 3) show that none of the species with small leaves or short leaf expansion times experienced high levels of loss of expanded leaf area$_{(excl)}$, but among species that take a long time to expand their leaves or have large leaves,

some species experienced high and others low levels of loss of expanded leaf area$_{(excl)}$. This suggests that some large-leaved species with longer leaf expansion times are employing defences other than rapid expansion to decrease their level of herbivore damage.

Herbivore damage has been shown by many authors to depend on a multitude of leaf traits. Leaf toughness is thought to be the most important determinant of herbivore damage (Feeny 1970, Coley 1983, Lowman and Box 1983), though chemical toxicity (especially tannin and phenol content), epicuticular waxes, trichome density, nitrogen content, phenology of leaf production and biotic defences have also been shown to significantly affect the likelihood of a leaf being attacked by herbivores (Feeny 1970, Coley 1983, Aide 1993, Folgarait and Davidson 1994, Gaume et al. 1997).

In this study the measured variable most closely related to mature-leaf toughness was SLA, leaf area per gram of dry mass. Low-SLA species have higher-density tissue, thicker leaf lamina, stronger veins or combinations of these (Garnier and Laurent 1994). SLA proved not to be a significant predictor of loss of expanded leaf area$_{(excl)}$ in this study, probably because leaf toughness does not develop fully until leaves have finished expanding, whereas measurements of leaf area loss were taken soon after leaf expansion ceased and consequently measured herbivore damage mainly during expansion. Leaves with high SLA generally had shorter leaf expansion times than did those with low SLA. This suggests that there may be a trade-off between rapid leaf expansion (leading to reduced herbivory during the expansion phase), and low SLA (which presumably reduces herbivore damage on mature leaves).

Leaf taste was also not significantly related to loss of expanded leaf area$_{(excl)}$. This could be the result of a poor correlation between repellence of substances to humans and insects, or because multiple leaf traits in combination confounded the results. However, few correlations between defensive characteristics were found.

Loss of expanded leaf area$_{(excl)}$ was lower on species with hairy expanding leaves. This was expected, as the presence of hairs has been shown to significantly reduce herbivore damage in previous work (Ribeiro et al. 1994), and is a defence type that can be employed during expansion, while leaf toughness and many secondary compounds cannot.

In summary, the results confirmed that larger-leaved species tend to have longer leaf expansion times. This was expected, but had not previously been quantified across a broad survey of species. Further, species with short expansion times and small leaf size did have low levels of loss of expanded leaf area$_{(excl)}$. This might provide a selection pressure towards reducing leaf expansion time via reducing leaf size.

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Appendix 1. Table of raw data. $LLA_{(total)}$ = loss of expanded leaf area, including whole branch loss (% leaf area lost); $LA_{(excl)}$ = loss of expanded leaf area, excluding instances where the whole branch and associated leaves were removed (% leaf area lost); exp = median expansion time (days); LA = mean leaf area (mm^2); SLA = specific leaf area (mm^2/mg). Species were defined as hairy if hairs on expanding leaves were visible to the naked eye. The final column contains results from taste tests: D = distasteful; N = neutral.

species	family	$LAA_{(total)}$	$LAA_{(excl)}$	exp	LA	SLA	hair	taste
Heath site								
Leucopogon microphyllus	Epacridaceae	8.57	1.54	19	2.7	9.11	no	yes
Philotheca salsolifolia	Rutaceae	0.48	0.48	27.5	6.1	4.36	no	yes
Tetratheca ericifolia	Tremandraceae	23.14	0.00	43	7.1	6.45	no	no
Darwinia fascicularis	Myrtaceae	36.11	0.00	25	8.9	7.79	no	yes
Banksia ericifolia	Proteaceae	16.00	1.25	40	14.3	5.23	yes	no
Pultenea elliptica	Fabaceae	15.61	2.63	34	21.3	10.69	yes	no
Hibbertia linearis	Dilleniaceae	25.69	5.06	50	30.8	6.82	no	yes
Epacris tubiflora	Epacridaceae	63.33	0.00	26	42.6	8.13	no	yes
Leucopogon esquamatus	Epacridaceae	44.00	0.00	37	43.5	8.16	no	no
Zieria laevigata	Rutaceae	11.66	12.71	74	62.8	5.31	no	yes
Hakea teretifolia	Proteaceae	39.33	1.11	55	70.2	2.45	no	no
Boronia ledifolia	Rutaceae	8.02	8.02	68	77.4	5.08	yes	yes
Grevillea sericea	Proteaceae	35.12	0.83	72	78.6	6.09	yes	no
Grevillea speciosa	Proteaceae	1.06	1.06	83	111.6	6.16	yes	yes
Eriostemon australasius	Rutaceae	13.70	7.54	96	212.7	7.26	no	yes
Isopogon anethifolius	Proteaceae	28.54	5.73	88	658.2	5.74	no	yes
Banksia serrata	Proteaceae	1.47	1.47	164	1721.1	2.84	yes	yes
Eucalyptus haemastoma	Myrtaceae	56.79	25.23	85	2121.0	5.40	no	yes
Angophora hispida	Myrtaceae	90.02	17.53	86	2334.4	3.63	no	yes
Terrace site								
Pultenea flexillis	Fabaceae	9.86	5.20	42	36.1	13.61	yes	no
Pimelea linifolia	Thymelaeaceae	2.43	2.43	26	37.5	13.59	no	no
Hibbertia obtusifolia	Dilleniaceae	11.34	11.34	40	43.9	9.95	no	yes
Grevillea buxifolia	Proteaceae	5.67	2.50	44	71.6	8.78	yes	no
Hakea gibbosa	Proteaceae	13.67	0.00	81.5	83.6	3.71	yes	yes
Grevillea sericea	Proteaceae	7.74	2.58	149	89.1	7.04	yes	no
Zieria pilosa	Rutaceae	41.47	21.23	73	162.2	10.30	no	yes
Xanthosia pilosa	Apiaceae	1.19	1.19	94	198.5	13.35	yes	yes
Crowea saligna	Rutaceae	38.93	9.62	50.5	213.4	10.74	no	yes
Hakea dactyloides	Proteceae	22.17	16.61	91	852.5	6.82	no	yes
Ceratopetalum gummiferum	Cunoniaceae	24.91	24.91	84	898.3	9.79	no	yes
Dodonea triquetra	Sapindaceae	31.99	31.99	94	1510.2	11.80	no	yes
Callicoma serratifolia	Cunoniaceae	19.62	9.07	102	2001.4	6.83	no	no
Pomaderris lanigera	Rhamnaceae	12.00	5.71	158	2964.6	8.61	yes	yes
Banksia serrata	Proteaceae	2.16	2.16	122	1721.1	2.84	yes	no
Banksia oblongifolia	Proteaceae	1.50	1.50	120	1783.5	3.48	yes	no
Acacia terminallis	Fabaceae	29.06	29.06	123	5267.9	6.19	no	yes

Appendix 1. (Continued)

species	family	$LAA_{(total)}$	$LAA_{(excl)}$	exp	LA	SLA	hair	taste
Diatreme site								
Prostanthera denticulata	Lamiaceae	49.32	3.33	43	13.4	19.41	yes	yes
Pultenea flexillis	Fabaceae	38.97	23.72	34	49.0	15.88	yes	no
Pultenea daphnoides	Fabaceae	11.84	11.84	43.5	134.3	8.64	no	no
Acacia floribunda	Fabaceae	55.47	10.08	85	150.1	8.45	no	yes
Pomaderris ferruginea	Rhamnaceae	45.78	41.90	118.5	718.9	10.22	yes	yes
Hardenbergia violacea	Fabaceae	86.05	10.20	49	808.7	8.96	no	no
Hibbertia dentata	Dilleniaceae	29.60	8.34	79	1153.0	11.41	yes	no
Glycine tabacina	Fabaceae	66.15	12.28	71	1313.0	16.44	yes	no
Lasiopetalum ferrugineum	Sterculiaceae	50.50	50.50	174	1470.0	8.67	no	no
Pandorea pandorana	Bignoniaceae	55.32	9.21	41	2995.4	13.33	no	yes
Xylomelum pyriforme	Proteceae	18.81	10.45	82	3262.4	5.82	no	yes
Syncarpia glomulifera	Myrtaceae	36.32	5.30	170	3270.9	5.94	yes	yes
Eucalyptus umbra	Myrtaceae	46.31	11.16	121	5283.6	3.54	no	yes
Cissus hypoglauca	Vitaceae	46.05	5.08	67	8706.1	11.11	no	no
Synoum glandulosum	Meliaceae	19.71	19.71	201	10604.6	9.91	no	no

Appendix 2. Results of the analysis of covariance tests used to determine whether regression lines from the three sites were significantly different in slope or elevation. Two degrees of freedom were available on tests for site differences, and the total number of species used was 51 in all tests except for the test on loss of expanded leaf area$_{(excl)}$ vs SLA on big leaves only ($n = 30$).

Variables	Tests for differences in slope		Tests for differences in elevation	
	F	P	F	P
(Log expansion time) vs (log leaf area)	0.30	0.74	1.53	0.23
(Log expansion time) vs (log leaf length)	0.39	0.94	0.39	0.68
(Log expansion time) vs (SLA)	0.69	0.51	10.81	<0.001
(Loss of expanded leaf area$_{(excl)}$) vs (log expansion time)	0.65	0.53	4.6	0.015
(Loss of expanded leaf area$_{(excl)}$) vs (log leaf area)	1.46	0.24	1.91	0.16
(Loss of expanded leaf area$_{(total)}$) vs (log expansion time)	0.11	0.90	7.77	0.001
(Proportion of leaf area loss due to whole branch removal) vs (log leaf area)	1.54	0.23	2.2	0.12
(Loss of expanded leaf area$_{(excl)}$) vs (SLA)-including all leaves	1.15	0.33	5.32	0.008
(Loss of expanded leaf area$_{(excl)}$) vs (SLA)-big (>100 mm^2) leaves only	0.2	0.82	0.28	0.76