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Herbivore damage along a latitudinal gradient: relative impacts of different feeding guilds

Nigel R. Andrew and Lesley Hughes

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We present the first broad-scale test for a latitudinal gradient in herbivory made with consistent methods, in similar habitat type, over the entire lifespan of leaves (phyllodes). We assessed the degree of chewing, sap-sucking and mining herbivory on *Acacia falcata* along its entire coastal latitudinal range (1150 km) in Australia. We found no significant differences in the rate of herbivory among latitudes. Mature phyllodes had a higher rate of herbivory compared to young phyllodes, and mining was higher on mature phyllodes from the most tropical latitude. We found significant differences in phyllode toughness and specific leaf (phyllode) area among latitudes, but no significant differences among latitudes in carbon: nitrogen. This study provides a useful model for further testing of the generalisation that herbivory is more intense in tropical versus temperate regions.

N. R. Andrew and L. Hughes, Key Centre for Biodiversity and Bioresources, Dept of Biological Sciences, Macquarie Univ., North Ryde, Sydney, NSW, 2109, Australia (nandrew@bio.mq.edu.au).

Many plant and animal taxa show a distinct increase in species richness towards the tropics (Rosenzweig 1995, Gaston 2000, Krebs 2001, Hillebrand 2004). Hypotheses put forward to explain latitudinal gradients in diversity include the ideas that the more continuously favourable environmental conditions, increased area and/or increased net primary productivity in the tropics promotes increased speciation (Rosenzweig 1995, Rosenzweig and Sandlin 1997, Rohde 1998, Chown and Gaston 2000, Gaston 2000), as well as non-biological explanations imposed by geometric constraints (Colwell and Lee 2000). Few of the assumptions underlying these theories, however, have been rigorously tested (Gaston 2000, Hillebrand 2004).

Rates of herbivory have generally been reported as being higher in the tropics than at more temperate latitudes (Coley and Aide 1991, Coley and Barone 1996). The relationships between herbivory and latitude reported by Coley and co-authors are broadly consistent with the idea that the more favourable climatic conditions in the tropics throughout the year allow insect herbivores to feed constantly, compared to temperate latitudes. Other hypotheses put forward to explain higher rates of herbivory in the tropics include increased levels of plant defences and longer leaf lifespans towards the tropics. Coley and Aide's (1991) generalisations have been widely accepted (paper cited 108 times as of November 2003: ISI 2003). However, these generalisations are based on literature compilations comparing studies that used a variety of methodologies, performed under a range of environmental conditions, and using plant species from a variety of phylogenies with different chemical and mechanical properties (Landsberg and Ohmart 1989, Coley and Aide 1991, Read et al. 2003).

In this study, we assessed leaf herbivory along a latitudinal gradient using standardised methods in order to reduce many of the confounding effects that may occur when comparisons are made between different plant species, habitat types and sampling techniques. To our knowledge, this is the first broad-scale test for a

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latitudinal gradient in herbivory that has been made with consistent methods, in similar habitat type over the entire lifespan of leaves (phyllodes). We assessed three major types of herbivory: two externally feeding types (phyllode-chewing, sap-sucking) and one internal (phyllode-mining).

Studies in which herbivore damage has been estimated at a single point in time have probably underestimated damage because leaves that have been completely eaten or dropped due to herbivore feeding are not included (Lowman 1984, Landsberg 1989). Long-term sampling has increased estimates of herbivory by up to 2.4 times for both young (Aide 1993, Jackson and Bach 1999) and mature leaves (Coley 1983, Lowman 1984). Rates of herbivory are affected by leaf age (Landsberg 1988, Coley and Aide 1991, Landsberg and Cork 1997, Jackson et al. 1999, Moles and Westoby 2000). Among latitudes, young tropical leaves are expected to face higher herbivory rates in general and also to experience a higher seasonal availability to herbivores due to a less severe climate, compared to young temperate leaves (Coley and Aide 1991). As individual leaves age, they may change in surface area, mechanical structural development, and chemical composition (Krischik and Denno 1983, Read et al. 2003). Young leaves tend to have higher water and nitrogen levels, and lower fibre content and toughness compared to older leaves (Feeny 1970, Coley 1983, Bowers and Stamp 1993, Read et al. 2003). Young leaves may also have relatively higher levels of defensive chemical compounds and reduced structural defences compared to older leaves (Coley 1983, Krischik and Denno 1983, Read et al. 2003). Once young leaves stop expanding, they begin to increase in structural complexity and leaf toughness (Coley 1983, Ernest 1989, Lowman and Heatwole 1992). However, different plant species may have mature leaves that are relatively tougher and stronger than the soft mature leaves of other species (Iddles et al. 2003, Read et al. 2003), or have higher levels of chemical defences (Feeny 1970).

Within a single host plant (with tough and strong mature foliage), we would expect that the rate of external herbivory (leaf-chewing and sap-sucking) would be higher on expanding leaves than on mature foliage. In contrast, due to the nature of herbivory by internal feeders (leaf-mining), relatively larger individuals will feed on more mature foliage compared to expanding foliage, and we would therefore expect an increase in mining damage as leaves mature. Furthermore, on a single species, we would expect a higher rate of herbivory on young tropical foliage from all three herbivory-types compared to more temperate juvenile foliage.

We addressed the following questions:

1) How do chemical and morphological traits of foliage differ among latitudes within the host plant species?
2) Do rates of herbivory (chewing, sap-sucking and mining) increase towards the tropics?
3) Are rates of herbivory more seasonal towards the more temperate latitudes compared to the tropics?
4) Do rates of herbivory differ between expanding versus mature foliage among latitudes?

Methods

We assessed herbivory on the phyllodinous shrub *Acacia falcata*. A phyllode is a reduced leaf in acacias, consisting of the petiole plus rachis, both flattened into a leaf-like structure with an entire margin (Bell 1991); true *Acacia* leaves are bipinnate. *A. falcata* is a shrubby species growing to 4 m in height and is common along the east coast of Australia. Four latitudes, spanning *A. falcata's* coastal range (1150 km, 9° of latitude) were chosen: Batemans Bay, New South Wales (NSW) (35° 40′S), Sydney, NSW (33°36′S), Grafton, NSW (29°46′S), and Gympie, Queensland (26°7′S). At each latitude, three sites where *A. falcata* was abundant were selected. All sites were less than 150 m in altitude in open forest habitat with a eucalypt overstorey. There was a reduction in average annual temperature of 4.3°C from north (Gympie) to south (Batemans Bay), but no directional trend in precipitation: Sydney (the second-most southerly site) had a significantly lower precipitation compared to the three other latitudes (Andrew and Hughes in press).

To assess total nitrogen (N) and total phosphorus (P), five soil core samples (each 654 cm^3) were taken per site, bulked, dried and sieved through 1 mm mesh. Total nitrogen was assessed using a LECO CHN-2000 analyser (LECO Corporation, St Joseph, MI, USA) and total phosphorus using ICPOES Method # 113 (Anonymous 2000).

We assessed three plant traits: carbon: nitrogen ratios (C:N), foliage toughness and specific leaf (phyllode) area (SLA). These traits were chosen because they encompass a range of chemical and mechanical properties that are quantifiable within and between plant species and relate to foliage defence and nutrition. Chemical and morphological traits of phyllodes were assessed at each site. All phyllodes sampled were fully expanded within the three months prior to collection and showed no visible signs of herbivory. For chemical traits, five phyllodes from each of five plants per site were collected. Dried leaves from each plant were bulked and ground. Carbon and nitrogen levels for each plant were measured using a LECO CHN-2000 analyser, and C:N ratios were then calculated. Phyllode toughness was assessed using a purpose built leaf fracture toughness tester (described in Wright and Cannon 2001). This device cuts the leaf/phyllode at a constant angle (20°) and at a constant speed. Mean force of fracture (as measured by the average force to cut the phyllode measured in Newtons [N]) divided by tissue thickness is measured as tissue toughness (Nm^{-1}, Wright and Cannon 2001). This method is similar to that used by Aranwela et al. (1999) and Darvell et al. (1996). Five phyllodes from each of five plants at each site were cut at the widest point, and a single average value of toughness was calculated for each phyllode (not including mid-vein). Specific leaf (phyllode) area (SLA: leaf area per unit leaf dry mass) was measured from the same phyllodes used for the toughness measurements. Fresh phyllodes were scanned on a flat bed scanner and phyllode area calculated using Delta-T Scan (Delta-T, Cambridge, UK), then oven dried for 48 h at 65°C and weighed. Average C:N, toughness and SLA per site were calculated and compared among latitudes using a one-way ANOVA, using sites as replicates.

Chewing herbivory is the most commonly studied type of herbivory, however, both mining and sap-sucking can cause significant reductions in photosynthetic tissue and plant growth (Landsberg and Wylie 1983, Fensham 1994, Coley and Barone 1996). Chewing herbivory is caused by organisms using mandibles to eat through leaves, and may be done by species from the orders Coleoptera (adults and larvae), Lepidoptera (larvae), Symphyta (sawfly larvae), Orthoptera, and Phasmatodea (Elliott et al. 1998). Sap-sucking damage is less conspicuous than chewing and more difficult to quantify, but phloem feeders can remove as much plant biomass as chewers (Leigh 1997). Individuals from the orders Hemiptera (Homoptera and Heteroptera) and Thysanoptera are identified as sap-suckers. These insects use their stylets (sucking mouthparts) to pierce the surface of the leaf and suck up the phloem sap, xylem or cell contents from mesophyll tissue (Elliott et al. 1998). Leaf-miners include larval Lepidoptera, Coleoptera, Diptera and Hymenoptera that feed within the upper and lower surface of the leaf (Elliott et al. 1998). Galling, another internal feeding type, was not assessed in this study since no foliar gallers were identified on *A. falcata*.

Herbivore damage was assessed every three months for two years, from February 2000 (spring) to November 2001 (summer). Initially, all phyllodes on one branch from 10 plants per site were sequentially numbered using a water-based permanent pen. Images of each phyllode were taken in-situ using a digital camera. Only phyllodes with images taken throughout the phyllode lifespan were included in the analysis. Three different types of herbivore damage (chewing, sap-sucking and mining) were identified and the area missing relative to total phyllode area was assessed using Image J software (Rasband 2003).

The rate of herbivory (chewing, sap-sucking and mining) per phyllode over three months (time) was calculated; rates for individual plants were averaged within sites. Due to one site at Gympie being burned during the sampling period, killing all plants being assessed, only two sites were analysed at this latitude. Herbivory was compared both among latitudes and times, and among latitudes and foliage age (expanding vs mature phyllodes), by a two-way multivariate analysis of variance (MANOVA), with sites as replicates within latitudes using Datadesk® 6.1 (Velleman 1997). Pillai's trace was the test statistic used (Tabachnick and Fidell 2001, Quinn and Keough 2002). One-way ANOVA's were then performed on component herbivory damage types.

Results

Soil total N and total P were marginally significant different among latitudes (Table 1a, b): Sydney had a marginally lower total N (0.07±0.02% w/w; P = 0.063) and total P (74.00±74.48 mg kg^{-1}; P = 0.056) compared to Gympie (total N: 0.20±0.08% w/w; Total P: 236.67± 41.63 mg kg^{-1}). Phyllode toughness exhibited a significant reduction towards the tropical latitudes, being significantly greater at Batemans Bay compared to Grafton and Gympie (Table 1c, Fig. 1a). SLA was significantly lower in Sydney compared to the more tropical latitudes (Table 1d, Fig. 1b). C:N did not significantly differ among latitudes (Table 1e, Fig. 1c).

Overall rates of herbivory did not significantly differ among latitudes (Table 2a, Fig. 2), ranging from 3.32%±0.92 (Grafton) to 5.60%±1.17 (Sydney) per three months. There was also no relationship between latitude and the percentage of phyllode area lost to the three different types of herbivores (Table 2b): rates of chewing herbivory among latitudes ranged from 1.03% to 3.74%; sap-sucking herbivory from 0.64% to 1.94%, and mining herbivory from 0.56% to 1.56%. There was no interaction between latitude and time for overall herbivory (Table 2a) or for the component damage types (Table 2b).

Surprisingly, the rate of overall herbivory on mature phyllodes (4.38%±2.83) was significantly higher than that of expanding phyllodes (2.75%±1.84; Table 3a). Leaf chewing damage was not significantly different among latitudes or phyllode age (Table 3b, Fig. 3a). Sap-sucking and mining damage was significantly more prevalent on mature (sap-suckers: 0.92%±0.42; miners:

Table 1. Summary of ANOVA statistics comparing site and plant traits among latitudes. Significant values in bold.

Variable	df	F	P
a) Total nitrogen	3.8	3.75	0.060
b) Total phosphorous	3.8	3.86	0.056
c) Toughness	3.8	5.82	**0.021**
d) SLA	3.8	5.46	**0.025**
e) Carbon:nitrogen	3.8	0.76	0.549

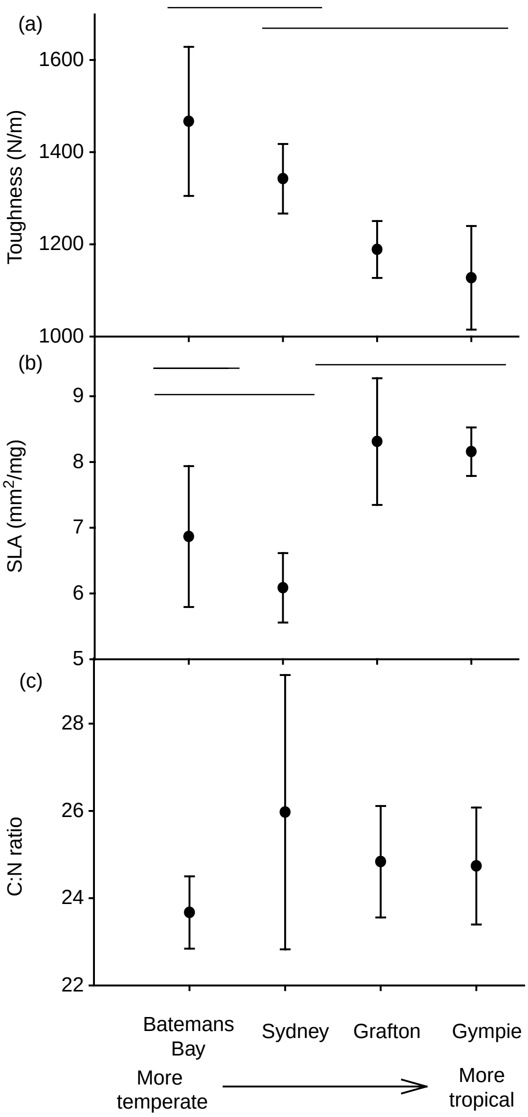

Fig. 1. Comparison of plant traits (mean ± sd) (a) phyllode toughness, (b) specific leaf (phyllode) area (SLA), (c) C:N of *Acacia falcata* phyllodes at four latitudes. Lines above figure indicate significant post-hoc differences among latitudes.

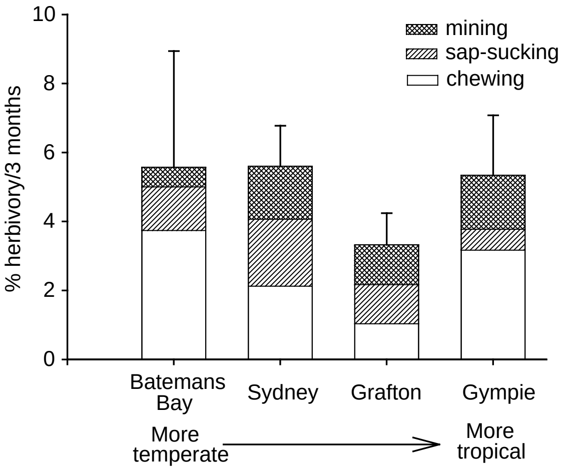

Fig. 2. Average phyllode herbivory (±sd) including chewing, sap-sucking and mining on *Acacia falcata* at four latitudes.

1.40% ± 1.02) compared to expanding phyllodes (sap-suckers: 0.39% ± 0.23; miners: 0.92% ± 0.41; Fig. 3b). There was no significant interaction between latitude and leaf age, however among the herbivory types, mining exhibited a marginally significant interaction between latitude and phyllode age: post hoc tests indicated that mature phyllodes from Gympie had higher rates of mining compared to all other phyllode ages and latitudes (Table 3b, Fig. 3c).

Discussion

In contrast to the general expectation that herbivory should increase towards the tropics, we found no relationship between latitude and the percentage of phyllode area lost to herbivores. It is possible that the difference between previous studies and the present study is due to some difference between Australian ecosystems and those found elsewhere. This idea is weakly supported by data from Morrow and Fox (1989) who found that herbivory on eucalypts in herbarium collections from eastern Australia showed

Table 2. Summary of MANOVA statistics (a) rate of herbivory at different latitudes and time and (b) ANOVA statistics for component herbivory types.

(a) Variable	df	Pillai trace	Approx. F	P
Latitude	9.168	0.19	1.29	0.2462
Time	3.168	0.48	1.53	0.0727
Latitude × time	9.168	0.77	0.91	0.6550

(b) Variable	df	Chewing		Sucking		Mining	
		F	P	F	P	F	P
Latitude	3.14	1.45	0.2393	0.78	0.5112	0.52	0.6703
Time	1.14	2.14	0.0543	1.51	0.1841	0.84	0.5627
Latitude × time	3.14	1.40	0.1565	0.77	0.7436	0.75	0.7657

Table 3. Summary of MANOVA statistics (a) rate of herbivory at different latitudes and leaf age (expanding and mature) and (b) ANOVA statistics for component herbivory types. Significant values in bold.

(a) Variable	df	Pillai trace	Approx. F	P
Latitude	9.42	0.75	1.57	0.1573
Age	3.12	0.58	5.55	**0.0127**
Latitude ×age	9.42	0.75	1.54	0.1647

(b) Variable	df	Chewing		Sucking		Mining	
		F	P	F	P	F	P
Latitude	3.14	1.18	0.3539	0.40	0.7581	7.22	**0.0037**
Age	1.14	0.14	0.7104	9.72	**0.008**	16.60	**0.0011**
Latitude ×age	3.14	1.49	0.2601	0.56	0.640	3.11	0.0607

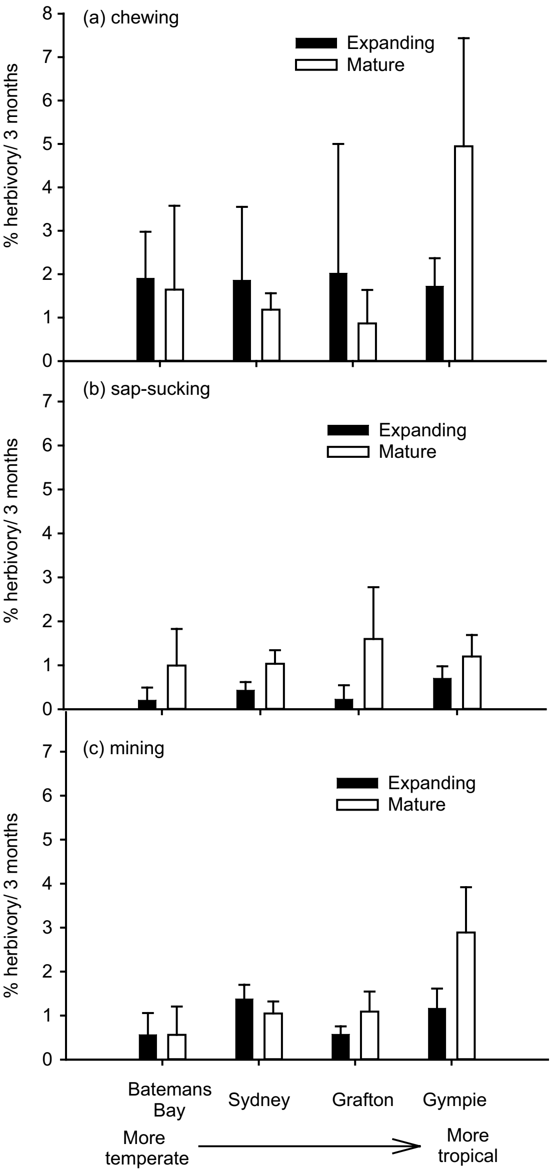

Fig. 3. Average phyllode herbivory (±sd) for (a) chewing, (b) sap-sucking and (c) mining for expanding and mature phyllodes on *Acacia falcata* at four latitudes.

temperate eucalypt species had lower levels of herbivory (7%) compared to more tropical species (10.5%), but had higher herbivory levels than evergreen oak leaves from North America (4%). However, it is also possible that the previously reported latitudinal gradient in herbivory is an artefact arising from comparing rates for different species across a variety of habitats. There are high levels of variation in rates of herbivory between individuals, species, stands, forests types and continents (Landsberg and Ohmart 1989, Coley and Aide 1991, Lowman 1997) and teasing apart the relative importance of different factors is difficult.

By pooling samples across leaves and sites within latitudes we have taken in account much of the variation that occurs within latitudes. Although this does reduce the statistical power of our analysis, we believe that it is an appropriate method to use in relation to the questions asked. Similarly, by sampling at a range of latitudes that encompass a 4.3°C temperature gradient and *A. falcata*'s entire coastal distribution from temperate to sub-tropical latitudes in comparable habitat, we believe that our sampling method was appropriate to assess latitudinal gradients in herbivory.

We found differences in SLA and phyllode toughness among latitudes, and phyllode toughness exhibited a directional change along the latitudinal gradient, decreasing towards the more tropical latitudes. C:N did not change among latitudes, consistent with rates of herbivory. This indicates that C:N may be a more important plant trait than SLA or toughness as a determinant of herbivory. Levels of plant nitrogen are known to regulate rates of insect herbivory and both insect abundance and diversity (Majer et al. 1992, Waring and Cobb 1992, White 1993, Landsberg and Gillieson 1995).

We found higher rates of herbivory on mature foliage compared to expanding foliage, which was also unexpected since previous studies have generally found higher rates of herbivory on young expanding leaves (Coley 1983, Lowman 1985, Ernest 1989). We believe that this result is due to differences in sap-sucking and mining herbivory, types of damage not generally reported in other studies. Sap-sucking damage was higher on mature foliage compared to young expanding foliage, possibly due to the dominant sap-sucking feeders (*Acizzia* psyllids, N. Andrew, unpubl.) on *Acacia falcata* preferring to meet their nitrogen requirements via the slower flow of nitrogen leaving senescing foliage (White 1993). Mining damage is expected to increase as leaves mature, since leaf miners increase in body size as the foliage matures and can potentially bypass chemical and mechanical defences on the exterior of the leaf (Faeth et al. 1981, Connor and Taverner 1997). We found mining to be significantly greater on mature phyllodes in general, and higher on those phyllodes assessed from the most tropical latitudes compared to other latitudes and phyllode ages, in accordance with our hypothesis. These findings are in contrast to studies on eucalypts in Australia, where sap-sucking and mining have generally been assessed as causing minimal damage compared to chewing (Landsberg and Wylie 1983, Fensham 1994). Chewing damage was not significantly different between expanding and mature leaves. Because we assessed herbivory every three months, the specific point in time when expanding leaves became mature leaves could not identified exactly and we may, therefore, have underestimated herbivory on juvenile leaves.

In summary, we found a general consistency in the rates of internally-based herbivory on *A. falcata* along a sub-tropical to temperate latitudinal range. These findings are consistent with the lack of differences in foliar C:N among latitudes and with levels pre- and post- seed predation compiled by Moles and Westoby (2003), but are in contrast to reports of foliar herbivory from studies based on compilations from different host plant species, forest types and geographic regions. While this study has been limited to a single host plant species, similar studies on a variety of species across their distributional range will determine if the patterns in these data can be generalised across a range of host plants and habitats.

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