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# Foliar defences and habitat adversity of three woody plant communities in Singapore

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## Summary

1. The concentrations of total phenolics and condensed tannins were measured in mature and immature leaves of 41 species of tree and shrub found growing wild in Singapore. The species came from *trema belukar*, the typical secondary forest produced by disturbance of primary lowland rain forest, *adinandra belukar*, an early successional community on extremely infertile soils, or mangrove. The *trema belukar* habitat has higher levels of available resources than the other two.

2. *Trema belukar* species had the highest mean level of total phenolics, significantly higher than the other two communities. The three communities did not differ significantly in foliar concentrations of condensed tannins. These results contradict the predictions of the resource-availability hypothesis of plant defence and are discussed in this light.

3. Immature leaves were generally about 70% higher than mature leaves in their total phenolic concentration and 78% higher in condensed tannin concentration across the three communities.

*Key-words:* Herbivory, mangrove, resource-availability hypothesis, tannins, tropical secondary forest

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## Introduction

Plants use a multitude of mechanisms to protect themselves from attack by herbivores but ecologists have discerned underlying patterns in this variety that have produced a number of theories of plant defence. Several of these theories relate level and types of defence to measures of habitat quality described variously as resource availability, stress, adversity or impoverishment (Coley, Bryant & Chapin 1985; Coley 1987; Southwood 1988; Taylor, Aarssen & Loehle 1990; Herms & Mattson 1992). Species of plant from resource-rich (low adversity or stress) habitats are hypothesized to be fast growing and to exhibit low levels of defence because the habitat conditions favour rapid growth and sufficient resources are available to replace any losses to herbivores (Coley *et al.* 1985; Coley 1987; Herms & Mattson 1992). Adverse habitats, low in available resources, favour slow-growing species with high levels of defences because losses to herbivores are not readily replaced (Coley *et al.* 1985; Coley 1987; Taylor *et al.* 1990; Herms & Mattson 1992). Resource shortage selects for increased leaf longevity, often expressed as evergreenness, and such leaves are protected through increased sclerophylly (Chabot & Hicks 1982; Turner 1994). Plant species of nutrient-poor sites are predicted to utilize defences that minimize expenditure of the valuable limiting

resources and have low maintenance costs (Coley *et al.* 1985; Coley 1987; Herms & Mattson 1992). These immobile or quantitative defences are largely complex carbon-based compounds such as structural materials like cellulose and lignin and phenolic compounds such as tannins (Coley *et al.* 1985; Coley 1987; Herms & Mattson 1992). If plants from resource-rich habitats do have defences to maintain they may use more toxic but more costly compounds like alkaloids or glycosides.

Evidence supporting the resource-availability hypothesis of plant defence, besides the general observations of the tendency for nutrient-poor habitats to support sclerophyllous, tanniniferous vegetation and fertile sites to be inhabited by softer-leaved plants (Beadle 1966; Janzen 1974; Givnish 1987; Turner 1994), is still fairly limited. Coley (1983) showed that pioneer tree species in a lowland tropical forest on Barro Colorado Island, Panama, had less fibrous and less tanniniferous foliage than persistent shade-tolerant species. She went on to show significant correlations between leaf life span and both condensed tannin concentration and fibre concentration for the sample of tropical trees (Coley 1988). Similar results were found in data gathered from the literature on a much wider geographic scale by Coley & Aide (1991). However, some studies have found higher condensed tannin concentrations in faster-growing species than

slower-growing ones (Newbery & de Foresta 1985; Baldwin & Schultz 1988).

Comparative studies on the fracture toughness and sclerophylly of three tropical woody plant communities have been conducted in Singapore (Choong *et al.* 1992). These compared two types of secondary forest, or *belukar* to use the local terminology, and mangrove forest. The two secondary forests are *trema belukar*, the community of fast-growing pioneer species characteristic of large gaps in primary rain forest (Choong *et al.* 1992), and *adinandra belukar*, the early successional community on land abandoned after exhaustive agriculture which shows closer floristic affinities with lowland heath forest than with mesomorphic lowland forest (Sim, Tan & Turner 1992). These communities were chosen for study because, generally being of low stature, canopy leaves are relatively easy to collect. Additionally, they provide a range of resource-availability levels. *Adinandra belukar* typically occurs on very acidic and infertile soils (Sim *et al.* 1992; Grubb, Turner & Burslem 1994), whereas *trema belukar* occurs on undegraded soils that are more fertile. Grubb *et al.* (1994) found higher foliar nutrient concentrations in a sample of *trema belukar* species than one of *adinandra belukar* species. Mangrove forests grow in conditions that are clearly adverse to most terrestrial plants, yet productivity levels in this community are, despite the saline and waterlogged soils, often high in comparison with dryland forests (Lugo & Snedaker 1974), although unlikely to reach the high rates of production exhibited by most tropical secondary forests (Brown & Lugo 1990). Therefore, the relative resource availability of mangrove and *adinandra belukar* would seem difficult to determine without data on stand productivity.

Choong *et al.* (1992) have already shown that *adinandra belukar* species have significantly tougher and more sclerophyllous leaves than *trema belukar* as would be predicted by the resource-availability hypothesis. The low values for toughness and sclerophylly found for many mangrove species were attributed to the short life span of the leaves. Salt accumulation by the leaves may necessitate their early shedding leading to an absence of selection in favour of toughening and sclerophylly.

The Singapore study has been extended to investigate the foliar chemical defences of the three forest types, in particular the concentrations of phenolic compounds and condensed tannins present. The rate of herbivory on developing leaves is often considerably higher than on mature, fully-expanded ones (Coley 1983; Coley & Aide 1991). Developing leaves must pass through a phase of being soft and relatively unfibrous making them more attractive to herbivores. Plants may therefore supply young leaves with high concentrations of deterrent chemicals to protect them (Coley & Aide 1991). For this reason the survey included immature and mature leaves from the three communities.

## Materials and methods

Fresh leaves from various tree and shrub species were tested for the concentration of total soluble phenolics using a Folin-Denis assay and condensed tannins using a vanillin assay. Samples of unshaded foliage were collected from trees growing in a variety of sites in Singapore (103° 50' E, 1° 20' N). The *adinandra belukar* species were mostly collected from Kent Ridge within the campus of the National University of Singapore. The cut branches were placed in sealed polyethylene bags during transportation to the laboratory where the cut ends of the shoots were recut under water and kept with the newly cut end under water until the foliage was sampled for analysis. The collected branches usually arrived at the laboratory within 1 h of being detached from the tree and the assays were usually begun within 24 h of collection. A total of 41 species was sampled which included all the common species (Wee & Corlett 1986; Sim *et al.* 1992) of the three communities found in Singapore. Each assay was conducted on three individuals per species but the total phenolics and condensed tannin assays were not always conducted on the same trees. On each branch sampled, a cork borer was used to cut discs of tissue from the laminae of both obviously immature and mature leaves. Damaged and senescent leaves were avoided. Leaves were judged immature if they were not fully expanded and were a clearly different colour or texture from mature ones. Ten leaf discs of each type were weighed and then dried at 80 °C overnight to determine the water content of the leaves. Other discs of known fresh weight were used for the assay.

Boiling water was used to extract soluble phenolic compounds which were assayed colorimetrically with Folin-Denis reagent according to the methods of Quarmby & Allen (1989). Tannic acid was used as the standard and the results expressed as mg tannic acid equivalents per g of tissue, both on a fresh and dry weight basis. Boiling methanol was used as the extractant for the condensed tannin assay following the method of Coley (1983). Catechin was employed as the standard and the results expressed as mg equivalents of catechin per g tissue on a fresh- and dry-weight basis.

The replicates for each species were used to calculate a species mean value of the total phenolic and condensed tannin concentrations and the ratio of these concentrations between immature and mature leaves on the plant. The mean values were then used to compare the three habitats largely by one-way analysis of variance. Some data were log-transformed in order for them to meet assumptions of homogeneity of variance.

## Results

The species tested and the mean values for the chemical assays are listed in Table 1. Nomenclature follows Turner (1993). Considerable differences between

**Table 1.** Foliar concentrations of total soluble phenolics and condensed tannins (mean  $\pm$  one SE,  $n=3$ ) in some trees from Singapore

Species	Total phenols [mg tannic acid equivalents (g fw) <sup>-1</sup> ]		Total phenols [mg tannic acid equivalents (g dw) <sup>-1</sup> ]		Condensed tannins [mg catechin equivalents (g fw) <sup>-1</sup> ]		Condensed tannins [mg catechin equivalents (g dw) <sup>-1</sup> ]	
	immature	mature	immature	mature	immature	mature	immature	mature
<b>Adinandra belukar</b>								
<i>Adinandra dumosa</i>	12.5 $\pm$ 3.1	6.9 $\pm$ 1.7	30.2 $\pm$ 8.8	15.5 $\pm$ 4.8	6.6 $\pm$ 1.9	7.7 $\pm$ 1.5	16.1 $\pm$ 5.4	17.1 $\pm$ 4.6
<i>Dillenia suffruticosa</i>	37.0 $\pm$ 3.5	20.4 $\pm$ 1.1	181 $\pm$ 195	54.5 $\pm$ 3.3	22.3 $\pm$ 0.8	26.2 $\pm$ 3.4	109 $\pm$ 6.6	69.9 $\pm$ 8.6
<i>Fagraea fragrans</i>	21.4 $\pm$ 0.6	14.1 $\pm$ 1.2	70.0 $\pm$ 2.0	37.4 $\pm$ 3.2	5.7 $\pm$ 1.5	6.0 $\pm$ 1.3	18.6 $\pm$ 4.9	15.9 $\pm$ 3.4
<i>Ficus grossularioides</i>	5.6 $\pm$ 0.2	4.4 $\pm$ 0.9	24.2 $\pm$ 1.4	14.7 $\pm$ 2.3	12.2 $\pm$ 4.2	10.1 $\pm$ 2.2	52.8 $\pm$ 17.8	34.8 $\pm$ 9.1
<i>Melastoma malabathricum</i>	13.2 $\pm$ 2.8	6.7 $\pm$ 1.9	48.3 $\pm$ 8.2	21.8 $\pm$ 4.8	14.5 $\pm$ 3.1	19.1 $\pm$ 9.9	54.7 $\pm$ 12.6	67.2 $\pm$ 36.3
<i>Myrica esculenta</i>	16.0 $\pm$ 3.2	15.9 $\pm$ 1.4	30.7 $\pm$ 6.8	30.7 $\pm$ 2.9	51.7 $\pm$ 9.8	30.8 $\pm$ 4.8	97.8 $\pm$ 16.2	59.5 $\pm$ 9.0
<i>Ploiarium alternifolium</i>	7.6 $\pm$ 1.7	6.6 $\pm$ 2.1	33.3 $\pm$ 5.8	25.4 $\pm$ 6.7	21.8 $\pm$ 0.6	19.7 $\pm$ 0.6	97.0 $\pm$ 5.4	79.0 $\pm$ 9.1
<i>Rhodamnia cinerea</i>	22.0 $\pm$ 4.2	26.2 $\pm$ 1.8	61.7 $\pm$ 12.4	50.8 $\pm$ 2.6	41.5 $\pm$ 20.2	78.6 $\pm$ 17.4	116 $\pm$ 57	154 $\pm$ 36
<i>Rhodomyrtus tomentosa</i>	9.8 $\pm$ 1.4	13.1 $\pm$ 1.7	22.9 $\pm$ 3.6	27.1 $\pm$ 3.1	8.6 $\pm$ 4.4	21.8 $\pm$ 4.4	19.7 $\pm$ 9.7	44.8 $\pm$ 8.5
<i>Vitex pinnata</i>	23.1 $\pm$ 1.7	26.1 $\pm$ 1.7	61.3 $\pm$ 10.7	53.8 $\pm$ 3.1	47.3 $\pm$ 10.0	20.7 $\pm$ 1.5	119 $\pm$ 17	42.7 $\pm$ 2.6
<b>Trema belukar</b>								
<i>Alstonia angustiloba</i>	15.8 $\pm$ 7.0	27.2 $\pm$ 24.2	107 $\pm$ 25.2	98.7 $\pm$ 48.6	58.4 $\pm$ 8.7	94.9 $\pm$ 33.2	353 $\pm$ 100	232 $\pm$ 46
<i>Arthrophyllum diversifolium</i>	26.9 $\pm$ 2.3	16.2 $\pm$ 5.9	122 $\pm$ 7.6	49.1 $\pm$ 17.9	3.4 $\pm$ 1.2	1.4 $\pm$ 0.5	15.4 $\pm$ 5.3	4.2 $\pm$ 1.4
<i>Cecropia peltata</i>	24.7 $\pm$ 6.0	17.6 $\pm$ 6.3	24.7 $\pm$ 6.0	38.7 $\pm$ 13.1	68.3 $\pm$ 5.8	34.4 $\pm$ 11.2	223 $\pm$ 277	76.6 $\pm$ 23.2
<i>Commersonia bartramia</i>	42.2 $\pm$ 5.7	50.3 $\pm$ 3.6	118 $\pm$ 13.1	135 $\pm$ 13	131 $\pm$ 24	89.0 $\pm$ 4.7	366 $\pm$ 66	239 $\pm$ 14
<i>Ficus fistulosa</i>	17.9 $\pm$ 5.9	9.4 $\pm$ 1.5	81.1 $\pm$ 37.3	29.6 $\pm$ 4.6	40.7 $\pm$ 5.8	17.8 $\pm$ 5.0	185 $\pm$ 82	55.8 $\pm$ 15.7
<i>Macaranga conifera</i>	54.0 $\pm$ 6.5	53.5 $\pm$ 3.0	155 $\pm$ 16.9	113 $\pm$ 5	24.4 $\pm$ 4.0	19.9 $\pm$ 1.7	72.4 $\pm$ 9.0	50.6 $\pm$ 3.1
<i>Macaranga gigantea</i>	65.0 $\pm$ 29.0	54.1 $\pm$ 27.2	211 $\pm$ 90	127 $\pm$ 65	117 $\pm$ 25	41.5 $\pm$ 4.5	375 $\pm$ 78	96.5 $\pm$ 11.0
<i>Macaranga heynei</i>	43.6 $\pm$ 7.4	53.9 $\pm$ 2.8	96.8 $\pm$ 22.3	120 $\pm$ 14	20.4 $\pm$ 2.9	16.4 $\pm$ 2.9	47.5 $\pm$ 12.2	35.2 $\pm$ 3.3
<i>Macaranga hypoleuca</i>	40.7 $\pm$ 11.8	41.3 $\pm$ 11.8	127 $\pm$ 44	85.6 $\pm$ 21.8	12.6 $\pm$ 0.6	13.8 $\pm$ 1.4	37.9 $\pm$ 3.6	29.2 $\pm$ 3.7
<i>Macaranga triloba</i>	98.9 $\pm$ 16.0	80.7 $\pm$ 8.9	272 $\pm$ 50	187 $\pm$ 22	9.6 $\pm$ 0.8	9.8 $\pm$ 1.1	26.2 $\pm$ 2.8	22.7 $\pm$ 2.6
<i>Mallotus paniculatus</i>	14.7 $\pm$ 0.3	27.6 $\pm$ 12.3	51.5 $\pm$ 9.3	63.9 $\pm$ 14.3	8.1 $\pm$ 3.3	10.5 $\pm$ 3.4	21.3 $\pm$ 7.8	24.3 $\pm$ 7.6
<i>Muntingia calabura</i>	39.0 $\pm$ 3.8	25.0 $\pm$ 2.9	109 $\pm$ 12	60.9 $\pm$ 7.9	12.5 $\pm$ 1.1	16.4 $\pm$ 0.7	35.0 $\pm$ 2.8	39.7 $\pm$ 1.7
<i>Sapium discolor</i>	44.1 $\pm$ 2.5	26.4 $\pm$ 7.9	121 $\pm$ 10	74.6 $\pm$ 22.4	3.8 $\pm$ 2.6	7.5 $\pm$ 5.1	9.7 $\pm$ 5.4	21.1 $\pm$ 13.7
<i>Trema cannabina</i>	25.9 $\pm$ 15.7	18.4 $\pm$ 12.0	84.3 $\pm$ 48.9	53.0 $\pm$ 33.8	5.8 $\pm$ 2.5	7.9 $\pm$ 3.9	19.6 $\pm$ 8.7	22.9 $\pm$ 11.0
<i>Trema tomentosa</i>	21.7 $\pm$ 7.4	18.3 $\pm$ 6.0	70.2 $\pm$ 24.2	48.2 $\pm$ 17.3	13.2 $\pm$ 7.2	21.0 $\pm$ 5.6	42.0 $\pm$ 23.4	54.8 $\pm$ 15.7
<b>Mangrove</b>								
<i>Avicennia alba</i>	11.9 $\pm$ 2.4	13.8 $\pm$ 2.6	41.0 $\pm$ 8.0	39.9 $\pm$ 5.5	1.2 $\pm$ 0.3	1.5 $\pm$ 0.1	4.3 $\pm$ 1.3	4.5 $\pm$ 0.5
<i>Avicennia marina</i>	14.1 $\pm$ 0.9	12.1 $\pm$ 2.4	48.1 $\pm$ 5.0	37.2 $\pm$ 8.6	1.3 $\pm$ 0.3	1.7 $\pm$ 0.8	4.3 $\pm$ 1.2	5.0 $\pm$ 2.4
<i>Avicennia officinalis</i>	10.2 $\pm$ 2.6	8.3 $\pm$ 0.2	47.1 $\pm$ 13.9	30.4 $\pm$ 3.7	1.3 $\pm$ 0.9	3.1 $\pm$ 2.0	5.3 $\pm$ 3.2	9.8 $\pm$ 5.1
<i>Avicennia rumphiana</i>	14.2 $\pm$ 1.4	12.0 $\pm$ 0.9	48.8 $\pm$ 5.6	32.1 $\pm$ 1.2	3.6 $\pm$ 1.3	4.7 $\pm$ 1.8	12.2 $\pm$ 4.4	13.2 $\pm$ 5.9
<i>Bruguiera cylindrica</i>	7.0 $\pm$ 1.5	3.2 $\pm$ 0.4	32.1 $\pm$ 7.1	12.4 $\pm$ 2.4	1.7 $\pm$ 0.9	0.9 $\pm$ 0.4	8.0 $\pm$ 4.0	3.4 $\pm$ 1.9
<i>Bruguiera gymnorhiza</i>	4.5 $\pm$ 0.8	4.8 $\pm$ 1.9	14.8 $\pm$ 3.5	15.6 $\pm$ 6.0	5.7 $\pm$ 0.3	10.8 $\pm$ 1.7	18.6 $\pm$ 0.6	34.4 $\pm$ 4.8
<i>Bruguiera parvifolia</i>	21.4 $\pm$ 7.1	29.3 $\pm$ 6.9	67.3 $\pm$ 23.3	83.9 $\pm$ 15.5	38.7 $\pm$ 11.6	41.5 $\pm$ 11.0	121 $\pm$ 37	122 $\pm$ 31
<i>Ceriops tagal</i>	16.7 $\pm$ 5.9	13.9 $\pm$ 3.3	49.6 $\pm$ 14.4	40.1 $\pm$ 7.9	34.1 $\pm$ 14.9	15.0 $\pm$ 2.5	123 $\pm$ 65	43.8 $\pm$ 5.4
<i>Excoecaria agallocha</i>	16.0 $\pm$ 1.4	11.9 $\pm$ 2.5	63.2 $\pm$ 9.9	49.2 $\pm$ 7.8	5.4 $\pm$ 3.3	1.3 $\pm$ 0.9	20.6 $\pm$ 11.7	5.2 $\pm$ 3.3
<i>Lumnitzera littorea</i>	14.3 $\pm$ 3.3	10.8 $\pm$ 2.2	58.4 $\pm$ 10.9	45.0 $\pm$ 5.2	20.1 $\pm$ 3.5	17.5 $\pm$ 5.2	85.6 $\pm$ 19.4	77.3 $\pm$ 27.5
<i>Lumnitzera racemosa</i>	10.0 $\pm$ 1.0	9.8 $\pm$ 0.4	55.4 $\pm$ 6.0	44.7 $\pm$ 2.6	17.3 $\pm$ 3.2	21.3 $\pm$ 4.9	94.5 $\pm$ 15.2	97.7 $\pm$ 23.1
<i>Rhizophora apiculata</i>	7.5 $\pm$ 3.2	5.1 $\pm$ 3.3	22.4 $\pm$ 8.8	16.6 $\pm$ 10.4	23.0 $\pm$ 1.8	11.5 $\pm$ 5.0	70.1 $\pm$ 10.1	40.3 $\pm$ 19.3
<i>Rhizophora mucronata</i>	24.0 $\pm$ 9.1	13.4 $\pm$ 9.1	80.8 $\pm$ 31.1	44.9 $\pm$ 30.3	79.0 $\pm$ 17.2	46.5 $\pm$ 9.3	262 $\pm$ 54	153 $\pm$ 26
<i>Rhizophora stylosa</i>	23.7 $\pm$ 14.4	9.4 $\pm$ 3.1	79.1 $\pm$ 48.7	30.7 $\pm$ 10.1	29.2 $\pm$ 6.6	19.3 $\pm$ 7.5	98.5 $\pm$ 22.0	62.7 $\pm$ 24.0
<i>Sonneratia alba</i>	18.1 $\pm$ 4.0	11.3 $\pm$ 1.2	64.4 $\pm$ 10.9	40.6 $\pm$ 2.5	2.1 $\pm$ 0.2	1.5 $\pm$ 0.4	7.6 $\pm$ 1.2	5.3 $\pm$ 1.1
<i>Xylocarpus granatum</i>	6.2 $\pm$ 2.0	5.9 $\pm$ 2.3	26.4 $\pm$ 8.6	22.7 $\pm$ 7.7	95.0 $\pm$ 32.8	24.5 $\pm$ 3.6	441 $\pm$ 226	93.1 $\pm$ 5.0

individuals within a species were observed in a number of cases leading to the large variances reported. There was a clear trend for the immature leaves to have higher phenolic and condensed tannin concentrations, particularly on a dry-weight basis.

The mean total phenolic concentration of the trema belukar was significantly higher than the value for adinandra belukar and mangrove for both mature and immature leaves (Table 2). There was no significant difference between the three habitats in mean condensed tannin concentration for either mature or immature leaves, whether expressed on a fresh- or dry-weight basis (Table 2). Kelly & Purvis (1993) have argued that ecological comparisons using multi-species samples can be invalidated by failure to control for taxonomic-relatedness within the samples. Whatever the validity of such an argument, in this case averaging the data by genus within each community did not materially alter the results of the habitat comparison.

There was no significant difference in the relative accumulation of total phenolics or condensed tannins in the immature leaves between the three habitats (e.g. on a dry-weight basis for total phenolics  $F=0.56$ ,  $P=0.58$ ; for condensed tannins  $F=0.98$ ,  $P=0.38$ ). On a dry-weight basis this averaged 70% for total phenolics and 78% for condensed tannins across the three communities, compared to an SLA in the young leaves 32% higher, on average, than in the old leaves indicating that the apparent decline in tannin concentration with development is not merely the dilution by late addition of structural material.

## Discussion

The results presented here are all based on direct analysis of fresh leaves, whereas many published data concern assays on dried leaves. Drying has been

shown to reduce apparent condensed tannin concentrations (Gartlan *et al.* 1980). One direct comparison that is valid, is with the study of total phenols from mangrove leaves presented by Kuthubutheen (1981). For the eight species in common between the two surveys, his results tend to be higher, although a paired *t*-test shows this difference to be not quite significant ( $t=2.13$ ,  $P=0.07$ ). In comparison with Coley's (1983) data from Barro Colorado Island, Panama, the mean total phenolic concentrations for trema belukar of 117 and 86 mg (g dw)<sup>-1</sup> for immature and mature leaves, respectively, are similar to the 127 and 77 mg (g dw)<sup>-1</sup> reported for the Panamanian pioneer species (Coley 1983). A comparison of values for condensed tannins assayed with vanillin between BCI pioneers and trema belukar, 122 versus 17 mg (g dw)<sup>-1</sup> (immature) and 67 versus 8 mg (g dw)<sup>-1</sup> (mature), are clearly very different, with trema belukar being higher even than the shade-tolerant species on BCI. The mature trema belukar leaves were also higher in condensed tannins than leaves from two tropical rain forests in Africa (McKey *et al.* 1978). The condensed tannin assay for Singapore may have given erroneously high results, although there appear to be grounds for considering the BCI species low in condensed tannins. Coley & Aide (1991) summarize data from the literature for a range of physical and chemical properties of leaves for species from different habitats. Their tropical gap class is clearly based on the BCI survey (Coley 1983) plus a few extra species, yet the mean condensed tannin concentration measured in quebracho tannin equivalents from a proanthocyanidin assay rises from 17 mg(g dw)<sup>-1</sup> at BCI for 22 species (Coley 1983) to 29.3 mg (g dw)<sup>-1</sup> for 28 species in the literature review. Coley (1986) reported *Cecropia peltata* reaching condensed tannin (proanthocyanidin) concentrations of 58 mg (g dw)<sup>-1</sup> and Waterman *et al.* (1988) a condensed tannin concentration in mature leaves of *Macaranga hypoleuca* of 162 mg (g dw)<sup>-1</sup>, indicating that at least some tropical pioneer trees possess highly tanniniferous foliage.

It is clear that the Singapore data provide no grounds to support the expectation of higher concentrations of chemical defences in resource-poor environments. An absence of this phenomenon with total phenolic concentrations has been found in other surveys, including the BCI study (Coley 1983) where the pioneer and persistent species were not significantly different in mean total phenolic concentrations. It is the failure of resource availability to effect clearly condensed tannin concentrations at the community level that is surprising. Some of the trema belukar species, such as *Arthrophyllum diversifolium*, *Sapium discolor* and *Macaranga triloba*, did show low levels of condensed tannins but others, such as *Commersonia bartramia*, *Alstonia angustiloba* and *Macaranga gigantea*, were high; higher than all the adinandra belukar species, except *Rhodamnia cinerea*. Similarly, a number of the adinandra belukar, and more markedly some of

**Table 2.** Foliar defensive chemical concentrations in tree species from three different habitats in Singapore. Each value represents mean  $\pm$  1 SE. Those values within a row followed by different letters are significantly different ( $P<0.05$ ) based upon a multiple-range test (95% confidence interval). The data for total phenolics were log-transformed prior to testing

	Age	Adinandra belukar ( <i>n</i> = 10)	Trema belukar ( <i>n</i> = 15)	Mangrove ( <i>n</i> = 16)
Total phenolics [mg (g fw) <sup>-1</sup> ]	immature	16.8 $\pm$ 3.0 <sup>a</sup>	36.3 $\pm$ 4.4 <sup>b</sup>	13.8 $\pm$ 1.5 <sup>a</sup>
	mature	14.0 $\pm$ 2.6 <sup>a</sup>	34.7 $\pm$ 5.2 <sup>b</sup>	10.9 $\pm$ 1.5 <sup>a</sup>
Total phenolics [mg (g dw) <sup>-1</sup> ]	immature	56.4 $\pm$ 14.9 <sup>a</sup>	116.7 $\pm$ 15.8 <sup>b</sup>	49.9 $\pm$ 4.8 <sup>a</sup>
	mature	33.2 $\pm$ 4.8 <sup>a</sup>	85.6 $\pm$ 11.3 <sup>b</sup>	36.6 $\pm$ 4.3 <sup>a</sup>
Condensed tannins [mg (g fw) <sup>-1</sup> ]	immature	23.2 $\pm$ 5.5 <sup>a</sup>	35.3 $\pm$ 10.6 <sup>a</sup>	22.4 $\pm$ 7.1 <sup>a</sup>
	mature	24.1 $\pm$ 6.6 <sup>a</sup>	26.8 $\pm$ 7.3 <sup>a</sup>	13.9 $\pm$ 3.6 <sup>a</sup>
Condensed tannins [mg (g dw) <sup>-1</sup> ]	immature	70.1 $\pm$ 13.4 <sup>a</sup>	121.9 $\pm$ 36.1 <sup>a</sup>	86.0 $\pm$ 29.3 <sup>a</sup>
	mature	58.5 $\pm$ 12.6 <sup>a</sup>	67.0 $\pm$ 18.7 <sup>a</sup>	48.2 $\pm$ 12.0 <sup>a</sup>



the mangroves, were very low in condensed tannins, including the belukar dominant *Adinandra dumosa*. The final conclusion from Singapore is that there is no evidence that resource shortage favours greater investment in foliar tannins.

A further possibility is that another class of chemical compounds acts as a more powerful and pervasive deterrent than those measured in this study. Goh, Soepadmo & Chuah (1991) have published a summary of a large-scale screening of Malaysian plant species for a variety of secondary chemicals, including qualitative tests for alkaloids, saponins and terpenes. Their survey overlaps well with the secondary-forest element from the Singapore survey, with only *Myrica esculenta*, *Cecropia peltata* and *Ficus fistulosa* not being included. Of the 22 species, Goh *et al.* (1991) found clear evidence for alkaloids being present in the leaves of only *Alstonia angustiloba* and saponins were found in *Rhodamnia cinerea* and *Rhodamnia tomentosa*. None of the species produced strongly positive results for the terpene test. These results obviously fail to produce any clear distinction between the two communities in their chemical defences and appear to be more influenced by phylogeny than ecology.

Mangrove species are often noted to be particularly tanniniferous (Janzen 1974; Tomlinson 1986; Hutchings & Saenger 1987) and it was surprising to find tannin concentrations in mangrove leaves in Singapore similar to those in tropical rain-forest pioneers. Choong *et al.* (1992) have shown that mangrove leaves are very low in crude fibre making them likely to be relatively palatable to herbivores unless other means of defence are present. The relatively short life-span of mangrove leaves (Choong *et al.* 1992) may not favour massive investment in tannins (*viz.* Coley *et al.* 1985) and the relative nutrient availability in the mangroves may make replacement of leaf tissue after herbivory relatively easy. One is left wondering why mangrove forests are not regularly defoliated by herbivores gorging on the succulent nutritious foliage. Possibly the salt in the environment greatly reduces the diversity of potential herbivores and the salt in the leaves may actually deter herbivores as much as tannins would (de Lacerda *et al.* 1986, but see Johnstone 1981).

Nearly all the species surveyed showed approaching twice the concentration of tannins in their immature leaves when compared to the mature leaves. Similar results have been reported for tropical trees elsewhere (Coley 1983; Coley & Aide 1991). Young leaves appear considerably more susceptible to herbivory, than mature ones. Coley (1983) measured a rate of loss about six times faster for young leaves. An accumulation of tannins in young leaves, when they are low in fibre content, is probably defensive, possibly more so against pathogens than herbivores, but from the Singapore study it appears to be a tactic employed across all the habitats and hence across a

range of resource-availability levels.

A number of interesting comparisons can be made within the communities studied. The five species of *Macaranga* from the trema belukar include two species habitually inhabited and defended by ants, *Macaranga hypoleuca* and *M. triloba*, with three non-myrmecophytic species (Corner 1988; Fiala *et al.* 1989). The two myrmecophytic species had the lowest condensed tannin concentrations of the five species studied. A similar, though less clear cut, result was found by Chuah *et al.* (1992) who studied the natural products from five species of this genus including two ant-inhabited species, *Macaranga hosei* and *Macaranga hullettii*. Of the five, *M. hullettii* and a non-ant species, *Macaranga heynei*, were the only ones which did not contain significant amounts of terpenoid components. Some evidence, therefore, that investment in defence by ants may reduce the requirement for investment in secondary chemicals.

The results for the mangroves allow a comparison between four species of *Avicennia* and the pre-eminent mangrove family the Rhizophoraceae. It is clear that the *Avicennia* species tend to show a low concentration of tannins in their foliage compared to most of the Rhizophoraceae. Janzen & Waterman (1984) also report a relatively low condensed tannin value for *Avicennia germinans* in Costa Rica. This is another example of the influence of phylogeny on defence type. Much research still needs to be done to disentangle phylogenetic and ecological factors influencing plant chemical defences.

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