

Research paper

## **Insect Folivory and Leaf Traits of Seven Hardwood Species in the Subtropical Rainforest of Fushan, Northeastern Taiwan**

Erh-Yang Lu,<sup>1,2)</sup> Chih-Yi Lee<sup>1)</sup>

### **[ Summary ]**

To understand insect herbivory in the subtropical rainforest of Fushan, northeastern Taiwan, we investigated seasonal patterns of insect folivory (quantified by leaf area loss) and leaf traits (toughness, total phenols, N, and P) of 7 common hardwood species from March to November 2006. We also examined the relationships between the leaf area loss and the 4 leaf traits.

The leaf area loss (rate of insect folivory) significantly differed among sampled months and species. Folivory mostly occurred in leaves before maturation. The area loss in young leaves, which accumulated until July, was the highest in *Pasania hancei* var. *ternaticupula* f. *ternaticupula* (13.00%), while the lowest was in *Meliosma squamulata* (2.96%), and ranged 4.25~7.02% in the other 5 species.

All 4 leaf traits significantly differed among sampled months. Young leaves sampled in April were tender, low in total phenols, and high in N and P. The leaf toughness and concentrations of total phenols and N also differed among species. The area loss in young leaves was significantly positively correlated with the N and P concentrations in young leaves (sampled in April). The greatest leaf area loss occurred in *P. hancei* with the highest N and P concentrations in its young leaves.

The results suggest that even in the same habitat, hardwood species face different pressures of insect folivory in the subtropical rainforest of Fushan. Higher folivory appeared to occur in species with higher foliar concentrations of N and P. It was also clear that insect folivores favored young, tender leaves rich in N and P and low in total phenols.

**Key words:** folivory, leaf traits, nitrogen, phosphorus, total phenols.

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## 研究報告

## 福山亞熱帶雨林闊葉樹昆蟲食葉程度與葉部特性

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## 摘 要

為了解福山亞熱帶雨林的昆蟲植食行為，本研究選取7個福山常見闊葉樹種來進行調查，分別量取各樹種的昆蟲食葉程度(以葉面積損失率進行量化)及4個葉部特性(硬度、總酚類化合物、氮、磷)在季節上的變化，並分析葉面積損失率及葉部特性間的關係。

昆蟲造成的葉面積損失率在採樣月分間具顯著差異，以4月剛發出新葉的損失率最低，也就是昆蟲取食集中在新葉期間，葉片成熟後昆蟲取食壓力大幅降低。葉面積損失率在樹種間亦具顯著差異，年輕葉累積的葉面積損失率(到7月)以三斗石櫟(13.00%)最高，綠樟最低(2.96%)，其餘5個樹種在4.25~7.02%之間。

4個葉部特性在月份間均具顯著差異，以4月的年輕葉之硬度及總酚類濃度最低，氮、磷濃度則最高。葉部硬度、總酚類化合物濃度、氮濃度在樹種間也具顯著差異，但是年輕葉及成熟葉在樹種間高低順序不一致。年輕葉的葉面積損失比率與年輕葉的氮、磷濃度具顯著正相關，三斗石櫟年輕葉中氮、磷濃度最高，被昆蟲取食的比率也是最高的。

這些結果顯示福山亞熱帶雨林的樹種即使是處在相同的環境中，來自昆蟲的取食壓力卻不一致，取食壓力的差異可能與其葉部特性有關。葉面積損失主要發生在葉部完全成熟前，這應與植食昆蟲偏好幼葉的柔軟、低總酚類化合物濃度、高氮及磷濃度有關。

關鍵詞：植食行為、葉部特性、氮、磷、總酚類化合物。

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## INTRODUCTION

In forest ecosystems, herbivory represents one of the major links in energy flows and material cycling. The importance of herbivory also includes effects on plant growth, seed production, community composition, and regeneration (Rausher and Ferry 1980, Marquis 1984, Schowalter et al. 1986, Marquis and Whelan 1994, Coley and Barone 1996, Belovsky and Slade 2000). Herbivorous insects are the most important herbivores in many forest ecosystems (Coley and Barone 1996). Insects feed on various plant organs, and those that chew on leaves garner the most attention. Insect herbivory (or folivory)

is often quantified by leaf area loss (LAL; Coley and Barone 1996). LAL can cause a reduction in the photosynthetic area, premature leaf shedding, and changes in the physical and chemical properties of leaves (Coley 1983, Lowman 1985, 1992, 1995, Lowman and Heatwole 1992, Coley and Barone 1996, Dajoz 2000, Marquis et al. 2001, MacDonald and Bach 2005, Unsicker and Mody 2005).

Many studies found that herbivory varied among species (Coley 1983, Lowman 1985, 1992, Lowman and Heatwole 1992, Barone 1998, Marquis et al. 2001, Xiang and Chen 2004, Unsicker and Mody 2005) and was re-

lated to differences in leaf traits (Coley 1983, Marquis et al. 2001, Forkner et al. 2004, Xiang and Chen 2004). Among leaf traits, N and P are elements essential to plant growth (Perry 1994), phenols are ubiquitous defense compounds (Schoonhoven et al. 2005), and leaf toughness is an indicator of the indigestible composition such as fibers and lignin (Coley 1983). These leaf traits may affect the host choice of herbivores and the amount of herbivory; therefore they have been the major topics of investigation in many studies (Rodriguez 1960, Feeny 1969, Coley 1983, Marquis et al. 2001, Peeters 2002, Forkner et al. 2004, Xiang and Chen 2004, MacDonald and Bach 2005).

This study was carried out in a subtropical rainforest of the Fushan Experimental Forest, northeastern Taiwan. With bountiful rainfall and favorable temperatures, this forest provides habitats for many plant species and herbivorous insects. A great diversity of large moths was reported in Fushan (Chao et al. 1999), and larvae of these moths are the primary leaf chewers in forests (Janzen 1988). This study selected 7 hardwood species common in Fushan to investigate herbivory. The main objectives included: (1) to understand the rate of insect folivory of the 7 species, (2) to examine seasonal patterns of insect folivory and leaf traits, and (3) to analyze relationships between the rate of insect folivory and leaf traits.

## MATERIALS AND METHODS

### Study site

The study site is located in the Fushan Experimental Forest, northeastern Taiwan (24°45'N, 121°35'E). The elevations range 650~1000 m. Fushan is warm and humid year round, with an ever-wet climate according to the classification of geographic-meteorolog-

ical zones in Taiwan by Su (1985). Based on the data of the Fushan meteorological observatory from 1993 to 2000, the mean annual temperature is 18.2°C, and the mean annual rainfall is 4225 mm, with 233 rainy days a year.

### Selected species

Based on a vegetation analysis of the Fushan Experimental Forest by Wang et al. (2000), 7 common hardwood species were selected for this study: *Castanopsis cuspidata* var. *carlesii* f. *sessilis* (Fagaceae), *Cyclobalanopsis longinux* (Fagaceae), *Pasania hancei* var. *ternaticupula* (Fagaceae), *Litsea acuminata* (Lauraceae), *Machilus thunbergii* (Lauraceae), *Meliosma squamulata* (Sabiaceae), and *Diospyros morrisiana* (Ebenaceae). *Diospyros morrisiana* is the only deciduous species, and the other 6 species are evergreen.

### Leaf sampling

In January and February 2005, 42 healthy trees from sunny locations were selected from the 7 species. The number of individuals sampled for each species was determined according to its abundance in this forest. Twelve individuals were selected for *Cas. cuspidata*, 8 for *L. acuminata* and *Mel. squamulata* each, 4 for *P. hancei*, *Cyc. longinux*, and *Mac. thunbergii* each, and only 2 for *D. morrisiana*. Most selected individuals were adult trees, but some were saplings. The diameters at breast height of the selected trees ranged 5.0~23.5 cm.

Leaf samples were collected 7 times in 2005. The 1st sampling of old leaves (which had emerged the previous year) was conducted on 24 March 2005, before the emergence of new leaves. On 29 April 2005, the newly emerged leaves had expanded to the full size of mature leaves, but were still tender and light green. The same cohorts of leaves were

sampled again on 2 June, 12 July, 11 August, 13 September, and 6 November. All leaves sampled in 7 mo were analyzed for their toughness and LAL, but only leaves sampled in March, April, June, July, and November were analyzed for their total phenol, N, and P concentrations. Leaves were sampled from healthy twigs in the middle or lower portions of well-lit crowns. At least 3 twigs were collected from each tree.

### LAL

In this study, the LAL was used to quantify the rate of insect folivory. The edges of wounds caused by chewing mouthparts of insects were mostly smooth and curvy, and differed from those punctured by swaying twigs or lacerated by mammals. The irregular wounds caused by the latter were discounted. After the leaves were removed from the sampled twigs and thoroughly mixed, 20~30 leaves were randomly chosen to be scanned to determine the LAL. In each individual, the percent LAL was calculated from the cumulative area loss of all 20~30 leaves.

### Leaf toughness

Using the design of Feeny (1970), a penetrometer used in this study was manufactured by the workshop of the Department of Mechanical Engineering, National Taiwan University. The toughness of 1 leaf from the middle portion of 1 twig of each tree was measured. The 3 points of measurements were chosen in the middle part of the leaf, and avoided midribs and major veins. The average toughness was then obtained for each tree.

### Leaf chemical analysis

After being oven-dried (45°C), ground, and sifted (mesh no. 60, 0.250 mm), total phenols of leaf samples were analyzed by the

Folin-Ciocalteu method (Waterman and Mole 1994), and N by the Kjeldahl method (Moore and Chapman 1986). The same solution prepared for the N analysis by the Kjeldahl method was then analyzed for P by inductively coupled emission plasmospectrometry (ICP).

### Statistical analysis

Analysis of variance (ANOVA) was used to determine whether LAL and leaf traits (toughness, total phenols, N, and P) significantly differed among species or sampled months. In addition, a correlation analysis was done to investigate the relationships between LAL and leaf traits.

## RESULTS

### LAL

The LAL was used to quantify the rate of insect folivory in this study. The LAL significantly differed among species and sampled months ( $p < 0.05$ ) (Table 1). In Fig. 1, the cumulative LAL (%) was plotted for old leaves (sampled in March) which had emerged before 2005 and new leaves which emerged in April 2005 (from April to November). The cumulative LAL was the lowest in the newly emerged leaves (in April), increased until leaf maturation (in June or July), and somewhat stabilized or fluctuated slightly afterwards.

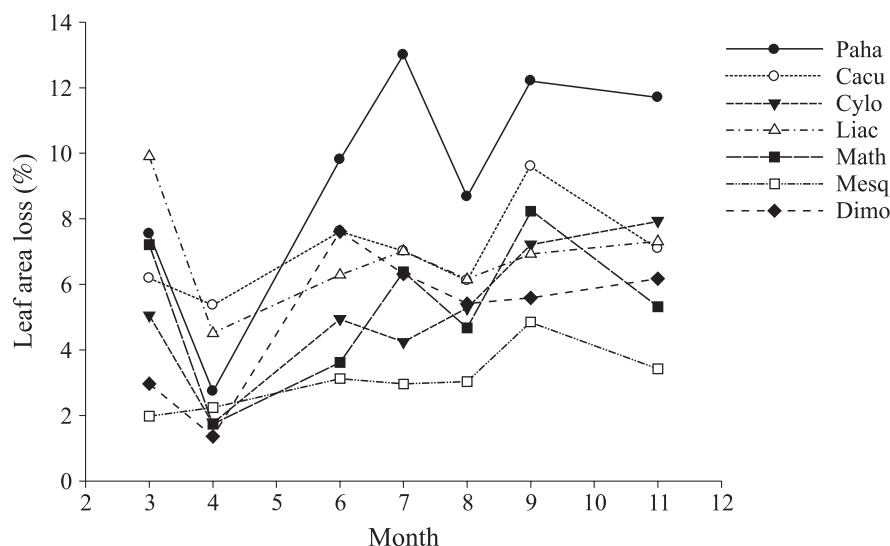
A comparison of the LAL between young and mature leaves is shown in Fig. 2. The LAL that accumulated until July was considered the loss in young leaves, while the LAL that accumulated from July to September was considered the additional loss in mature leaves. The area loss in young leaves was the highest in *P. hancei* (13.00%), the lowest in *Mel. squamulata* (2.96%), and ranged 4.25~7.02% in the other 5 species. The area loss in mature leaves was substantially lower

**Table 1. ANOVA of the effects of species and sampled months on the leaf area loss and leaf traits<sup>1)</sup>**

	Species	Month	Species × Month
Leaf area loss	< 0.0001 <sup>2)</sup>	0.0002	0.9067
Toughness	< 0.0001	< 0.0001	< 0.0001
Total phenols	< 0.0001	< 0.0001	< 0.0001
N	< 0.0001	< 0.0001	< 0.0001
P	0.0946	< 0.0001	0.3165

<sup>1)</sup> Data of leaf area loss and leaf toughness include samples collected in all 7 mo (March, April, June, July, August, September, and November), while data of N, P, and total phenols include samples collected in 5 mo (March, April, June, July, and November). In each sampled month, there were at least 4 individuals for each species except for *Diospyros morrisiana* (which had only 2 individuals).

<sup>2)</sup> Probability for a greater *F* value.



**Fig. 1.** Cumulative area loss of old leaves (March) which emerged before 2005 and new leaves that emerged in April 2005 (from April to November). Each point is the mean of at least 4 individuals for each species except for *Diospyros morrisiana* (Dimo) (which had only 2 individuals).

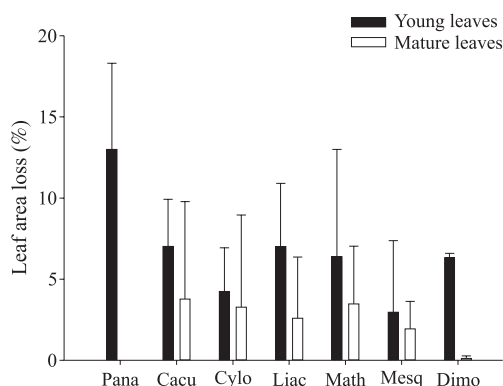
**Paha**, *Pasania hancei* var. *ternaticupula* f. *ternaticupula*; **Cacu**, *Canstanopsis cuspidata* var. *carlesii* f. *sessilis*; **Cylo**, *Cyclobalanopsis longinux* var. *longinux*; **Liac**, *Litsea acuminata*; **Math**, *Machilus thunbergii*; **Mesq**, *Meliosma squamulata*; **Dimo**, *Diospyros morrisiana*.

than that in young leaves. Notably in *P. hancei* and *D. morrisiana*, the area loss in mature leaves was negligible or nonexistent.

#### Leaf traits

Leaf toughness, total phenol concentra-

tion, and N concentration significantly differed among species and sampled months ( $p < 0.05$ ), but the leaf P concentration significantly differed only among sampled months ( $p < 0.05$ ) (Table 1). In addition, the interactions of species and month were significant for leaf



**Fig. 2.** Leaf area loss in young and mature leaves. The leaf area loss which had accumulated until July was considered loss in young leaves, while the leaf area loss that accumulated from July to September was considered additional loss in mature leaves. For each individual, the area loss in mature leaves was counted as “zero” if the calculated additional loss was “negative”. Each point is the mean of at least 4 individuals for each species except for *Diospyros morrisiana* (Dimo) (which had only 2 individuals). ANOVA results: an insignificant species effect ( $p = 0.2779$ ), a significant effect of leaf age ( $p = 0.0001$ ), and an insignificant interaction of species and leaf age ( $p = 0.0537$ ). Species codes are explained in the legend to Fig. 1.

toughness, total phenol concentration, and N concentration ( $p < 0.05$ ), suggesting that seasonal patterns of leaf traits varied with species.

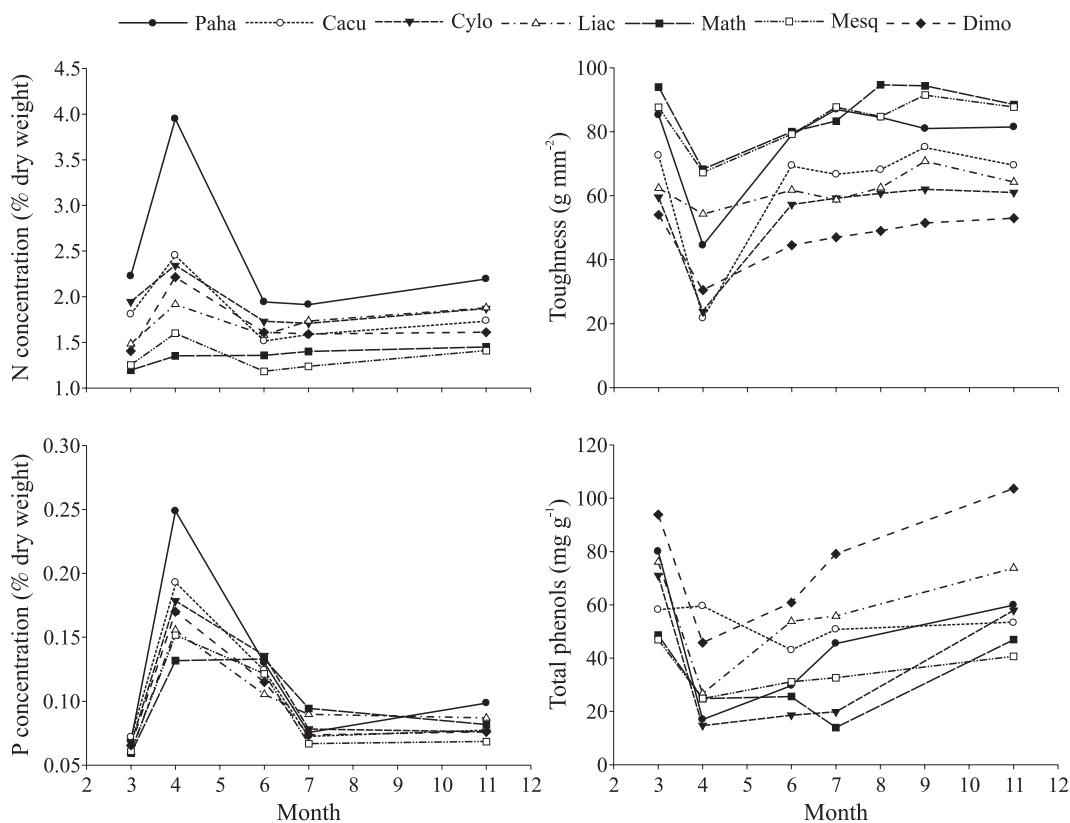
The leaf toughness was the lowest in April, increased afterwards, and stabilized after July (Fig. 3). The toughness in young leaves (April) was the highest in *L. acuminata*, *Mac. thunbergii*, and *Mel. squamulata* ( $54\text{--}68\text{ g mm}^{-2}$ ), followed by *P. hancei* and *D. morrisiana* ( $31\text{--}45\text{ g mm}^{-2}$ ), and was the lowest in *Cas. cuspidata* and *Cyc. longinix* ( $22\text{--}24\text{ g mm}^{-2}$ ). The toughness of mature

leaves (July) was the highest in *Mac. thunbergii*, *Mel. squamulata*, and *P. hancei* ( $83\text{--}88\text{ g mm}^{-2}$ ), followed by *Cas. cuspidata*, *Cyc. longinix*, and *L. acuminata* ( $59\text{--}67\text{ g mm}^{-2}$ ), and the lowest in *D. morrisiana* ( $47\text{ g mm}^{-2}$ ).

The leaf concentration of total phenols generally increased with leaf age, and reached the highest in November. Total phenols in young leaves (April) were the highest in *Cas. cuspidata* ( $60\text{ mg g}^{-1}$ ), followed by *D. morrisiana* ( $46\text{ mg g}^{-1}$ ), and were the lowest in *P. hancei* and *Cyc. longinix* ( $15\text{--}17\text{ mg g}^{-1}$ ). The other 3 species ranged  $25\text{--}27\text{ mg g}^{-1}$ . Total phenols in mature leaves (July) were the highest in *D. morrisiana* ( $79\text{ mg g}^{-1}$ ), followed by *L. acuminata*, *P. hancei*, and *Cas. cuspidata* ( $45\text{--}56\text{ mg g}^{-1}$ ), with the lowest in *Cyc. longinix* and *Mac. thunbergii* ( $14\text{--}20\text{ mg g}^{-1}$ ).

The leaf N concentration was the highest in April, and substantially decreased in June. Leaf N concentrations changed little afterwards. The N concentration in young leaves (April) was the highest in *P. hancei* (3.95%), followed by *Cas. cuspidata*, *Cyc. longinix*, and *D. morrisiana* (2.22–2.45%), and was the lowest in *Mel. squamulata* and *Mac. thunbergii* (1.60 and 1.35% respectively). The leaf N concentration in mature leaves (July) was still the highest in *P. hancei* (1.91%), followed by *L. acuminata* and *Cyc. longinix* (1.71–1.73%), and was still the lowest in *Mac. thunbergii* and *Mel. squamulata* (1.40 and 1.24% respectively).

The leaf P concentration was the highest in April, and substantially decreased in June and July. Leaf P concentrations changed little afterwards. The P concentration in young leaves (April) was the highest in *P. hancei* (0.249%), followed *Cas. cuspidata* (0.193%), and was the lowest in *Mel. squamulata* (0.132%). Leaf P concentration in mature leaves (July) was slightly higher in *Mac.*



**Fig. 3.** Leaf traits of 7 species from March to November of 2005. Each point is the mean of at least 4 individuals except for *Diospyros morrisiana* (Dimo) (which had only 2 individuals). Species codes are explained in the legend to Fig. 1.

*thunbergii* and *L. acuminata* (0.090~0.094%), and was slightly lower in the other 5 species (0.067~0.078%).

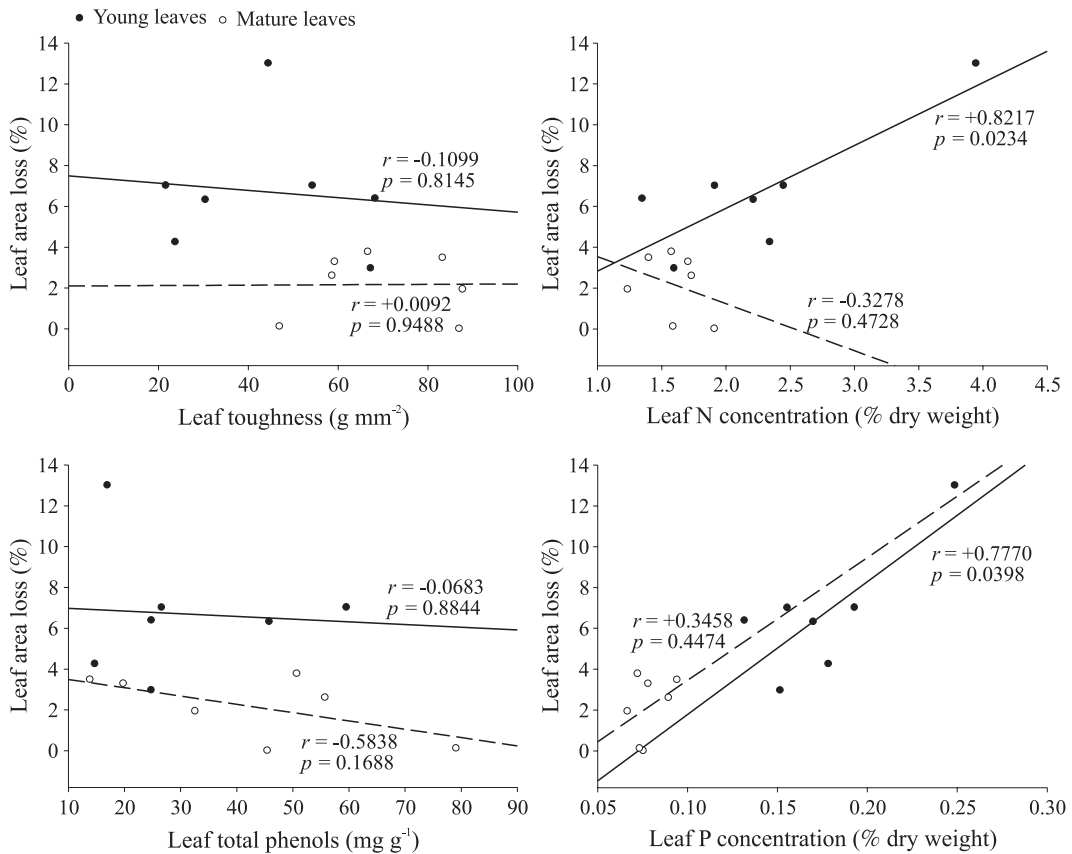
**Correlations between LAL and leaf traits**

The LAL in young leaves was significantly positively correlated with the N and P concentrations of young leaves ( $p < 0.05$ ), whereas the area loss in mature leaves was significantly correlated with none of the 4 leaf traits of mature leaves ( $p > 0.05$ ) (Fig. 4). Among the 7 species, *P. hancei* clearly stood out because of its highest LAL as well as the highest N and P concentrations in young leaves.

**DISCUSSION**

**Species selection**

Compared to temperate forests, rainforests in the subtropics and tropics have greater species diversity and more-complex structures. In a study of subtropical rainforests in Australia, Lowman (1985) found that none of the species accounted for more than 5% of the canopy cover. In contrast, *Nothofagus moorei* was the single most important species in the temperate rainforest of Australia, making up 75% of the canopy cover (Selman and Lowman 1983). Located in the subtropics, the rainforest at Fushan is composed of numerous



**Fig. 4.** Correlations of leaf area loss with leaf toughness, total phenols, N, and P in young (filled circles with solid lines) and mature (open circles with dashed lines) leaves. The leaf area loss in young and mature leaves was the same as in Fig. 2. Traits of young leaves are from samples in April, while those of mature leaves are from samples in July. Each point is the mean of at least 4 individuals for each species except for *Diospyros morrisiana* (which had only 2 individuals).

dominant species. Therefore, the selection of species is of great importance in terms of obtaining representative results. Based on a vegetation analysis at Fushan by Wang et al. (2000), 7 common species were selected in this study: *Cas. cuspidata*, *Cyc. longinix*, *P. hancei*, *L. acuminata*, *Mac. thunbergii*, *Mel. squamulata*, and *D. morrisiana*. These species make up more than half of the canopy in the forest, and thus the results of this study can provide information on herbivory which is representative of Fushan.

#### Insect folivory at Fushan

In this study, the LAL was  $> 10\%$  only in *P. hancei*, with all the other 6 species substantially  $< 10\%$  (Figs. 1, 2). Compared to rates of insect folivory reported for many forests in temperate and tropical areas (compiled by Schowalter 2006), the LAL of these 7 species fell well within the range of those forests. Lowman (1995) stressed that the rates of folivory could tremendously differ among the methods used to assess folivory. The rate obtained by tagging and long-term



observation was higher by several fold than that determined by discrete sampling. Discrete sampling may underestimate folivory because this method does not account for the loss from complete leaf consumption or the early/premature shedding of heavily damaged leaves (Lowman 1995). This study found that the LAL was at the lower end in March (for old leaves which had emerged the previous year) and November, supporting the possibility that more-damaged leaves had been shed earlier.

### Species variations

This study found that the rate of insect folivory significantly varied with species (Table 1). Among the 7 species, the LAL was the highest in *P. hancei*, and the lowest in *Mel. squamulata* (Figs. 1, 2). In spite of growing in the same habitats, these species faced different pressures of herbivory. Similar results were found in many previous studies (Coley 1983, Lowman 1985, 1992, Lowman and Heatwole 1992, Barone 1998, Marquis et al. 2001, Xiang and Chen 2004, Unsicker and Mody 2005). Comparing the taxa gave no consistent conclusions on rates of insect folivory. Values of LAL obviously differed among the 3 species of the Fagaceae, but were rather similar between the 2 species of the Lauraceae.

Species variations in the rate of insect folivory could be related to differences in leaf traits of the species (Coley 1983, Marquis et al. 2001, Forkner et al. 2004, Xiang and Chen 2004). This study also found that each species had distinct leaf traits (Table 1, Fig. 3), and the area loss in young leaves was significantly positively correlated with the N and P concentrations in young leaves (Fig. 4). Insect folivores obviously favored the young leaves of *P. hancei* which are rich in N and P. This result supports the theory of Coley and Barone

(1996), who hypothesized that greater palatability was associated with higher nutritional quality and lower defensive compounds.

An analysis of correlations also suggested that factors other than leaf traits influenced the rate of insect folivory. As in a study by Pérez-Harguindeguy et al. (2003), the rate of herbivory was only weakly related to leaf traits. In addition to leaf traits, the behaviors of herbivorous insects are also important. Slansky and Feeny (1977) reported higher daily consumption rates of food plants that were lower in N by the larvae of cabbage butterfly (*Pieris rapae*), suggesting higher herbivory pressure in plants with low N concentrations. In addition, monophagous and oligophagous insects may have evolved different detoxifying mechanisms to reduce the effects of defense chemicals on the rate of consumption (Howe and Westley 1988). In the future, the behaviors or host preferences of insect folivores should be included in the investigation in order to further understand species variations in insect herbivory.

### Seasonal variations

This study found significant seasonal patterns of insect folivory in the forest of Fushan (Figs. 1, 2). Insects mostly consumed young leaves, and rarely fed on mature leaves. Similar results were found in many previous studies (Coley 1983, Lowman 1985, 1992, Coley and Aide 1991, Kudo 1996, Marquis et al. 2001). The preference for young leaves is probably related to leaf traits as well, which change with leaf aging (Chapin and Kedrowski 1983, Coley 1983, Aide and Zimmerman 1990, Kudo 1996, Alonso and Herrera 2000, Riipi et al. 2002, Forkner et al. 2004, Brunt et al. 2006). In this study, leaves became tougher, higher in total phenols, and lower in N and P with each progressive sampling from April (Fig. 3). Obviously, young leaves pos-

sess characteristics that attract insect folivores (Coley and Barone 1996). This also explains why the area loss in young leaves was significantly correlated with the N and P concentrations in young leaves (Fig. 4).

## CONCLUSIONS

By investigating 7 hardwood species common to the subtropical rainforest of Fushan, this study found that the LAL, which was used to quantify the rate of insect folivory, was > 10% in only 1 species and < 10% in 6 species. In spite of growing in the same habitats, these species faced different pressures of insect folivory. Species variations in the rate of insect folivory were related to the N and P concentrations in the young leaves. Insect folivores appeared to favor young leaves of *P. hancei* which are rich in N and P. In fact, insect folivory mainly occurred on young leaves of all 7 species, which were tender, low in total phenols, and high in N and P, indicating greater palatability for insects. In the field, many more factors could influence the rate of herbivory. Therefore, more-detailed and -extensive studies are required to further our understanding of herbivory.

## ACKNOWLEDGEMENTS

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## LITERATURE CITED

**Aide TM, Zimmerman JK. 1990.** Patterns of insect herbivory, growth, and survivorship in juveniles of a neotropical liana. *Ecology* 71:1412-21.

**Alonso C, Herrera CM. 2000.** Seasonal variation in leaf characteristic and food selection by larval noctuids on an evergreen Mediterranean shrub. *Acta Oecol* 21:257-65.

**Barone JA. 1998.** Host-specificity of folivorous insects in a moist tropical forest. *J Anim Ecol* 67:400-9.

**Belovsky GE, Slade JB. 2000.** Insect herbivory accelerates nutrient cycling and increases plant production. *Proc Natl Acad Sci USA* 97:14412-7.

**Brunt C, Read J, Sanson GD. 2006.** Changes in resource concentration and defense during leaf development in a tough-leaved (*Nothofagus moorei*) and soft-leaved (*Toona ciliata*) species. *Oecologia* 148:583-92.

**Chao JT, Fan YB, Warneke A, Jaung LM, Chen YM. 1999.** Larger moths (Lepidoptera: Bombycoidea and Sphingoidea) of the Fushan Experimental Forest, northern Taiwan. *Taiwan J For Sci* 14:469-78. [in Chinese with English summary].

**Chapin FS III, Kedrowski RA. 1983.** Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64:376-91.

**Coley PD. 1983.** Herbivory and defense characteristics of tree species in a lowland tropical forest. *Ecol Monogr* 53:209-33.

**Coley PD, Aide TM. 1991.** Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW, editors. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. New York: J Wiley. 639 p.

**Coley PD, Barone JA. 1996.** Herbivory and plant defense in tropical forests. *Ann Rev Ecol Syst* 27:305-35.

**Dajoz R. 2000.** *Insects and forests: the role and diversity of insects in the forest environment*. New York: Intercept. 668 p.

**Feeny P. 1969.** Inhibitory effect of oak leaf

tannins on the hydrolysis of proteins by trypsin. *Phytochemistry* 8:2119-26.

**Feeny P. 1970.** Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-81.

**Forkner RE, Marquis RJ, Lill JT. 2004.** Feeny revisited: condensed tannins as anti-herbivore defenses in leaf-chewing herbivore communities of *Quercus*. *Ecol Entomol* 29: 174-87.

**Howe FH, Westley LC. 1988.** Ecological relationship of plants and animals. New York: Oxford Univ Press. 273 p.

**Janzen DH. 1988.** Ecological characterization of a Costa Rican dry forest caterpillar fauna. *Biotropica* 20:120-35.

**Kudo G. 1996.** Herbivory pattern and induced responses to simulated herbivory in *Quercus monogolica* var. *grosseserrata*. *Ecol Res* 11:283-9.

**Lowman MD. 1985.** Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Aust J Ecol* 10:7-24.

**Lowman MD. 1992.** Leaf growth dynamics and herbivory in five species of Australian rain-forest canopy trees. *J Ecol* 80:433-47.

**Lowman MD. 1995.** Herbivory as a canopy process in rain forest trees. In: Lowman MD, Nadkarni N, editors. *Forest canopies*. San Diego, CA: Academic Press. p 431-55.

**Lowman MD, Heatwole H. 1992.** Spatial and temporal variability in defoliation of Australian eucalypts. *Ecology* 73:129-42.

**MacDonald KP, Bach CE. 2005.** Resistance and tolerance to herbivory in *Salix cordata* are affected by different environmental factors. *Ecol Entomol* 30:581-9.

**Marquis RJ. 1984.** Leaf herbivore decrease fitness of a tropical plant. *Science* 226:537-9.

**Marquis RJ, Diniz IR, Morais HC. 2001.** Patterns and correlates of the interspecific

variation in foliar insect herbivory and pathogen attack in Brazilian Cerrado. *J Trop Ecol* 17:127-48.

**Marquis RJ, Whelan CJ. 1994.** Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007-14.

**Moore PD, Chapman SB. 1986.** *Methods in plant ecology*. 2<sup>nd</sup> ed. Oxford, London: Blackwell Scientific Publications. 589 p.

**Peeters PJ. 2002.** Correlations between leaf structural traits and the densities of herbivorous insect guilds. *Biol J Linn Soc* 77:43-65.

**Pérez-Harguindeguy N, Diaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabido M. 2003.** Leaf traits and herbivore selection in the field and in cafeteria experiments. *Aust J Ecol* 28:642-50.

**Perry DA. 1994.** *Forest ecosystems*. Baltimore, MD, London: Johns Hopkins Univ Press. 649 p.

**Rausher MD, Feeny P. 1980.** Herbivory, plant density, and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata*. *Ecology* 61:905-17.

**Riipi M, et al. 2002.** Seasonal changes in birch leaf chemistry: Are there trade-offs between leaf growth and accumulation of phenolics? *Oecologia* 130:380-90.

**Rodriguez JG. 1960.** Nutrition of the host and reaction to pests. *Publ Am Assoc Advanc Sci* 61:149-67.

**Schoonhoven LM, van Loon JJA, Dicke M. 2005.** *Insect-plant biology*. New York: Oxford Univ Press. 421 p.

**Schowalter TD. 2006.** *Insect ecology: an ecosystem approach*. 2<sup>nd</sup> ed. Burlington, MA: Academic Press. 572 p.

**Schowalter TD, Hargrove WW, Crossley DA. 1986.** Herbivory in forested ecosystems. *Annu Rev Entomol* 31:177-96.

**Selman B, Lowman MD. 1983.** The biology and herbivory rates of *Novacastria nothofagi* Selman (Coleoptera: Chrysomelidae), a new

genus and species on *Nothofagus moorei* in Australian temperate rain forests. *Aust J Zool* 31:179-91.

**Slansky F, Feeny P. 1977.** Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecol Monogr* 47:209-28.

**Su HJ. 1985.** Studies on the climate and vegetation types of the natural forests in Taiwan (III): a scheme of geographical climatic regions. *Q J Chin For* 18:33-44.

**Unsicker SB, Mody K. 2005.** Influence of tree species and compass bearing on insect folivory of nine common tree species in the West Afri-

can savanna. *J Trop Ecol* 21:227-31.

**Wang HH, Pan FJ, Liu CK, Yu JH, Hung SF. 2000.** Vegetation classification and ordination of a permanent plot in the Fushan Experimental Forest, northern Taiwan. *Taiwan J For Sci* 15:411-28. [in Chinese with English summary].

**Waterman PG, Mole S. 1994.** Analysis of phenolic plant metabolites. Oxford, London: Blackwell Scientific Publications. p 66-103.

**Xiang H, Chen J. 2004.** Interspecific variation of plant traits associated with resistance to herbivory among four species of *Ficus* (Moraceae). *Ann Bot* 94:377-84.