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Studies on Herbivory and Its Influencing Factors of Plants in Subtropical Evergreen Broad-leaved Forest

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摘 要

植物与昆虫都是森林生态系统的重要组成成分，两者在森林生态系统的物质循环和能量流动过程中具有重要作用。昆虫食叶是森林常见的特征，而植物则在昆虫取食的压力下进化出多种防御策略，两者在长期的相互作用过程中形成了复杂的协同进化关系，成为进化生物学和生态学研究的热点。

常绿阔叶林是我国亚热带地区的地带性植被，具有许多与热带森林和温带森林明显不同的种类组成和群落特征，尽管对亚热带常绿阔叶林已开展了系统的研究，但有关植物与食叶昆虫之间相互作用的研究还不多见，而这些研究对揭示常绿阔叶林生态系统维持和受损生态系统的恢复都具有重要的意义。本论文选择位于我国亚热带南部的梅花山和中北部的浙江天童两地常绿阔叶林中的代表植物作为研究对象，通过野外跟踪观测、室内分析，研究了叶片虫食状的多样性特征、植物叶片虫食的时间和空间动态、出叶物候和叶片特性与叶片虫食的关系，总结出植物对虫食所采取的应对策略。研究结果如下：

1 对浙江天童常绿阔叶林 11 种常绿乔灌木叶片虫食状类型和格局的观测分析表明：（1）11 种植物中共有 16 种叶片虫食状类型, 每种植物的叶片虫食状类型数在 10–13 种之间，其中缘食状最常见，虫瘿最少；（2）叶片虫食状格局分为 3 种类型：一种取食状占优势的单优格局（如马银花和檵木）、两种虫食状(缘食状和顶食状)共占优势的双优格局（木荷）和三种以上虫食状占优势的多优格局（如栲树、连蕊茶和格药柃等）；（3）乔木的叶片取食状多样性指数(2.040)高于灌木(1.882), 优势种多样性指数高于伴生种, 但差异均不显著，多样性指数反映了虫食状类型和出现频率的综合差异；（4）16 种虫食状类型中有 8 对显著正相关, 4 对显著负相关, 可能反映出不同类型昆虫取食植物的趋同和差异。

2 对浙江天童常绿阔叶林中 11 种常绿乔灌木叶片虫食动态的研究表明：（1）11 种植物平均虫食率为 11.87%，幼叶期虫食率占总虫食率的 56.9%；平均虫食频度为 50.15%，幼叶期虫食频度占总虫食频度的 62.30%；（2）虫食动态有三种格局：春季幼叶期虫食为主的单峰格局（如格药柃、栲树和苦槠）、春季幼叶期虫食为主和夏季虫食为辅的双峰格局（如米槠、青冈、和莲蕊茶等）；春季幼叶期虫食为主和夏秋两季节虫食为辅的三峰格局（如木荷）；（3）不同生活型植物叶

片虫食率间存在一定的差异，乔木叶片的平均虫食率(18.66%) 显著高于灌木叶片的平均虫食率(6.21%; t=2.260, p=0.050)；而优势种的平均虫食率(13.00%)与伴生种(10.51%)没有显著差异。

3 对福建梅花山和浙江天童代表植物幼叶期虫食跟踪调查研究的结果发现幼叶期存在三种虫食格局：前食型虫食格局（如格药柃、两广石栎和上杭锥等)、后食型虫食格局（如建润楠、黄樟和黄瑞木）和中间型虫食格局（如辣汁树、栲树和木荷等)，表明亚热带植物幼叶期对虫食防御的能力及对策的差异，前食型虫食格局的植物为逃避策略，而后食型虫食格局的植物为抵抗策略，而中间型虫食格局的植物则不明确或二者兼有。

4 对木荷林林下、林窗以及竹林林下 3 种不同生境下的木荷幼树叶片虫食率与虫食频度进行了调查分析，结果发现（1）木荷林林下木荷幼树叶片的虫食率(14.14%)显著高于竹林林下(5.71%; $p<0.05$)，木荷林林下(12.28%)低于木荷林林窗(14.72%)，但不显著；（2）大部分受损叶片的虫食率低于 10%，昆虫对叶片仅为适量取食，叶面积大量损失的情况较少；（3）木荷幼树叶片虫食频度与虫食率极显著正相关($p<0.01$)。以上结果表明昆虫取食植物叶片随生境的变化而变化。

5 对福建梅花山代表植物的出叶时间、展叶速度、展叶期、出叶格局以及植物幼叶期的叶片虫食关系的分析表明：（1）植物幼叶期叶片平均虫食率为 8.59%，平均虫食频度为 33.29%；（2）82%的植物于 4 月份抽生新叶，乔木与灌木的出叶时间差异不显著。出叶时间对幼叶期虫食率无显著影响。展叶速度与出叶时间显著正相关($R=0.38, p<0.05$)，出叶越早的植物展叶越慢，出叶越晚的植物展叶越快。乔木的平均展叶速度显著快于灌木($t=2.196, p<0.05$)，展叶速度与幼叶期的虫食率显著正相关($R=0.35, p=0.039$)，展叶速度越快的植物幼叶期虫食率越高，反之越低；（3）乔木的出叶同步性低于灌木，但二者差异并不显著，植物的出叶同步性对虫食无显著影响，但与虫食频度显著正相关($R=0.35, p=0.030$)，即出叶同步性越高，被昆虫攻击的叶片越多，表明叶片数量是昆虫取食的重要选择因素；（4）展叶期与展叶速度极显著负相关($R=-0.423, p=0.008$)，但展叶期同虫食率并无显著相关性。

6 叶片的叶绿素含量、含水量、比叶重、叶片硬度与幼叶期叶片虫食率和虫食频度相关性分析表明：（1）叶绿素含量与比叶重极显著负相关($p<0.001$)，同叶片硬

度显著负相关($p=0.012$)，比叶重同叶片硬度极显著正相关($p<0.001$)；（2）植物叶片虫食率与叶片含水量显著正相关($p=0.034$)，而同叶绿素含量、比叶重和叶片硬度均没有显著相关性；（3）77%的植物其幼叶的虫食与含水量正相关，而且 5 种植物 (两广石栎、苦槠、木荷、甜槠和连蕊茶)达显著水平；73%的植物其幼叶的虫食与比叶重负相关，3 种植物(两广石栎、苦槠和木荷)达显著水平；68%的植物其幼叶虫食与叶片硬度负相关，4 种植物(两广石栎、米槠、青冈和木荷)达显著水平，但建润楠与叶片硬度显著正相关；（4）叶片硬度对成熟叶片的虫食没有显著影响；比叶重与成熟叶片的虫食率负相关，但只有马银花和连蕊茶达显著水平；叶片含水量与成熟叶片的虫食率正相关，且格药柃和细齿柃达显著水平；叶绿素含量与成熟叶片的虫食率负相关，且青冈、木荷和连蕊茶达到显著水平；（5）虫食率与虫食频度极显著正相关($p=0.004$)，虫食频度可以反映虫食率的大小。

7 综合上述研究发现常绿阔叶林植物对昆虫取食所采取的策略可分为三种类型，即防御、逃避及二者间的过渡类型：（1） 叶片含水量低但硬度大的植物，叶片中营养含量低但出叶时间早且生长缓慢，叶片虫食率低，此类植物(如黄樟、辣汁树和黄瑞木等)以防御的方式抵抗昆虫的取食；（2） 叶片含水量高但硬度低的植物，叶片中营养含量高、出叶时间晚且生长快速，但又局限于资源的配置可能导致化学防御物质含量少，叶片虫食率较高，此类植物(如两广石栎、甜槠、苦槠和木荷等)倾向于快速的生长以逃避昆虫的取食；（3）处于此两类之间的植物的应对策略并不明确，可能是防御和逃避之间的过渡类型但也可能采取其他策略。

关键词：常绿阔叶林, 叶片, 物候, 叶片特性, 虫食, 动态, 防御对策

ABSTRACT

Plants and insect herbivores are integral to the forest ecosystem, playing important roles in food webs, nutrient cycling and energy transfer. Herbivory on leaves by insect is common in the forest, and plants have consequently developed multiple strategies against insect herbivores. The evolutionary relationship between herbivores and plants has resulted in an impressive variety of adaptations and interactions, and studies of that relationship have become a most interesting focus in evolutionary biology and ecology.

Evergreen broad-leaved forest is the regional vegetation in eastern China, and differs from tropical and temperate forest in both species diversity and community structure. Although research into subtropical evergreen broad-leaved forest had been conducted from many perspectives, study of the interaction between plant and insect herbivores is rare. However, the interaction between plants and herbivores is very important for maintaining and restoring evergreen broad-leaved forest. In this study, plants in Mt. Meihuashan of Fujian province and the Tiantong region of Zhejiang province were investigated. Through field research, monitoring and data analyses in the lab, herbivory pattern diversity, leaf phenology, leaf traits, temporal and spatial patterns of herbivory were researched into. And the strategies plants used to battle herbivores were summarized according to the results, which are as follows:

1 The study investigated herbivory patterns on leaves of 11 evergreen plant species in Tiantong National Forest Park. As a result, (1) 16 kinds of insect herbivory patterns were identified on the leaves of 11 evergreen tree species, and from 10 to 13 for leaves from the same species. The frequency of Edge Defoliation was the highest (28.7%) and that of Gall was the lowest (0.5%). (2) Based on the number of dominant insect herbivory patterns in a species, three distribution types in 11 species were identified: (i) mono-dominant distribution-type with only one dominant insect herbivory pattern in a species(*Rhododendron ovatum* and *Loropetalum chinense)*; (ii) bi-dominant distribution-type with two dominant insect herbivory patterns in a species(*Schima superba*); and (iii) multi-dominant distribution-type with three or more than three dominant insect herbivory patterns in other 8 tree species. (3) Although the average index of six arbor species (2.040) was higher than that of five shrub species (1.882) and the average index of dominant species was higher than that of companion species, there was no significant difference between them. (4) Correlation analysis showed that there were significantly positive correlations among eight pairs of insect herbivory patterns and significantly negative correlation among four pairs of insect herbivory patterns. This may suggest similarity and difference in insect herbivory selection.

2 The dynamics of herbivory on 11 plants was investigated in Tiantong, Zhejiang province. The results were as follows: (1) Average herbivory on plant leaves was 11.87%, and 56.9% of herbivory occurred during leaf expansion. Herbivory frequency was 50.15%, and 62.30% of herbivory frequency occurred during leaf expanison. (2) Herbivory patterns could be classified into three categories according to the herbivory intensity in different seasons: mono-peak herbivory pattern with leaf damage occurring mainly in spring (*Eurya muricala* , *Castanopsis fargesii* and *C. sclerophylla*); bi-peak herbivory pattern with leaf damage occurring not only in spring but also in summer (*Castanopsis carlesii, Cyclobalanopsis glauca, Camellia fraternal* and *Rhododendron ovatum*); tri-peak herbivory pattern with damage occurring in spring, summer and autumn (*Schima superba*). (3) Life form affected herbivory on leaves. Herbivory on arbors leaves was significantly higher (18.66%) than that on shrubs (6.21%; t=2.260, p=0.050). Although herbivory on leaves of dominant species (13.00%) was higher than companion species (10.51%), there was no significant difference between them (p>0.05).

3 As indicated by the Mt. MeiHuaShan and Tiantong monitoring project, herbivory during the leaf expansion period can be classified into 3 categories according to time: (1) Pre-herbivory, meaning the majority of herbivories occurred before the leaves reached full size; (2) Post-herbivory, meaning the majority of herbivory occurred in several days after the leaves reached full size; and (3) mid-herbivory, that is, herbivory occurred during leaf expansion and development. The patterns of herbivory on young leaves were the results of strategies applied by plants. Plants that suffered pre-herbivory damage might employ “escape” strategy to reduce leaf losses. Plants that suffered post-herbivory damage might employ ‘defense’ strategy to reduce leaf losses. Nonetheless, plants of the mid-herbivory pattern depend on other factors or employ both strategies.

4 The effects of habitat on herbivory in juveniles of *Schima superba* was investigated in Tiantong. The results suggested, (1) for shade leaves, the rates of herbivory were significantly higher (14.14%) in *S. superba* than that in bamboo forest (5.71%; $p<0.05$). However, in *S. superba* forest, herbivory on leaves showed no significant difference between in shade (12.28%) and in light gap (14.72%). (2) for the majority of damaged leaves, leaf area losses were under 10%. It means that herbivory was moderate rather than serious as assumed before. (3) There was a significantly positive correlation between herbivory and herbivory frequency.

5 Timing of leaf emergence, leaf expansion rate, duration of leaf expansion, leaf emergence pattern and herbivory on young leaves were investigated in Mt. MeiHuaShan. The relationships between leaf phenology and leaf herbivory were examined. The results were as follows: (1) Herbivory on young leaves was 8.59% and herbivory frequency was 33.29%. (2) 82% of the species leafed out in April and there was no significant difference on leaf emergence time between arbors and shrubs. No significant correlation was found between the timing of leaf emergence and herbivory on young leaves. There was significant correlation between leaf expansion rate and leaf emergence time ($R=0.38$, $p<0.05$). The earlier the species leafed out, the slower it expanded. The leaf expansion rate of arbors was significantly more rapid than that of shrubs ($t=2.196$, $p<0.05$). Significant relationship was found between leaf expansion rate and herbivory on young leaves ($R=0.35$, $p=0.039$). The more rapid the leaves expanding, the greater damage it suffered. (3) In terms of synchrony of leafing out, there was no significant difference between arbors and shrubs. There was no significant correlation between synchrony of leafing out and herbivory on young leaves, but significant relationship was found between it and herbivory frequency ($R=0.35$, $p=0.030$). It means the more synchronous the species leafed out, the more leaves were attacked. (4) Duration of leaf expansion differed by almost 60 days and were significantly related to leaf expansion rate (R=-0.423, p=0.008). However, no significant relationship was found between duration of leaf expansion and herivory on young leaves.

6 To study the effects of leaf traits on herbivory, chlorophyll content, water content, LMA (Leaf mass per area) and leaf toughness of young leaves and herbivory were studies in Mt. Meihuashan. The relationship between leaf traits and herbivory was examined. The results were as follows: (1) Chlorophyll content was significantly negatively correlated with LMA ($p<0.001$) and leaf toughness ($p=0.012$), and LMA was significantly positively correlated with leaf toughness ($p<0.001$). (2) Herbivory was significantly positively related to water content ($p=0.034$). However, no significant correlations were found between herbivory and chlorophyll, LMA and leaf toughness. (3) The herbivory on young leaves of 77% of the species examined was positively correlated with water content, and it was significant for *Lithocarpus synbalanus*, *Castanopsis sclerophylla, Schima superba*, *Castanopisis eyrei* and *Camellia fraterna*. The herbivory on young leaves of 73% of all species was negatively correlated with LMA, and it was significant for *Lithocarpus synbalanus*, *Castanopsis sclerophylla* and *Schima superba*. (4) The herbivory of 68% of all species was negatively correlated with leaf toughness, and it is significant for *Lithocarpus synbalanus*, *Castanopsis carlesii, Cyclobalanopsis glauca* and *S. superba*. However, herbivory on the leaves of *Machilus oreophila* was positively correlated with leaf toughness. Herbivory was not significantly related to chlorophyll content. For mature leaves, herbivory was not significantly correlated with leaf toughness. Herbivory on mature leaves was negatively correlated with LMA, but it was significant only for *Rhododendron ovatum* and *Camellia fraterna*. And herbivory was also negatively correlated with chlorophyll content, but it was significant only for *Cyclobalanopsis glauca, S. superba* and *Camellia fraterna*. However, herbivory on mature leaves was positively correlated with water content, and it was significant for *Eurya weissiae* and *Eurya nitida*. (5) Significant relationship was found between herbivory and herbivory frequency ($p=0.004$) on mature leaves.

7 Three strategies were identified according to the results mentioned above. (1) The species that leafed out earlier with lower leaf water content, higher leaf toughness and lower leaf expansion rate, such as *Cinnamomum porrectum, C. tsangii* and *Adinandra millettii*, might employ 'defense' strategy to reduce leaf losses. (2) The species that leafed out later with higher leaf water content, lower leaf toughness and higher leaf expansion rate, such as *Lithocarpus synbalanu*s, *Castanopsis sclerophylla, Schima superba* and *Castanopisis eyrei,* might employ 'escape' strategy to reduce herbivory. (3) The strategies used by other species are not clear and they might employ either of the two strategies or other ways to reduce herbivory.

Key words: Subtropical evergreen broad-leaved forest, Leaf, Leaf phenology, Leaf traits, Herbivory, Dynamic, Defense strategy

目 录

研究目的和意义

植物和植食昆虫作为生态系统的重要组分，两者总数占地球生物的将近一半，相互关系十分复杂；一方面昆虫通过取食叶片降低植物的适合度(Marquis, 1984; Bazzaz *et al.*, 1987; Mothershead and Marquis, 2000; Elle and Hare, 2002; Steets and Ashman, 2004)、影响植物竞争和群落动态(Avila-Sakar *et al.*, 2003; Davidson, 1993; Strauss *et al.*, 2001)，另一方面植物在昆虫强大取食压力下进化出多种类型的防御手段，减少昆虫取食(Coley and Barone, 1996; 蔡志权和曹坤芳, 2002)；两者相互作用不仅塑造了生物界丰富多样的生态适应类型和错综复杂的营养关系(Coley, 1983; Hartley and Jones, 2003; Kursar and Coley, 2003)，而且推动了生态系统的物质循环和能量流动(Coley, 1983; Herrera and Pellmyr, 2002)。因此，揭示植物与昆虫的相互关系不仅是进化生物学的核心问题，也是生态学研究的重要内容(Coley, 1983; ; 钦俊德, 1987; Herrera and Pellmyr, 2002; 阎凤鸣, 2003; 张大勇等, 2004)。

叶片是植物地上部分最易被昆虫取食的器官之一，因而也是昆虫取食和植物防御作用最强烈的部位之一。由于叶片的发生、发育具有明显的节律变化和阶段差异，因而与之相适应的昆虫食叶也表现出一定的动态变化。大量的研究表明昆虫对植物叶片的取食具有明显的时空格局 (Coley, 1983; Lowman, 1987; 孙谷畴, 1990; 郑征等, 2001; 于晓东等, 2001; 蔡志权和曹坤芳, 2002; Kursar and Coley, 2003)，其中最明显的格局就是昆虫对幼叶和成熟叶的取食差异(Kursar and Coley, 2003)。Coley 等人的调查发现热带植物叶片的虫食有 68%发生在幼叶期，幼叶日损失率是成熟叶的 5-25 倍(Coley, 1983)；我国西双版纳季雨林植物叶片虫食也表现出相似的格局(张大勇等, 2004)；而温带植物叶片的虫食大部分发生在成熟叶，仅有 27%在幼叶期，表现出完全相反的虫食格局(Coley and Barone, 1996)。

那么，是什么因素导致了昆虫对幼叶和成熟叶取食有如此大的差异呢？尽管影响因素很多，但其中一个重要原因是与幼叶和成熟叶结构和性质的差异及防御水平不同有关。对热带植物叶片发育的跟踪观测发现，叶片在发育过程中营养、形态结构和次生代谢物的含量发生明显的变化(Coley and Barone, 1996; Kursar and Coley, 2003)，幼叶期叶片的含水量和含氮量高、次生代谢物（主要为酚类和单宁类等化合物）的含量低，因而适口性好，有利于昆虫取食；但随着叶片的发育，许多植物叶片的表面形成毛或蜡质、结构硬化、次生代谢物的含量增加，而含水量和含氮量下降，因此叶片适口性降低，不利于昆虫的取食(Coley, 1983; Coley and Barone, 1996; Kursar and coley, 2003; Theis and Lerdau, 2003)，其中硬度的增加被认为是成熟叶防御昆虫取食的最有效方式(Kursar and Coley, 2003)。成熟叶的这种防御方式被称为组成式防御(Kursar and Coley, 2003)，是一种需要资源投入的防御方式(Iwasa et al., 1996; Kursar and Coley, 2003; Stamp, 2003)，对快速生长的幼叶来说，这种防御投资影响到叶片的生长，不可能成为其最佳选择(Kursar and Coley, 2003)；但面对幼叶强大的被取食压力，植物则采取了另外一种被称为“逃避”（escape）和忍耐(tolerance)的策略，就是通过加快展叶速度来缩短易被昆虫取食的时间（逃避）或者是通过延缓叶片变绿来减少因取食而造成的损失（忍耐）(Aide, 1989; Kursar and Coley, 1992)。

如果说热带植物由于叶片寿命长（几年甚至十几年）、幼叶期相对较短（仅1周左右）(Coley and Barone, 1996)，于是权衡的结果是加大对成熟叶的防御投资；那么温带植物叶片寿命短（几个月或更短）、幼叶期相对较长，是否会加大对幼叶投资或形成其它与热带植物完全不同的防御方式，从而导致两者完全不同的食叶格局？亚热带常绿阔叶林植物叶片寿命、叶片扩展速度和幼叶期长度等特征既不同于温带植物也不同于热带植物，那么它们又是如何权衡对幼叶和成熟叶的保护的？我们尚无答案。

叶片发生节律（物候）被认为是植物适应不利环境（如低温和干旱）或应对生物取食压力节律变化的一种发育方式，通常有同步抽叶和连续抽叶两种方式，但是即使在气候波动很小的热带低地雨林地区，叶片的发生也并非全年连续不断，而是具有一定的抽叶高峰，这被认为是有利于减少食草动物的取食(Aide, 1992)。然而，在高度季节性的环境中（如温带落叶林或热带干旱林），物候一向被认为是由温度或湿度季节性变化引起的生理胁迫制约的，与生物压力无关，但目前已有一些研究认为叶片发生节律也是季节性森林植物防御昆虫食叶的一种对策(Aide, 1992; 1993; Van Asch and Visser, 2007)。一些学者对热带季节性干旱林植物的研究发现，大多数植物选择在雨季来临之前抽叶，以避开昆虫出现的高峰，

或者是采取高度集中式的同步抽叶方式，让动物饱食生厌（satiation）；因此同种植物在旱季抽生的叶或同步抽生的叶受到昆虫的取食明显低于湿季或非同步抽生的叶(Coley, 1983; Lowman, 1987; 1992; Aide, 1992; 1993; Murali and Sukumar, 1993; 张大勇等, 2004)。亚热带常绿阔叶林也属于季节性森林，叶片的抽生表现出一定的节律变化，在我国东部亚热带地区，许多植物一年有两次抽叶高峰，一次在初春（与低温相对应）、另一次在夏末（与干旱相对应）（个人观察），这种发育节律是否也是逃避昆虫取食的一种策略？如果是，那么两次抽叶对策的差异是什么？

不同地区植物叶片的发生节律和发育过程明显不同，而同一地区不同生活型的植物、同一生活型不同亲缘关系植物叶片的发生节律和发育过程也存在着不同程度的差异。那么面临同样取食压力具有相同生活型的植物是否具有相似的虫食格局和防御对策？具有不同生活型的植物又是否表现出明显不同的虫食格局或防御对策呢？目前对热带雨林植物的研究发现，昆虫对林窗种类叶片取食明显高于林下耐荫植物，对先锋种类的取食高于演替中后期种类，这被认为是由于两类植物具有明显不同的防御对策所致(Coley, 1983)，可见生活方式不同影响到了叶片的虫食和防御。但生活型或生活史相同的植物可能具有不同的亲缘关系，而昆虫的取食通常又具有一定的选择性，因此同样生活型或生活史植物实际所面临的取食压力是不同的，那么它们也就可能采取不同的防御模式。Kursar 和 Coley(2003) 提出了一个关于热带植物幼叶的逃避/防御连续谱假说（Escape/defense continuum theory）用于解释植物防御种间差异。该假说认为不同的选择压力不断重复地作用于不同植物在防御策略上的权衡将导致不同植物或个体选择不同的防御策略，也就是说防御类型并非固定不变，由于生理限制决定了一个种只能拥有一个有限的防御组合，大多数植物的防御对策可以归到一个逃避和防御的连续谱中；连续谱的一端是采取“防御”策略的种类（具有有效的化学防御、叶扩展速度慢、正常变绿和低损失率），另一端是采取“逃避”策略的种类（具有低效的化学防御，叶扩展速度快、延迟变绿和高损失率），因此幼叶损失率的种间差异是植物具有不同防御组合的结果。尽管这一假说似乎很好地解释了植物防御对策差异的类型和原因，但该假说由于是针对热带植物幼叶防御研究结果提出的，因此是否适用于成熟叶或其它地区的植物，尚待检验。

由于动-植物相互作用研究在进化生物学研究中的重要地位，近三十年来人们开展了大量的理论和实践研究，提出了许多植物防御的假说(Stamp, 2003; 张大勇等, 2004)，较有影响的有最适防御假说、碳-氮平衡假说、生长率假说和生长-分化平衡假说等，每一个假说分别从不同角度提出假设，试图预测植物在防御水平上差异；每一个假设既有一定的合理性，又都有一定的局限性，仍需要仔细加以检验(Herms and Mattson, 1992; Tuomi *et al.*, 1999; Stamp, 2003)，特别是来自对自然群落研究的实践(Coley and Barone, 1996)。总的看来，目前国外对有关昆虫取食动态与植物防御的文献主要集中在对热带森林和部分温带森林植物的研究(Coley, 1983; Lowman, 1992; Aide, 1992; Kursar and Coley, 2003)，有关亚热带常绿阔叶林植物叶片防御的研究鲜见报道。

亚热带常绿阔叶林是陆地生态系统重要类型之一，我国是其分布的主体，作为这一地区的地带性植被，在生物多样性保育、环境保护和可持续发展等方面发挥着重要作用。植物和昆虫是其主要组分，两者在常绿阔叶林多样性的创造、群落结构稳定以及推动物质循环和能量流动等方面具有重要作用。目前常绿阔叶林面积大大减少，片断化现象和结构受损严重，许多昆虫-植物相互作用关系尚未被认识就已经消失，因此开展对常绿阔叶林昆虫与植物相互关系的研究是一项十分紧迫的任务。亚热带常绿阔叶林具有优势种明显、伴生种丰富，不同层次常绿和落叶层片混交、叶片时空格局明显，同一群落中具有不同亲缘关系的相同生活型和不同生活型同时存在，以及叶片特征和发生方式明显不同于热带和温带植物等特点，为开展昆虫取食和植物防御理论研究提供了理想的素材。

几十年来我国对常绿阔叶林生态系统的各个组分已有了较为细致的研究，为本项目开展提供了广泛的背景知识。近十几年来，一些学者从能量角度调查了南亚热带常绿季风林和常绿阔叶林虫食量动态，包括对主要种叶片虫食时空格局的研究(陈章和等, 1993; 彭少麟和任海; 1998; 孙谷畴, 1990; 江红等, 2005)；近年来我们对浙江天童常绿阔叶林 17 种常绿乔灌木成熟叶片的虫食格局也进行了初步的研究，为进一步深入开展植物防御理论的研究奠定了基础，但这些研究都缺少对叶片防御变化与虫食动态关系的连续观测，而这对探讨植物防御对策和建立防御理论是必不可少的。

因此，本文以浙江天童和福建梅花山的常绿阔叶林植物为研究对象，探讨亚

热带常绿阔叶林植物叶片虫食的变化规律及其潜在机制。本项目的意义在于通过研究叶片虫食规律，揭示昆虫-植物相互作用机制，丰富人们对昆虫-植物关系多样性认识，检验并充实已有植物防御理论；同时进一步深化我们对常绿阔叶林结构与功能的理解，为常绿阔叶林受损指标的筛选与生态恢复和森林虫害的监测与防治提供科学依据。

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第一章 植物叶片虫食与防御研究进展

叶片是植物的光合器官，昆虫对植物叶片的取食危害必然影响叶片的光合作用能力，进而影响到植物的生长、竞争和生殖分配（Marquis, 1984; Morrison and Reekle, 1995; Thomson, 2003; Corcket, E. *et al.* 2003）。由于植物出叶时间、叶片寿命和出叶方式存在明显的种间差异，同时群落组成、结构和动态变化及昆虫自身食性的差异（Coley and Barone, 1996），导致群落中叶片虫食具有明显的时空格局。植物在虫食压力下进化出化学、生理、机械和物候等方面的防御机制（Karban *et al.*,1997; Herrera and Pellmyr, 2002），反过来控制昆虫的取食，进而影响昆虫种群的发展(Karban *et al.*, 1997)；昆虫与植物之间相互作用的多样性是生态系统多样性的重要方面，对维持生态系统的稳定具有重要作用 (Coley and Barone, 1996; Herrera and Pellmyr, 2002)。本研究以亚热带常绿阔叶林植物为研究对象，从以下四个方面对植物叶片的虫食与防御进行综述和分析：1）植物叶片虫食状的多样性；2）植物叶片的虫食及时间动态；3）植物叶片虫食的空间动态；4）植物对昆虫食叶的防御策略。

1 关于植物叶片虫食多样性

在植食性昆虫中, 既有仅取食1种或少数几种植物的专食性或狭食性昆虫(specialist), 也有食性不专的广食性类型(generalist)(阎凤鸣, 2003)。这种食性的差异使得群落中植物叶片的虫食状格局复杂多样。

由于昆虫口器和取食行为的差异, 不同类型的昆虫取食叶片后通常在叶片上留下不同形态和大小的痕迹, 即虫食状(insect herbivory pattern) 或取食状(eating pattern)(于晓东等, 2001; 江红等, 2005)。Houard、Buhr和Schnaider曾分别描述了欧洲和地中海地区植物遭受昆虫危害产生的虫瘿、潜叶及其他虫食状, 并给出了根据这些虫食状鉴定昆虫种类的方法(于晓东等, 2001)。Needham和Herring分别介绍了潜叶昆虫的生活史以及与叶片的关系, 提出根据植物叶片上潜叶痕迹判断昆虫种类的方法(于晓东等, 2001)。Skuhravy′等在斯洛伐克西南部9种栎树的叶片上发现78种昆虫(于晓东等, 2001); 于晓东等(2001)在温带森林的辽东栎

(*Q. liaotungensis*)叶片上识别出9种虫食状类型及相应的5目15科20多种昆虫；江红等(2005)在亚热带常绿阔叶林中的石栎(*Lithocarpus glaber*)上识别出15种虫食状类型。可见，分析叶片的虫食状可以间接地帮助我们认识植食性昆虫的类型，并可能作为监测森林虫害的有用指标。

2 关于植物叶片虫食强度

植物群落的组成及结构的不同，致使不同地区的植物叶片虫食率存在差异。Pimentel(1988)对 93 个不同植被类型的虫食率进行了统计，世界上植物初级生产量的 7%为昆虫所消耗。热带森林中的叶片年虫食率高于温带阔叶林。在温带地区每年虫食率的均值为 7.1%，而热带湿润地区耐阴物种的年平均虫食率为 11.1%（Coley and Barone, 1996）。中国南亚热带常绿阔叶林的年虫食率为 7.03%(陈章和等, 1993)，低于热带和温带地区的年虫食率，虽然不连续的随即取样调查容易导致低估（Lowman，1984)，但以上研究结果表明虫食的差异在不同地区间是真实存在的。这种纬度的差异反映了植物所面临的虫食压力的差异，也反映了昆虫无论是种类还是数量在各纬度地区是不同的，而温度在其中起到了关键作用(Kursar, *et al.*,1999)。

每年10%的叶片损失看起来并不严重，但它却足以降低植物的适合度。如将一种阴生灌木(Piper arieianum)去叶10%，将会减弱其生长及种子繁殖、推迟开花，并降低种子的生活力(Marquis, 1984; 1994）。未遭受破坏的巴拿马天蓬树的种苗年存活率为85%，而种苗叶面积损失8%时其存活率为0%（Clark and Clark, 1985）。而且，多数植物仅分配10%的资源用于繁殖(Bazzaz, *et al.*, 1987)，这种资源分配明显影响适合度。因此，虫食对植物的生长和存活有非常大的影响，且这种现象在热带地区比温带地区更为突出，而对亚热带地区植物叶片虫食的研究则不多见，只有在中国南亚热带地区曾进行过尝试(陈章和等, 1993; 彭少麟, 1996)。

3 关于植物叶片虫食格局

3.1 时间格局

昆虫对植物叶片的取食是植物群落的常见特征(Cyr and Pace, 1993)，但昆虫

取食叶片具有明显的季节性，即叶虫食量年内变化较大，呈现出明显的时间格局(Wolda, 1988; Coley and Barone, 1996)。植物叶片的虫食全年在雨季有一个高峰期，而旱季11~4月的幼叶虫食量仅占全年的1.16%。少数植物在秋季会出现第二个虫食高峰期。虫食全年的时间变化反映了昆虫种群数量随季节的变化而出现波动(郑征等, 2001)。热带的研究表明旱季时昆虫种群数量被抑制，在雨季刚开始时有一个明显的增加，之后缓慢的增长直至下一个旱季来临(Wolda, 1978; Janzen,1985; Lowman,1985; Marquis and Braker, 1994, Murali and Sukumar, 1993)。虫食率的季节变化同昆虫的季节变化有相似的趋势。

幼嫩叶片比成熟叶片遭受更高的虫食损失(Feeny, 1970; Coley, 1983; Coley and Aide, 1989; Kursar and Coley, 2003)。热带耐阴植物 68%的叶片虫食发生在正展叶的幼叶上，这种现象被称为“物候窗” (Coley and Barone, 1996)。幼叶的日均虫食面积是成熟叶片的 20 多倍(Coley, 1983; Coley and Kursar, 1996; Coley and Barone, 1996)。中国西双版纳热带季节雨林中的植物幼叶的虫食量占总虫食量的 72.9%(郑征等, 2001)。虽然常绿植物的叶片可以存活较长时间，但超过 70%的叶片损失发生在幼叶展开时的几周内(Coley and Kursar, 1996)，幼叶的高含水量、高 N 素含量、低硬度是形成这种虫食格局的原因之一(kursar and Coley, 2003)。尽管展叶期的叶片具有适口性高的特点，但温带植物叶片虫食主要发生在成熟叶片上，展叶期的虫食率仅占全年虫食率的 27% (Coley and Barone, 1996)。因此，在多种因素的影响下不同地区植物叶片虫食的时间格局存在较大差异。

3. 2 空间格局

昆虫对不同生境中植物叶片的取食存在明显差异(Lowman, 1984; 1985; Givnish, 1988)。在热带和温带对虫食空间变化的研究表明冠层叶片虫食率低于林下、阳生叶片的虫食率低于阴生叶片，空间变化源于植物叶片营养、水份、次生物质、捕食者和小气候等条件的不同(Lowman, 1984; Coley 1983; Barone, 1994; Coley and Barone, 1996; Lee, 1999)。虫食格局的空间变化是植物防御策略随生境变化的体现，并对植物防御策略的自然选择方向和速度产生影响。Bazzaz (1987) 认为虫食的空间变化影响植株的存活率或繁殖成功率，并改变该物种的种群结构。反过来植物群落类型、植物密度和光照等生境条件均会导致植物虫食的空间

变化(Lowman, 1984)。在新南威尔士及澳大利亚的热带和温带雨林中发现阳生叶片所遭受的损伤明显要少于阴生叶片，且虫食在林下层比林冠层发生的更为严重(Loman, 1992)。巴拿马热带雨林 32 种幼树在林下层的研究也发现了相似的格局，林冠层植食性昆虫所造成的损失较小(Barone, 1994)， 但在冠层病原菌所造成的损失可能更为严重。对温带辽东栎叶片不同坡向虫食的研究认为阳坡叶片所遭受的虫食比阴坡严重(于晓东等, 2001)。

植物化学成分的区别、局部小气候的差异或食叶昆虫被捕食率的不同，已被认为是冠层虫食量减少的可能原因。阳生叶片比阴生叶片更小、硬度更大，且所含次生防御物质更高(Lowman and Box, 1983; Lowman,1985; Givnish, 1988)。树冠处更热、更干且风更大的典型小气候，会对许多植食性昆虫产生很大的影响(Lowman,1985)。鸟类的捕食，相对于林下层也可能会减小林冠层植食性昆虫的数量。在波多黎各的研究表明，一种蜥蜴是林冠层植食性昆虫的主要捕食者，因而降低了树冠叶片的植食率，但它们的影响是否在林冠层比林下层更大还不清楚。

关于植物化学、微气候及捕食者作用可能会随植食者大小和群体的不同而有所差异。林下层虫食更高的趋势表明，许多植物防御，尤其是叶片的物候期和延迟变绿，可能是林下层植物面对虫食压力产生的结果，关于植物对虫食的防御将在下一个小节中论述。

4 关于植物对昆虫食叶的防御策略

地区间森林植物的防御水平存在差异(Coley and Barone, 1996)。热带森林中植物的整体防御水平和防御多样性比亚热带和温带的森林都高，这种较强的防御能力部分上是应对对巨大虫食压力的进化结果。热带植物的叶片寿命均较长，热带低地雨林中林地植物叶片的平均寿命为 3 年，最长可达 14 年，因此较高虫食率与较长叶片寿命的组合会使热带叶片产生更高的防御。热带植物中，近 70%的叶片损失是在幼叶生长期发生的，这表明热带幼叶的防御策略和防御水平更高。温带地区的格局则恰恰相反，其幼叶的防御不如老叶。目前所知的植物防御策略有以下几种：

4.1 生理防御

叶片的营养含量在物种和叶片年龄间存在差异。蛋白质、水分和纤维含量是由于光合能力的差异或是保护叶片免于物理损伤而形成的结果。有研究认为叶片的营养含量差异部分是由昆虫和病原菌的选择而导致(Moran and Hamilton, 1980)。较低的N含量和水分含量会影响食叶昆虫的取食(Stamp and Casey, 1993)。幼叶几乎都比老叶具有更高的N含量和水分含量——这是细胞生长所无法避免的生理过程(Coley and Aide, 1991)。正是幼叶的这种高营养含量吸引了昆虫的取食，因此虫食压力可能会使植物选择将不必要的N从叶片中去除(Coley and Barone, 1996)。一项对非洲、东南亚和中美洲4片低地雨林中200多种物种的调查发现，幼叶含N量与叶片生长速率间显著正相关(Coley and Kursar, 1996; Kursar and Coley, 2003)。快速的叶片生长需要高的N含量，这大概是为了构成重要的新陈代谢酶。虽然在长势较慢的叶片中没有生理制约阻止其具有高N含量，但是缓慢的生长不需要高N含量，虫食的选择作用应该会使植物倾向于低含N水平。幼叶的高含N水平可能反映了生长需求与植食者适口性间的平衡。纤维会引起植食者的消化和机能问题，纤维含量和硬度是常用的对纤维素含量的度量，二者都与植食显著负相关。热带植物老叶的硬度是温带地区的2倍。热带植物幼叶的硬度也高于温带，但是二者的硬度均显著低于成熟叶片(Coley and Aide, 1991)。硬度是非常有效的防御，热带和亚热带植物的幼叶一旦长得足够大就马上变硬。尽管生长期在物种间的差异很大，但是几乎所有的物种都会在叶片停止生长后的几天内迅速变硬。热带植物的叶片虫食率在叶片开始变硬的3-5天内下降了4倍。因此，虫食的选择会使植物叶片尽可能快的硬化。

4.2 物候防御

昆虫同植物协同进化，在物候上形成较高的同步性(van Asch M and Visser ME, 2007)，因此植物应对虫食的另一种策略是通过改变叶片生长的物候期达到逃避昆虫取食的目的(Feeny, 1976; McKey, 1979; Lieberman and Lieberman, 1984; Aide, 1988)。这可用两种方式完成。1）叶片生长可在一年中昆虫数量最低时开始，这段时期在多数森林中为旱季。2）叶片同步爆发式生长，用大量的叶片使昆虫饱食，以此来保证一些叶片可以逃避虫食。

4.2.1 昆虫数量低时的叶片生长

在一年中昆虫数量较低的时期，幼叶的虫食率较低。在Ghana东南部的Acrra热带干旱林中，幼叶的虫食损失在雨季刚开始时最低(Lieberman and Lieberman, 1984)。同样，印度南部的干旱林中，在旱季萌发大量新叶的植物所遭受的损失显著低于那些在雨季萌发新叶的树种(Murali and Sukumar, 1993)。Aide（1992）通过试验让一种通常在旱季植食者数量较少时长新叶的灌木Hybanthus prunifolius在雨季出叶，结果雨季出叶造成了严重的虫食损失。然而，这种为了逃避植食而表现出的叶片生长的季节性变化，是否为旱季并不明显的森林中的植物所应用，因为短暂的旱季并不会使昆虫的数量有很大的下降(Wolda, 1988)。那么，旱季或雨季初期的低虫食率是否是叶片生长的决定性因素呢？有研究表明降水、光照和虫食，在决定叶片生长期的进化中起到了十分关键的作用（Rathcke and Lacey, 1985; Van Vlokenburgh, 1999; Moles and Westoby, 2000; Sun *et al.*, 2006）。落叶林中的旱季，水分胁迫是限制叶片生长的关键因素。旱季较短且水分胁迫较轻的湿润林中，植物会在阳光最充足的时间内出叶，以此避开雨季时光照不足的限制(van Schaik *et al.*, 1993; Wright and van Schaik, 1994; Reich, 1995)。昆虫对植物叶片生长的影响目前却很难进行评估，主要因为在旱季末，昆虫数量少与光照充足相重合所导致(Van Schaik *et al.*, 1993; Wright, 1996)。了解影响植物叶片生长因素的一种方法是观察在旱季昆虫依然丰富的森林中的叶片生长(Wright and van Schaik, 1994)。例如叶片生长在光照强度和昆虫数量均最大时达到峰值，便表明光照相对虫食在决定叶片生长时更重要(Wright and van Schaik, 1994)。但是，在虫食影响叶片生长的作用被完全弄清楚前，还需要进行大量的比较性研究。

4.2.2 叶片生长的同步性

叶片的同步性生长也是一种逃避植食的策略。在Ghana，出叶同步性性越高的树种虫食率越低(Lieberman and Lieberman, 1984)。Aide(1991) 在热带森林中发现在叶片大量生长的季节之外生长的叶片遭受的虫食显著高于同步出叶的叶片，这表明虫食压力是影响植物出叶同步性的可能因素。但连续长叶的植物所遭受的虫食率也较低，可能是化学防御所造成。

4.2.3 快速展叶

幼叶的虫食构成了热带叶片终生损伤的大部分，所以缩短生长期可以减小虫食损失。快速的叶片生长会给狭食性昆虫搜寻宿主带来不便，并且会缩短被广食性昆虫所接触取食的时间。Aide 和 Londoño(1989)发现专门取食 *Gustavia superba* 这种快速生长植物幼叶的昆虫仅有 3 天的时间来成功的产卵，尽管其幼虫具有罕见的快速发育期。Ernest(1989)发现在缓慢生长的 Pentagonia 叶片上的虫食损失是生长快速的叶片上的 2 倍，而 Kursar 和 Coley(2003)发现生长速度越快的植物其虫食率越高，是因为展叶速度快的叶片含有的营养物质高，而次生物质少。

总之，植物叶片的虫食动态与防御策略受到多方面因素的影响，植物的叶片虫食和防御策略是生物因素和非生物因素综合影响的结果。目前大部分研究在热带和温带进行，而亚热带植物与昆虫相互关系的研究亟待开展，以揭示该地区植物与昆虫的相互影响关系，为亚热带地区尤其是中国东部地区亚热带常绿阔叶林的恢复和保持提供理论和数据支持。

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第二章 研究方法和技术路线

1 研究目标

(1) 揭示亚热带常绿阔叶林植物叶片虫食时空变化规律;

(2) 揭示不同生活型和亲缘关系植物虫食的种间差异;

(3) 探讨植物出叶物候和叶片特性对虫食影响的潜在机制。

2 研究内容

亚热带常绿阔叶林是陆地生态系统重要类型之一，我国是其分布的主体 。亚热带常绿阔叶林具有优势种明显、伴生种丰富，不同层次常绿和落叶层片混交、叶片时空格局明显，同一群落中具有不同亲缘关系的相同生活型和不同生活型同时存在，以及叶片特征和发生方式明显不同于热带和温带植物等特点，为开展昆虫取食和植物防御理论研究提供了理想的素材。本论文通过对物种丰富的常绿阔叶林植物的出叶物候的差异及群落叶片物候整体特征的调查、叶片特性的整体特征及其随时间的变化、各植物种叶片的昆虫取食状况的时空格局的调查，旨在揭示常绿阔叶林中昆虫取食植物叶片的基本特征，探讨亚热带地区植物－昆虫的相互关系，即为阐明常绿阔叶林植物－昆虫关系提供依据，也为进一步开展该项工作奠定基础。

因此，本研究拟解决以下 4 个方面的问题：1）常绿阔叶林植物叶片虫食的多样性，包括虫食状、虫食率和虫食频度的基本特征？2）植物叶片虫食的时空动态格局，包括植物叶片虫食的时间动态和空间动态？3）植物叶片虫食的影响因素，包括物候因素和叶片特性因素对有何种虫食影响？4）总结常绿阔叶林植物对虫食的应对策略？

3 研究地点和材料

研究于 2005 年在浙江省宁波市天童国家森林公园内展开，此地属于中亚热带地区，华东师范大学在此建有野外观测站。这里的气候为温暖湿润的亚热带季

风气候，全年温和多雨，四季分明。此地年均温度为 16.2℃；最热月为 7 月，平均温度为 28.1℃；最冷月为 1 月，平均温度为 4.2℃；无霜期 237.8 天。年平均降雨量为 1374.7mm，多集中在夏季(6-8 月)，占全年雨量的 35-40%,冬季冷而干燥，雨量仅占全年的 10-15%，春季雨量一般大于秋季。受梅雨锋系和台风影响，年内降水主要有两个高峰，各在 5、6 月和 7、8 月。地带性植被是以栲树、米槠和木荷为优势种的常绿阔叶林(宋永昌和王祥荣, 1995)。

2006 年研究转移到福建梅花山国家级自然保护区内中国华南虎园内进行，该地处东经 116°45′25″～116°57′24″，北纬 25°15′24″～25°35′44″，位于福建西南部，是武夷山脉南段与博平岭之间的玳瑁山麓，上杭、连城、新罗 3 县(区)交界的毗连地带，土地总面积 22168.5hm^2。保护区位于中亚热带的南缘，气候具有从南亚热带向中亚热带过渡的特点。年平均气温 13～18℃，1 月平均气温 7.5～8.3℃，7 月平均气温 22.9～23.8℃，极端最低气温-5.5℃，极端最高气温 35℃；日均气温≥10℃的活动积温 4500℃～5100℃；年平均降水量 1700～2200mm；全年无霜期 290d；年平均相对湿度 70％～96％。年平均蒸发量在 1000mm 左右。

该区森林植被保存完好，植物种类丰富，被子植物共有 147 科 654 属 1499 种和变种。地带性植被为以罗浮锥（*Castanopsis fabri*）、甜槠(*C. eyrei*)、米槠(*C. carlesii*)和木荷(*Schima superba*)为建群种组成的常绿阔叶林(见福建梅花山国家级自然保护区经营方案)。

通过详细查看，翻阅资料，结合本研究的目的，在浙江天童森林公园内选择了以下常绿阔叶植物种，六种乔木中优势种分别为栲树、米槠和木荷，石栎、苦槠和青冈为伴生种以及 12 种灌木种，其中连蕊茶和马银花为优势种，山矾、披针叶山矾、细齿柃，细枝柃和檵木为伴生种。以上植物均处于构成森林公园景观的主要成分的木荷 ´ 栲树群丛(*Schimeto-Castanopsietum fargessii* Association)中。群落分为两个乔木层(高 10-20m; 6-8m)，一个灌木层(2-3m)和一个草本层。为进一步研究，2006 年在福建梅花山扩大了对物种的调查范围，共选择了 16 科 41 种植物进行了调查。所选择植物生长于以甜槠、木荷和罗浮栲等为建群种的常绿阔叶林内。为便于研究，本研究所选择的植物均为 1-2m 高的植株个体。详细物种目录见文后附录。

4 研究路线

为揭示常绿阔叶林昆虫取食叶片的基本特征以及植物和昆虫之间相互作用的复杂关系，本课题的研究路线为：首先，调查各植物种的出叶物候、叶片特性随时间的变化以及叶片的虫食率和虫食频度的种间差异和空间差异，并调查虫食状的多样性；然后，根据所调查的结果分析出叶物候、叶片特性、生境和叶片虫食之间的关系；最后，根据所分析的各因子和虫食的互相影响，归纳总结植物对昆虫取食的防御策略。出叶物候主要包括出叶的时间、展叶速度、展叶期和展叶格局四个方面；叶片特性包括叶绿色含量、叶片含水量、比叶重和叶片硬度四个方面。具体技术路线如图 1 所示。

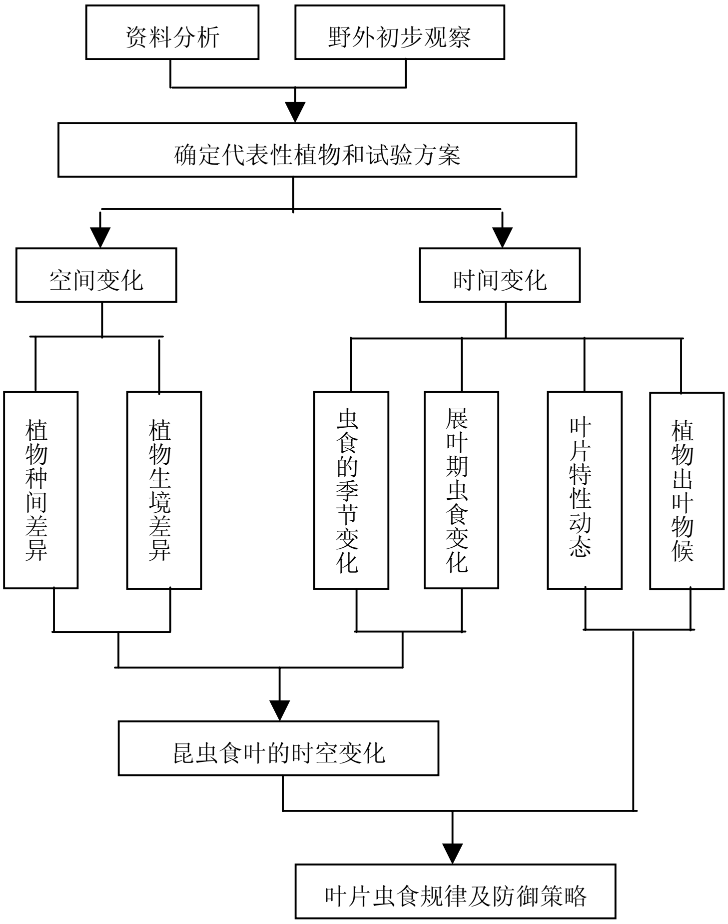

图 1 植物叶片虫食动态及其影响因素研究的技术路线

Fig.1 Technological process of herbivory on leaves and its influencing factors of plant in ergreen broad-leaved forest.

5 研究方法

研究方法详见各章节。

第三章 植物叶片虫食状分析

摘要：为探讨昆虫对植物叶片的取食行为和伤害方式，作者选择浙江天童常绿阔叶林内的 11 种常绿乔灌木为对象，对叶片虫食状类型和格局进行分析。结果如下: (1)共发现 16 种虫食状类型，每种植物叶片虫食状类型数在 10–13 种之间，每种虫食状出现频率在 0.5–28.7%之间。缘食状出现频率最高(28.7%)，虫瘿出现频率最低(0.5%)。(2)叶片虫食状分布格局可分为 3 种类型，即一种虫食状占绝对优势的单优格局，如马银花(*Rhododendron ovatum*)和檵木(*Loropetalum chinense*)；两种虫食状(缘食状和顶食状)共占优势的双优格局，仅有木荷(*Schima superba*)；3 种及 3 种以上虫食状占优势的多优格局(其余 8 种植物)。(3)叶片虫食状多样性指数变化在 1.57–2.23 之间，最高为苦槠(*Castanopsis sclerophylla*)，最低为马银花；乔木的多样性指数(2.040)高于灌木(1.882)，优势种多样性指数高于伴生种，但差异均不显著； 多样性指数反映了虫食状类型和出现频率的综合差异。(4)16 种虫食状类型中有 8 对显著正相关，4 对显著负相关，可能反映出不同类型昆虫取食植物的趋同和差异。

关键词：亚热带常绿阔叶林，叶片虫食状，多样性，分布格局

前言

昆虫取食叶片导致叶片缺失或叶组织损伤的现象十分普遍 (Cyr and Pace, 1993)。而叶面积的损伤又直接影响到植物的光合作用，进而减弱植物的生长和竞争能力，并最终导致植物适合度下降(Strauss *et al*., 2001; Thomson *et al*., 2003; Avila-Sakar *et al*., 2003)。昆虫与植物在长期的相互作用、协同进化过程中形成十分复杂的种间关系，这种关系在塑造热带森林的生物多样性和群落结构方面具有重要作用(Coley and Barone, 1996)。

在植食性昆虫中，既有仅取食1种或少数几种植物的专食性或狭食性昆虫(specialist)，也有食性不专的广食性类型(generalist)(阎凤鸣, 2003)。这种食性的差异使得群落中植物叶片的虫食状格局复杂多样。

由于昆虫口器和取食行为的差异，不同类型的昆虫取食叶片后通常在叶片

上留下不同形态和大小的痕迹，即虫食状(insect herbivory pattern) 或取食状(eating pattern)(于晓东等, 2001; 江红等, 2005)。Houard、Buhr和Schnaider曾分别描述了欧洲和地中海地区植物遭受昆虫危害产生的虫瘿、潜叶及其他虫食状，并给出了根据这些虫食状鉴定昆虫种类的方法(于晓东等, 2001)。Needham和Herring分别介绍了潜叶昆虫的生活史以及与叶片的关系，提出根据植物叶片上潜叶痕迹判断昆虫种类的方法(于晓东等, 2001)。Skuhravy′等在斯洛伐克西南部9种栎树的叶片上发现78种昆虫(于晓东等, 2001); 于晓东等(2001)在温带森林的辽东栎(*Q. liaotungensis*)叶片上识别出9种虫食状类型及相应的5目15科20多种昆虫; 江红等(2005)在亚热带常绿阔叶林中的石栎(*Lithocarpus glaber*)上识别出15种虫食状类型。可见，分析叶片的虫食状可以间接地帮助我们认识植食性昆虫的类型，并可能作为监测森林虫害的有用指标。

常绿阔叶林是我国亚热带地区的地带性植被，其中孕育着丰富多样的植物和昆虫种类。尽管目前人们对常绿阔叶林群落和生态系统已进行了大量的研究，但多集中于植物方面的探讨，关于植物叶片虫食状类型及其与取食昆虫之间相互关系的研究却鲜见报道。本项研究对浙江天童常绿阔叶林中11种常见常绿乔灌木叶片的虫食状类型、分布格局及种间差异进行了初步的分析，为进一步研究植食性昆虫与植物之间的相互关系提供基础资料。

1 研究区概况

天童国家森林公园位于浙江省鄞县东南部(29°48′ N, 121°47′ E)，距宁波市28 km，面积349 hm^2。主峰太白山海拔653.3 m，一般山峰海拔300 m左右。年均温为16.2℃，年均降雨量1,374.7 mm。地带性土壤为山地黄红壤。该区森林植被保存良好，植物种类丰富，共有种子植物148科506属968种;地带性植被为以栲树(*Castanopsis fargesii*)、米槠(*C. carlesii*)和木荷(*Schima superba*)为建群种组成的常绿阔叶林(宋永昌等, 1995)。据初步统计，该区植食性昆虫有8目90科272种(未发表数据)。

本研究选择常绿阔叶林中较为常见的11种常绿乔灌木为取样对象，其中乔木6种，3种为优势种，即木荷、栲树和米槠，3种为伴生种，即石栎(*Lithocarpus glaber*)、苦槠(*Castanopsis sclerophylla*)和青冈(*Cyclobalanopsis glauca*)；灌木5种，

2种为优势种，即连蕊茶(*Camellia fraterna*)和马银花(*Rhododendron ovatum*)，3种为伴生种，即檵木(*Loropetalum chinense*)、细齿柃(*Eurya nitida*)、细枝柃(*E. loquaiana*)。

2 取样方法

2.1 叶片采集

取样在2004年10月上中旬完成，每种在林内随机选择5株样木，每株冠层取2–3个枝条，统一收集当年成熟的所有叶片。为了检验植株冠层取样方位可能对取样结果的影响，选择栲树和木荷为代表植物，分别从每株大树的东、南、西、北和中5个不同方位各采2–3个枝条，共收集木荷叶片629片、栲树叶片1,983片。利用ANOVA检验，发现取样方位对栲树和木荷叶片虫食状类型和频率无显著性影响(栲树F=0.769, P=0.582>0.05；木荷F=0.836, P=0.541>0.05)。因此对其余种类的采样不再考虑方位，但尽可能采集冠层阳面的枝条，每种植物采集的叶片数不低于400片，样本数高于Morrow等(1978)的取样要求。

2.2 叶片虫食状的鉴定

昆虫取食叶片后在叶片上留下各种不同的取食痕迹，根据留下的痕迹大小、形状、位置和排列进行识别、分类。对少数难区别的类型采取多人鉴定的方法，尽可能减少人为因素的干扰。

2.3 叶片虫食状多样性指数

为反映每种植物叶片虫食状在类型和出现频率上的综合差异，本文选择多样性指数(Shannon-Wiener指数)来加以度量，即

$$H=-\sum_{i=1}^{n} P_i \log_2 P_i$$

式中P_i是第i种虫食状类型在所有虫食状类型中的比例，n是虫食状类型总数。

2.4　叶片虫食状频率

虫食状频率(%)=100×某种虫食状所占的叶片数/所有虫食状所占的叶片总数。本文所有数据分析和作图在Excel和SPSS软件上完成。

表1　叶片虫食状的类型和分布

Table 1　Types and distribution of insect herbivory pattern of 11 species

虫食状类型 Type of insect herbivory pattern	植物种 Species											平均值 Mean
	Cf	*Ss*	*Cc*	*Cs*	*Lg*	*Cg*	*Lc*	*Caf*	*Ro*	*En*	*El*	
	虫食频率 Herbivory frequency (%)											
缘食状Edge defoliation (EF)	27.3	32.4	28.3	13.1	22.7	16.2	44.4	29.7	51.7	26.5	24.1	28.7
顶食状Top defoliation (TD)	15.5	28.4	11.3	17.9	25.7	11.1	13.7	17.6	8.0	10.3	7.2	15.2
掏食状Excavating defoliation (EX)	10.1	6.9	2.4	7.9	0.2	29.3	10.1	12.6	16.5	14.2	7.2	10.7
切叶状Leaf cutting (LC)	3.6	5.1	8.9	15.1	19.6	8.1	6.0	13.5	9.2	9.7	5.1	9.5
大孔状Big perforation (BP)	8.3	9.8	10.4	11.0	8.1	6.1	0.8	9.0	4.2	17.1	5.1	8.2
小孔状Small perforation (SP)	5.9	3.2	15.2	10.0	6.1	8.1	11.7	8.6	6.1	11.6	20.0	9.7
阴面食状Lower epidermis defoliation (LEF)	3.0	4.9	9.5	9.0	1.7	10.6	2.4	2.3	1.1	5.8	12.3	5.7
阳面食状Upper epidermis defoliation (UEF)	2.5	8.3	3.6	8.7	0.7	6.6	10.1	4.5	0.0	0.6	5.6	4.7
细长条状Slender defoliation (SLD)	15.6	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.4	1.0	0.0	1.8
长条状Striped defoliation (STD)	5.6	0.0	5.1	0.0	0.2	0.0	0.4	0.0	0.4	0.0	0.5	1.1
连续小孔状Successive pinhole (SUP)	0.0	0.0	0.0	0.0	12.6	0.0	0.0	0.0	1.1	0.0	0.5	1.3
叶中脉状Middle vein defoliation (MVD)	1.3	0.7	1.5	1.8	0.0	1.0	0.0	0.5	0.4	1.0	1.0	0.8
泡状Bloth-shaped mine (BM)	0.7	0.2	1.2	1.5	1.1	1.0	0.0	0.0	0.0	0.0	0.0	0.5
潜叶状Leaf mine (LM)	0.5	0.0	0.3	3.6	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.6
褶皱状Rugate defoliation (RD)	0.0	0.0	0.0	0.3	1.3	0.0	0.4	0.5	0.8	0.3	9.2	1.2
虫瘿Gall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	1.9	2.1	0.5

Cf: 栲树; *Ss*: 木荷; *Cc*: 米槠; *Cs*: 苦槠; *Lg*: 石栎; *Cg*: 青冈; *Lc*: 檵木; *Caf*: 连蕊茶; *Ro*: 马银花; *En*: 细齿柃; *El*: 细枝柃。

Cf, Castanopsis fargesii; Ss, Schima superba; Cc, Castanopsis carlesii; Cs, Castanopsis sclerophylla; Lg, Lithocarpus glaber; Cg, Cyclobalanopsis glauca; Lc, Loropetalum chinense; Caf, Camellia fraterna; Ro, Rhododendron ovatum; En, Eurya nitida; El, Eurya loquaiana

3　结果与分析

3.1　叶片虫食状类型及分布

11种常绿乔灌木叶片上共识别出16种虫食状类型(表1, 图1)。每种植物叶片的虫食状类型在10–13种之间, 最多的13种(包括栲树、米槠和细枝柃), 最少的10种(仅有檵木)(表2)。

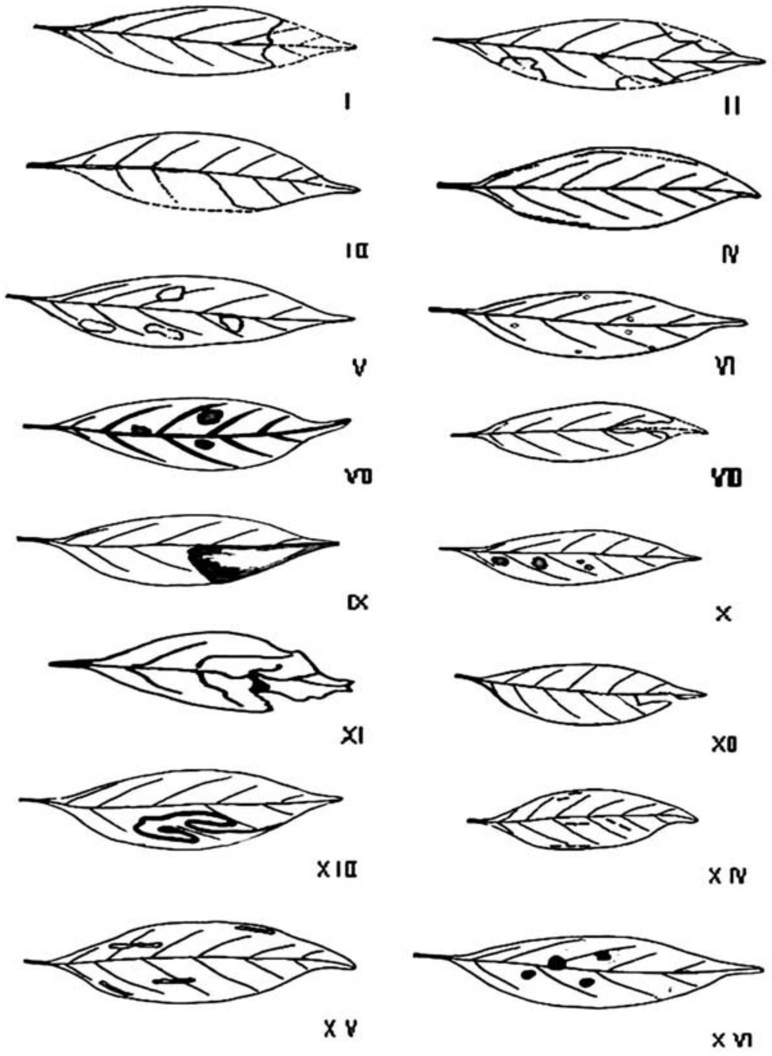

图**1**　11种常绿乔灌木叶片上的16种虫食状示意图
Fig. 1 Sketch map for 16 insect herbivory patterns of 11 species
I: 顶食状; II: 缘食状; III: 切叶状; Ⅳ: 连续小孔状; Ⅴ: 大孔状; Ⅵ: 小孔状; Ⅶ: 阴面食状; VIII: 叶中脉状; Ⅸ: 泡状; Ⅹ: 阳面食状; XI: 褶皱状; Ⅻ: 掏食状; ⅩⅢ: 潜叶状; ⅩⅣ: 细长条状; ⅩⅤ: 长条状; ⅩⅥ: 虫瘿
I, Top defoliation; II, Edge defoliation; III, Leaf cutting; Ⅳ, Successive pinhole; Ⅴ, Big perforation; Ⅵ, Small perforation; Ⅶ, Lower epidermis defoliation; VIII, Vein defoliation; Ⅸ, Bloth-shaped mine; Ⅹ, Upper epidermis defoliation; Ⅺ, Rugate defoliation; Ⅻ, Excavating defoliation; ⅩⅢ, Leaf mine; ⅩⅣ, Slender defoliation; ⅩⅤ, Striped defoliation; ⅩⅥ, Gall

不同植物之间既可能拥有相同的虫食状，也可能具有不同的虫食状类型。16种虫食状类型中，缘食状、顶食状、掏食状、切叶状、小孔状、大孔状和阴面食状在11种植物叶片上均有分布，阳面食状仅在马银花上未出现，叶中脉状在石栎和檵木上未出现；褶皱状和潜叶状仅出现在乔木种类叶片上，虫瘿仅出现在连蕊茶、细齿柃和细枝柃3种灌木的叶片上，长条状、细长条状虽在多种植物叶片上出现，但频率并不高(表1)。

对所有11种植物叶片虫食状的统计结果表明，缘食状、顶食状、掏食状、切

叶状、大孔状、小孔状、阴面食状和阳面食状不仅出现在大多数植物上，而且出现频率也较高(均在4.0%以上)，其中出现频率最高的是缘食状，占28.7%；其他8种虫食状频率均低于1.8%，其中频率最低的为虫瘿，仅占0.5%(表1)。此外，某些虫食状在某些植物种占有相对较高的频率，如栲树的细长条状占15.6%、石栎的连续小孔状占12.6%和细枝柃的褶皱状占9.2%(表1)。

16种虫食状可分为3种类型：(1)一种虫食状占绝对优势的单优格局，如马银花和檵木，在这两种植物上缘食状所占比例分别达到51.7%和44.4%；(2)两种虫食状(缘食状和顶食状)占优势的类型，即双优格局，仅有木荷，两种虫食状之和占50%以上；(3)其余8种植物为3种或3种以上虫食状占优势的多优格局。

3.2　叶片虫食状多样性分析

11种植物叶片虫食状多样性指数变化在1.57–2.23之间，最高为苦槠(2.23)，最低为马银花(1.57)。总体上看，虫食状类型多的，多样性指数也高，但二者的相关性不显著(F=0.578, P= 0.062)(表2)。马银花、檵木和木荷等的多样性指数较低，是由于虫食状类型较少而且为单优或双优的格局所致 (表2)。虫食状类型与多样性高低并非呈明显的正相关，多样性指数大小基本反映了这种植物虫食状的多样性特征。

表2　11种植物叶片虫食状多样性

Table 2 Diversity of insect herbivory patternof 11 species

	植物种 Species										
	Cf	*Ss*	*Cc*	*Cs*	*Lg*	*Cg*	*Lc*	*Caf*	*Ro*	*En*	*El*
叶片数 No. of sample	503	476	463	408	496	496	459	450	412	480	464
虫食状 No. of herbivory pattern	13	10	13	12	12	11	10	11	12	12	13
Shannon–Wiener指数 Shannon–Wiener index	2.13	1.80	2.15	2.23	1.88	2.06	1.69	1.96	1.57	2.02	2.17

物种代号同表1。 Symbol of species refer to table 1.

尽管6种乔木的平均虫食状多样性(2.040)高于5种灌木(1.882)，但叶片虫食状多样性指数高低在乔木和灌木之间无显著差异(F=1.637, P =0.233)。优势种和伴生种之间也无显著性差异(F=0.424, P =0.531, 表2)。

3.3　叶片虫食状间相关性分析

16种虫食状间的相关分析表明有8对虫食状类型显著正相关，它们是阴面食状—叶中脉状，阴面食状—小孔状，细长条状—长条状，切叶状—连续小孔状，

潜叶状—叶中脉状，潜叶状—泡状，褶皱状—小孔状，褶皱状—虫瘿；有4对虫食状类型间显著负相关，即缘食状—阴面食状，缘食状—泡状，缘食状—潜叶状，顶食状—小孔状；其他类型间无显著相关性(表3)。

表3　16种叶片虫食状之间的相关性

Table 3 The Pearson Correlations among insect herbivory pattern of 11 species

	TD	EX	LC	BP	SP	LEF	UEF	SLD	STD	SUP	MVD	BM	LM	RD	Gall
EF	–0.186	–0.002	–0.323	–0.473	–0.164	–0.627*	–0.162	–0.033	0.006	–0.127	–0.585	–0.660*	–0.631*	–0.103	–0.133
TD		–0.443	0.360	0.174	–0.638*	–0.373	0.208	–0.036	–0.159	0.468	–0.241	0.245	0.010	–0.352	–0.383
EX			–0.259	–0.137	–0.174	0.138	0.053	–0.063	–0.286	–0.433	0.026	–0.177	0.269	–0.190	0.032
LC				0.263	–0.171	–0.212	–0.268	–0.408	–0.361	0.684*	–0.169	0.442	0.257	–0.187	–0.071
BP					–0.051	0.157	–0.335	0.074	0.067	–0.043	0.500	0.207	0.137	–0.267	0.321
SP						0.654*	0.124	–0.203	0.107	–0.243	0.289	–0.084	–0.040	0.683*	0.579
LEF							0.337	–0.186	0.044	–0.345	0.674*	0.339	0.461	0.463	0.272
UEF								–0.257	–0.235	–0.412	0.115	0.078	0.417	0.020	–0.197
SLD									0.798*	–0.141	0.326	0.137	–0.051	–0.175	–0.192
STD										–0.158	0.439	0.317	–0.113	–0.156	–0.274
SUP											–0.499	0.293	–0.188	0.053	–0.184
MVD												0.520	0.624*	–0.006	0.037
BM													0.698*	–0.299	–0.554
LM														–0.203	–0.315
RD															0.620*

虫食状代号参见表1.*表示在0.05水平上相关性显著($P<0.05$) Symbol of herbivory pattern refer to table 1. * At the 0.05 level, correlations are significant ($P<0.05$)

4　讨论

由于口器和取食方式的不同，植食性昆虫通常被分为咀嚼类(chewers)、潜叶类(miners)、刺吸类(sucking insects)、造瘿类(gall-makers)和穿洞类(borer)五大类(Abrahamson,1989)，其中前四类都有取食叶片的类型，每种类型的昆虫在取食叶片后会留下不同形态的虫食状。其中咀嚼类昆虫可因口器大小、取食行为不同，还可以形成形态各异的虫食状。本项研究在11种植物中共识别出16种虫食状类型，仅比江红等(2005)观察到的15种虫食状多出造瘿类一种类型，与于晓东(2001)观察到的9种虫食状相比，增加的8种类型都是咀嚼类昆虫取食形成的。但本研究未对蚜虫等刺吸类昆虫形成的虫食状进行识别。本文的分类方法基本上涵盖了本区植物叶片的虫食状类型，可作为今后研究的参考。本次识别出石栎的12种虫食状类型少于江红等(2005)观察到的15种类型数，可能是由于样本数和取样时间不同所至，需要进一步研究。

16种叶片虫食状类型出现的频率存在明显差异，而且在不同植物种类间存在着差异。在11种植物叶片上出现频率较高的虫食状类型有8种，即缘食状、顶食状、掏食状、切叶状、大孔状、小孔状、阴面食状和阳面食状，其中缘食状是最常见的类型，出现频率最高，其次是顶食状，其他6种虫食状出现的频率依次降低；这与于晓东等(2001)和江红等(2005)研究的结果基本一致。我们根据每种植物中优势虫食状数的差异，首次将11种植物叶片虫食状分布格局分为3种类型，即单优格局、 双优格局和多优格局，反映出昆虫对叶片的取食在不同植物间既存在明显的共性，也有一定的差异。

植食性昆虫既有专食性(specialist)又有广食性(generalist) (钦俊德, 1987)，群落中的每种植物都可能受到两种类型昆虫的共同取食，也可能仅受到一种昆虫类型的取食，结果就可能在叶片上遗留的虫食状类型的相互关系中得以反映。因此虫食状的相关性就可能是昆虫食性分化和昆虫相互关系的具体体现。本研究中的16种虫食状类型间的相关分析表明有8对虫食状之间显著正相关，4对显著负相关。正相关反映不同类型的昆虫可能取食相同的食物和分化的生活空间，从而可以共同存在； 而负相关反映出昆虫间取食食物的差异以及相似的生活空间，从而互相排斥，虫食状的相关性结果不仅有助于我们对昆虫食性选择性的认识，而且可以加深理解不同种类昆虫的相互关系。

江红等(2005)的研究和本项研究都未对昆虫作相应的观察，尽管我们发现少数虫食状与取食昆虫之间存在很好的对应关系，如本区的潜叶状由北美斑潜蝇所为(私人观察)，但由于昆虫取食的复杂性，不同的虫食状(如缘食状、顶食状和掏食状)可能是一种昆虫所为，也可能是口器相似的不同昆虫所致，如同种昆虫取食叶片后留下顶食、掏食、缘食等不同的虫食状，这些虫食状都从叶的边缘开始取食。有些昆虫在低龄时由于取食能力差，只产生阴面食状和阳面食状，而长大后可以留下缘食状的取食痕迹，也可将叶片吃穿，产生孔状取食痕迹(私人观察)，也就是说虫食状类型与昆虫之间的关系相当复杂。

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第四章 植物展叶期间叶片虫食动态

摘要：植物叶展叶期是叶片遭受虫食较严重的时期，为研究植物叶片展叶期间的虫食动态，本文调查了福建梅花山常绿阔叶林中植物叶片展叶期间的虫食情况，并对比了不同植物叶片的虫食格局，结果如下：1）展叶期间叶片展开之前的低龄叶日均虫食面积显著高于展叶后的高龄叶片(t=2.368, p=0.029)，低龄叶和高龄叶的日均虫食面积在乔木和灌木之间均没有显著差异；2）植物叶片展叶期的虫食有三种格局：(i)展叶初期虫食面积较小，随叶片展开逐渐增加，而展叶完成后虫食面积快速下降的前食型虫食格局；(ii)展叶初期叶片的日均虫食面积非常低，直至叶片展开后虫食面积缓慢增加的后食型虫食格局；(iii)展叶完成前后的虫食变化缓慢的中间型虫食格局。以上结果表明，植物叶片展叶前的虫食高于展叶后，且有多种虫食动态格局。

关键词：常绿阔叶林, 叶片展叶期, 虫食, 动态

前言

植物叶片展叶期是叶片遭受虫食最严重的时期(Coley 1983; Crawley, 1983; Lowman, 1985, Aide, 1993)，热带雨林中 70%的叶片损失发生在叶片展叶期(Coley and Aide, 1991)。叶片展叶期的虫食对植物生长的影响大于叶片成熟后(Krisckik and Denno,1983; Jurik and Chabot, 1986; Mendoza, *et al.*, 1987)，并严重影响植物的生长和繁殖(Louda, 1984; Crawley, 1985)，进而影响群落结构和功能。在长期的自然进化中，植物和昆虫形成了复杂的相互关系，在巨大的虫食压力下植物进化出多种策略防御昆虫的取食(Coley and Barone, 1996)。

叶片展叶期间植物的防御策略和植物对资源的获取能力有关，生长缓慢的植物对次生物质的投入大于生长快速的植物(Coley, *et al.*, 1985)，而且叶片的次生物质含量高于成熟叶片(Mckey, 1979; Coley and Aide, 1991)。叶片发育过程中叶片的高含水量和 N 素含量对昆虫的吸引导致叶片虫食率较高，在快速生长的植物中表现尤为明显(Kursar and Coley, 2003)。硬度是叶片有效的防御方式之一(Lowman and Box, 1983; Coley, 1983; Juniper and Southwood, 1986)，但幼叶无法

利用叶片的硬度进行防御，只能利用其他的防御方式，如快速生长逃避以及利用次生物质抵抗虫食(Coley and Barone, 1996; Kursar, *et al.*, 1999)。由于植物叶片展叶期间的防御方式多样，所以叶片展叶期的虫食动态存在差异并反映出这一时期植物防御方式的种间差异(Kursar and Coley, 2003)，因此叶片展叶期的虫食动态是了解植物防御虫食对策的重要基础。

对叶片展叶期的虫食动态及其防御方式，目前只有在热带森林中有少量研究(Kursar and Coley, 2003)。热带雨林植物叶片展叶期的虫食动态有三种格局：1）耐阴植物幼叶的防御能力差，展叶期和展叶后的虫食动态变化大，展叶后的虫食显著低于展叶期间；2）向阳植物叶片具有寿命短且防御能力差的成年叶片，展叶期间与展叶后的虫食动态变化小，展叶后的虫食同展叶期间没有显著的差异；3）植物幼叶具有较好的防御能力，虫食在展叶期和展叶后的变化处于以上两种格局之间。以上研究是对植物多样性和昆虫多样性均较高的热带森林研究的结果，但对亚热带常绿阔叶林植物幼叶的虫食及其动态的研究目前还没有相关报道。

亚热带常绿阔叶林是处于热带雨林与温带落叶阔叶林之间的重要过渡类型，夏季炎热多雨，冬季少雨而寒冷，其群落构成及生物习性与热带和温带均有较大差别(李博, 2000)，叶片展叶期的虫食动态也可能与热带雨林存在差异，因此本项研究的主要目的是探讨亚热带常绿阔叶林植物叶片发育期的虫食动态特征，以期对本地区植物叶片发育期的虫食有深入的认识。

1 材料与方法

1.1 研究区概况

本研究分别在中国福建梅花山国家级自然保护区和浙江天童国家森林公园内进行。研究地详情参见第二章。

1.2 研究材料

本文分别研究了梅花山 6 个科的 19 种植物，包括 11 种乔木和 8 种灌木。浙江天童 4 科 10 种植物，包括 4 种乔木和 6 种灌木（表 1)。为便于调查，所选择

的植株均为生长于林下的高 1~2 米的植株。记录了不同植物种幼叶期间的昆虫取食面积。

表 1 低龄叶(age≤0)和高龄叶片(age>10)的日均虫食面积

Table 1 Herbivory (cm^2d^{-1}) on young leaves (age≤0) and mature leaves (age>10).

	植物种	生活型	优势度	低龄叶虫食	SE	高龄叶虫食	SE
	Species	LF	DI	(cm^2d^{-1})		(cm^2d^{-1})	
福建梅花山	罗浮锥	T	C	0.025	0.009	0.004	0.004
	细叶青冈	T	C	0.044	0.016	0	0
	建润楠	T	C	0.052	0.026	0.178	0.102
	黄樟	T	C	0.058	0.044	0.059	0.037
	上杭锥	T	D	0.066	0.03	0	0
	杨梅	T	C	0.067	0.025	0	0
	栲树	T	C	0.082	0.037	0.025	0.013
	甜槠	T	D	0.083	0.038	0.002	0.001
	两广石栎	T	C	0.136	0.049	0	0
	木荷	T	D	0.197	0.05	0.016	0.009
	深山含笑	T	D	0.396	0.259	0	0
	小叶乌饭树	S	D	0.012	0.005	0.003	0.003
	黄瑞木	S	C	0.024	0.013	0.018	0.007
	辣汁树	S	C	0.026	0.013	0.022	0.022
	连蕊茶	S	C	0.062	0.017	0.14	0.14
	格药柃	S	D	0.07	0.042	0	0
	鹿角杜鹃	S	D	0.103	0.054	0.036	0.033
	乌饭树	S	D	0.11	0.067	0.105	0.104
	石笔木	S	C	0.207	0.162	0.107	0.052
浙江天童	格药柃	S	D	0.009	0.001	0	0
	连蕊茶	S	D	0.008	0.002	0.005	0.001
	细齿柃	S	C	0.003	0.001	0.028	0.017
	山矾	S	C	0.013	0.005	0	0
	披针叶山矾	S	C	0.003	0.001	0	0
	马银花	S	D	0.004	0.004	0.001	0.001
	苦槠	T	C	0.060	0.02	0	0
	米槠	T	D	0.008	0.003	0.002	0.001
	青冈	T	C	0.061	0.032	0.001	0.001
	木荷	T	D	0.021	0.011	0.000	0

注: 植物种按生活型分为乔木(T)和灌木(S), 优势种(D)和伴生种(C)。日均虫食面积是每叶每天的虫食面积的平均值。

Note: Plant species are classified into Tree (T) and Shrub (S) by life form (LF) and dominant species (D) and Companion species (C) by dominance index. Herbivory (cm^2d^{-1}) is average leaf area losses to herbivores every day.

1.3 研究方法

1.3.1 样本标记

每种植物选择 6－10 棵健壮植株，每株选择三根枝条。每三天调查一次每根枝条上所抽生的叶片数，同时选择枝条中部的 3 片记录其每次的叶面积，直至叶片面积在连续三次的观测中不再增加为止，即认定该叶片展叶结束。为避免破坏幼嫩的叶片，用有色塑料线标记在芽附近的老叶上，利用叶芽上叶片的节位确定叶片的个数和位置。

1.3.2 展叶期叶片日均虫食面积的测定

叶片展叶期间，每 3 天用带网格的透明塑料片(10 格/cm2)测量叶片虫食面积(在塑料片上依据叶片剩余部分描绘后测得)和潜在完整叶片面积(剩余面积与虫食面积之和)。叶片虫食状包括缘食、孔状、潜叶以及由昆虫造成的任何形状的叶片损失(王宏伟等, 2006)。本次研究以昆虫取食为研究目的，因此主要考虑昆虫的作用而排除了微生物和真菌的影响。本文所有数据用 ORIGIN 6.0 分析处理。

1.3.3 昆虫幼虫的生长测定

选择取食木荷叶片的鳞翅目的一种蛾类幼虫为饲养对象，首先抓取若干成虫放置于一透气容器中，待成虫产卵后，将成虫移去。卵孵化后，选择健壮幼虫 10 条，分放于 5 个透气容器中，每日采摘新鲜木荷叶片喂养并测量每日虫食面积。前期每 2 天测定一次体重，待幼虫进入快速生长期后每日测定一次体重，至幼虫化蛹为止。

2 结果与分析

2.1 植物展叶期叶片日均虫食面积的比较

2.1.1 梅花山

(1) 低龄叶的日均虫食面积(0.096 cm^2d^{-1})显著高于高龄叶片的日均虫食面积(0.038 cm^2d^{-1}) ($t = 2.368$, $N=19$, $p = 0.029$, 图 2)。

(2) 叶片展叶期日均虫食面积存在种间差异(表 1)。日均虫食面积最大的为深山含笑 (0.396 cm^2d^{-1})，是日均虫食面积最小的小叶乌饭树的 30 多倍。高龄叶片日均虫食面积最大的是连蕊茶(0.14cm^2d^{-1})，而格药柃、细叶青冈、上杭锥、杨梅和两

广石栎的高龄叶片均没有昆虫取食。

(3) 乔木低龄叶的日均虫食面积(0.11cm^{2}d^{-1})大于灌木(0.077cm^{2}d^{-1})，高龄叶日均虫食面积(0.026 cm^{2}d^{-1})却小于灌木(0.054 cm^{2}d^{-1})，即展叶完成后灌木的虫食高于乔木，但二者没有显著差异(t=0.775, p=0.449; t=-1.116, p=0.28)。

2.1.2 天童

(1) 低龄叶片的日均虫食面积大于高龄叶片(表 1)，但差异并不显著(p=0.060)，细齿柃高龄叶片的日均虫食面积大于低龄叶片导致了差异显著性的降低。

(2) 乔木种植物的低龄叶片虫食面积显著大于灌木种(t=-2.828, p=0.022)，但高龄叶片间并无显著差异。

梅花山植物的低龄叶片日均虫食面积(0.095cm^{2}d^{-1})显著大于天童植物的低龄叶片日均虫食面积(0.019cm^{2}d^{-1}, t=-2.627, p=0.014)，但高龄叶片间并无显著差异(p=0.063)。

2.2 植物展叶期叶片虫食动态比较

2.2.1 梅花山

梅花山 19 种植物叶片展叶期的日均虫食面积均较高，且在叶片发育过程中存在变化(图 2)。叶片发育过程中日均虫食面积变化很大，且虫食格局存在种间差异，可以分为三类：

(1)**前食型虫食格局**，格药柃、两广石栎、上杭锥、深山含笑、甜槠、细叶青冈和杨梅七种植物在叶片展开前的日均虫食面积高于展叶后叶片的日均虫食面积。叶片虫食面积在叶片展开初期虫食面积(cm^{2}d^{-1})均较低，而完全展开时的虫食面积相对最高，叶片完全展开后虫食面积快速的下降，并在较长一段时间内没有虫食(表 1, 图 2)，表明叶片展开前的防御水平较低；

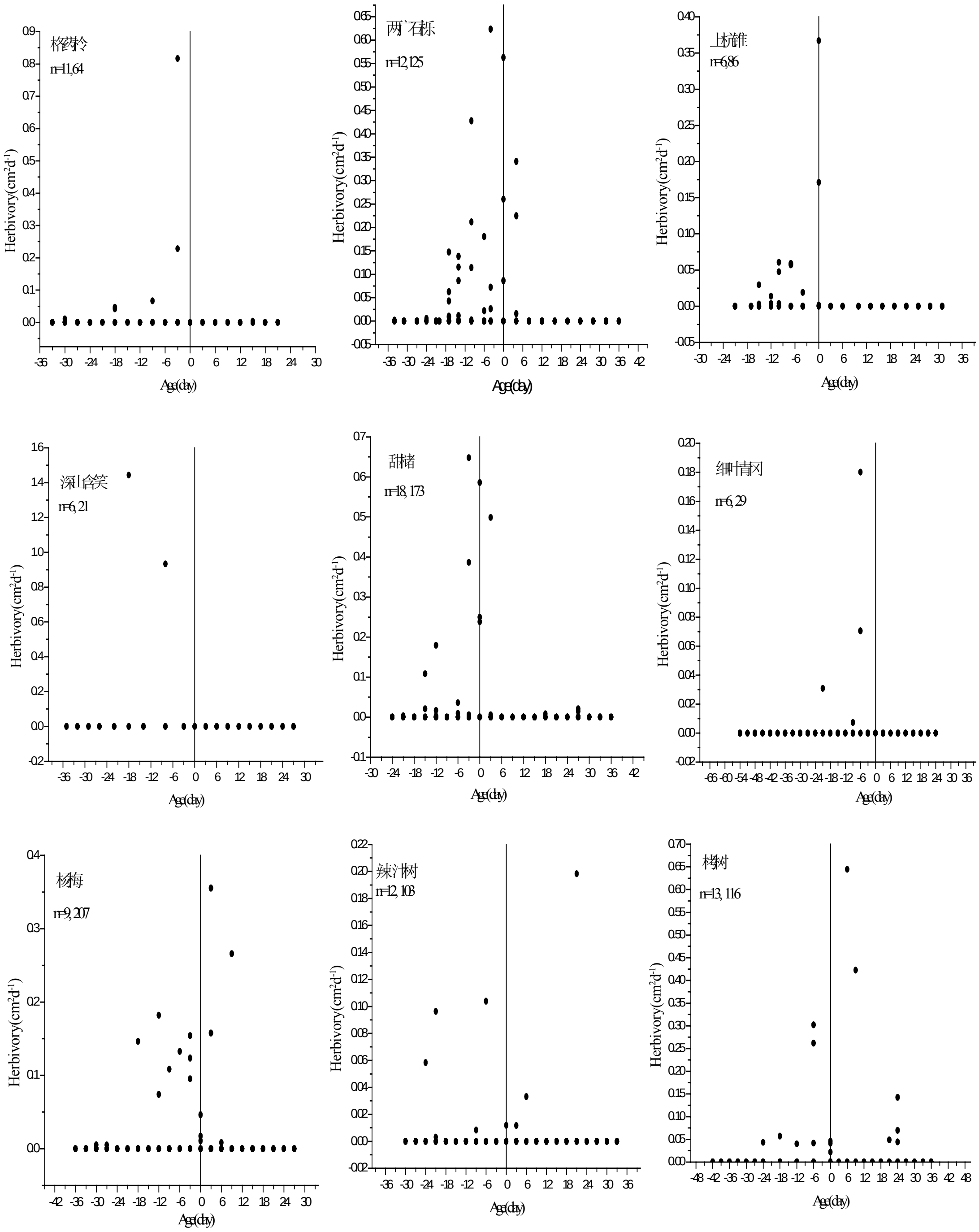
(2)**后食型虫食格局**，建润楠、黄樟和黄瑞木三种植物在叶片展开前的虫食面积非常低，在展叶将要结束时虫食率快速上升，并一直延续到叶片展开后较长的一段时间，表明此类植物叶片展开前的防御水平较高，而展叶后叶片防御水平下降；

(3)**中间型虫食格局**，辣汁树、栲树、鹿角杜鹃、罗浮栲、石笔木、乌饭、小叶乌饭和木荷八种植物在展叶期间的日均虫食面积虽然也高于展叶后叶片的日均虫食面积(表 1, 图 2)，且变化并不剧烈。连蕊茶叶片展开后的日均虫食面积高于

叶片展开前，但变化不如后食型剧烈，这九种植物在叶片展开后的较长一段时间内仍然有虫食发生，表明此类植物的防御水平在叶片展叶期间变化不大。

2.2.2 天童

浙江天童 10 种植物幼叶期间的虫食动态同梅花山的植物相似。春季格药柃和山矾的幼叶虫食动态以及秋季米槠的幼叶虫食动态为前食型虫食格局，其余春季 8 种植物和秋季 4 种植物为中间型虫食格局(图 3)，在天童没有发现后食型虫食格局。表明天童植物叶片在展叶期间的防御水平没有大的变化。



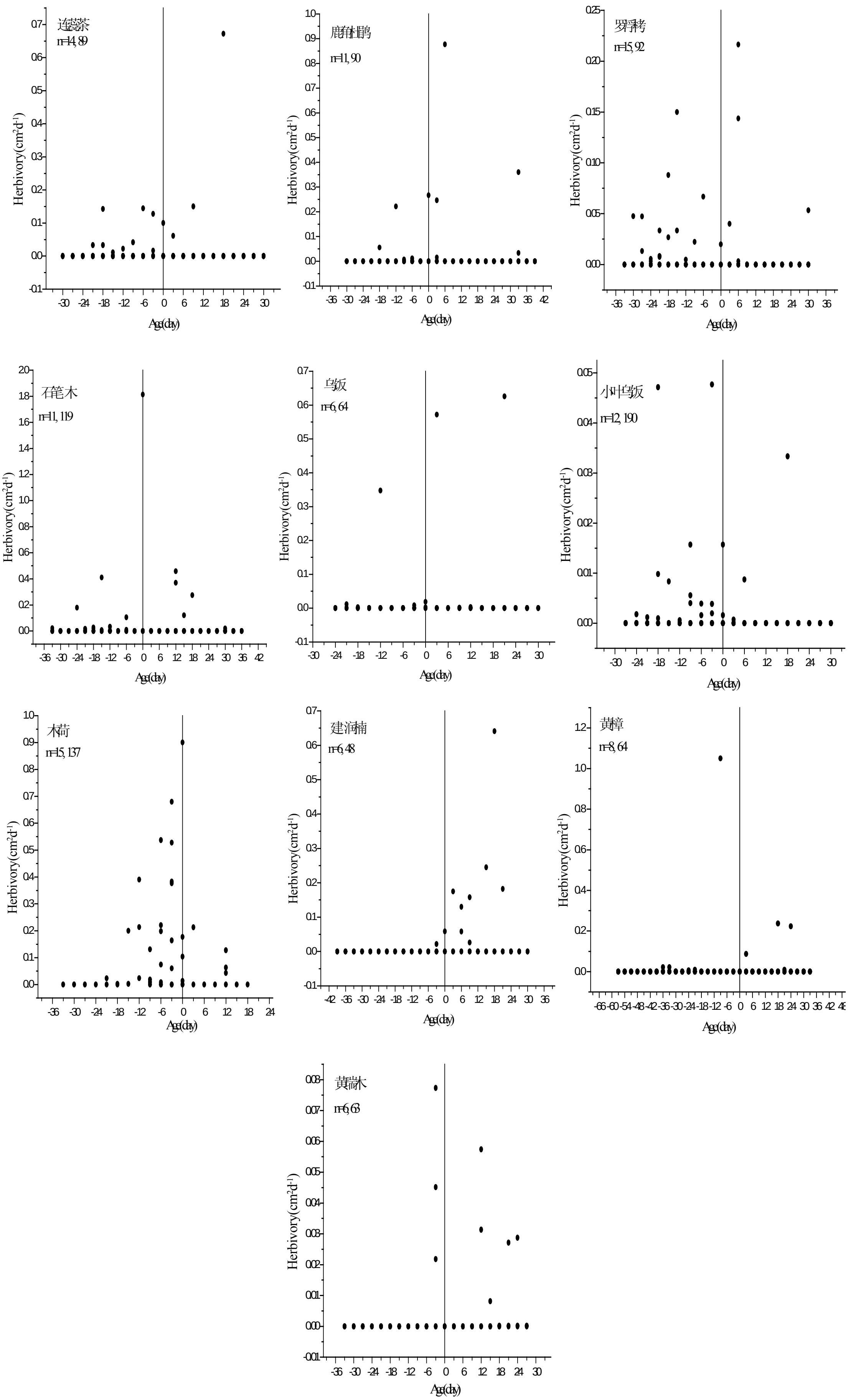
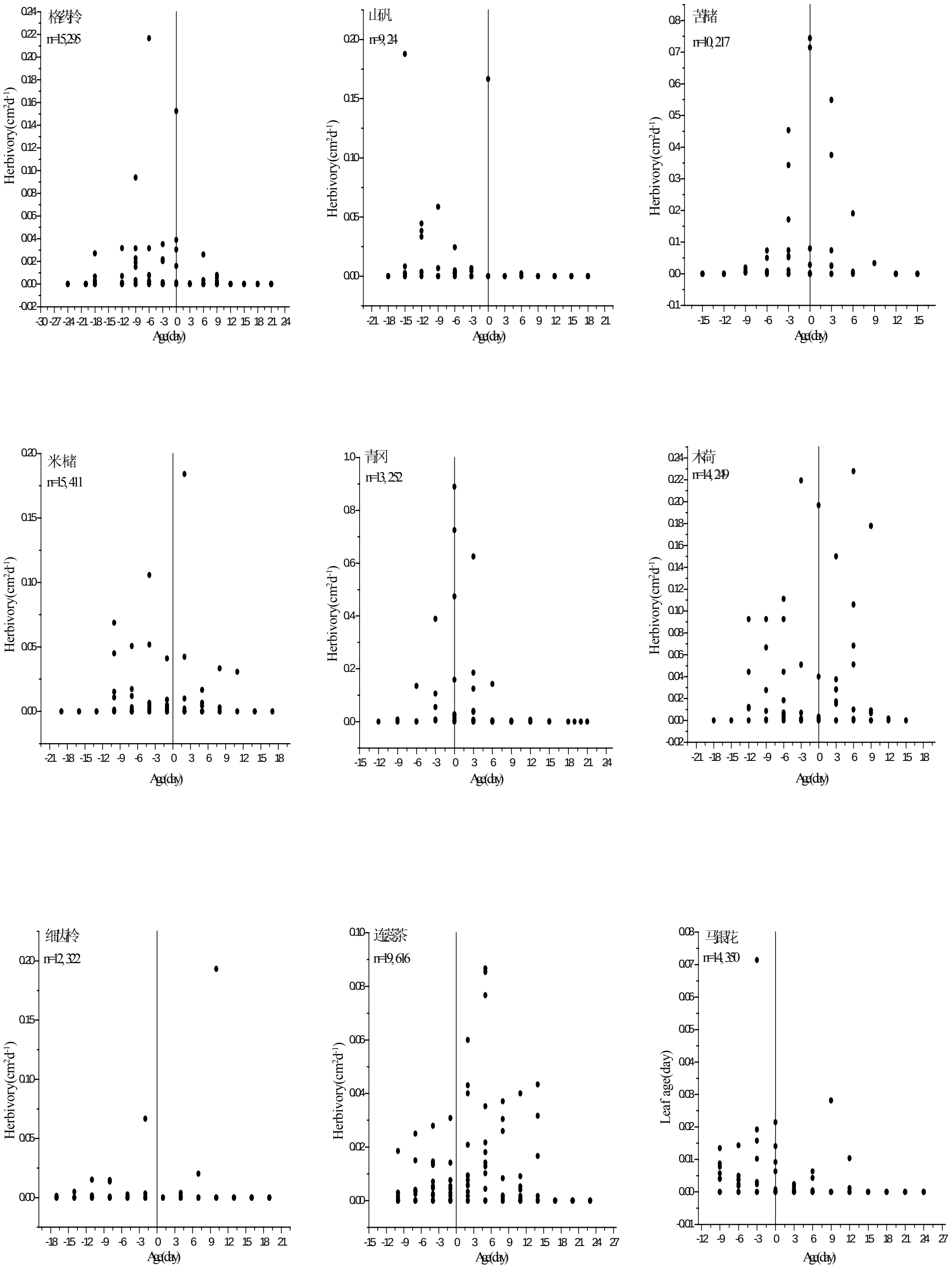

连蕊茶
n=14, 89
鹿角杜鹃
n=11, 90
罗浮柿
n=15, 92
石笔木
n=11, 119
乌饭
n=6, 64
小叶乌饭
n=12, 190
木荷
n=15, 137
建润楠
n=6, 48
黄樟
n=8, 64
黄瑞木
n=6, 63
Herbivory(cm²d⁻¹)
Age(day)

图 2 梅花山植物幼叶期的虫食时间格局

Fig.2 Patterns of herbivory on leaves of plants in Mt. Meihuashan.



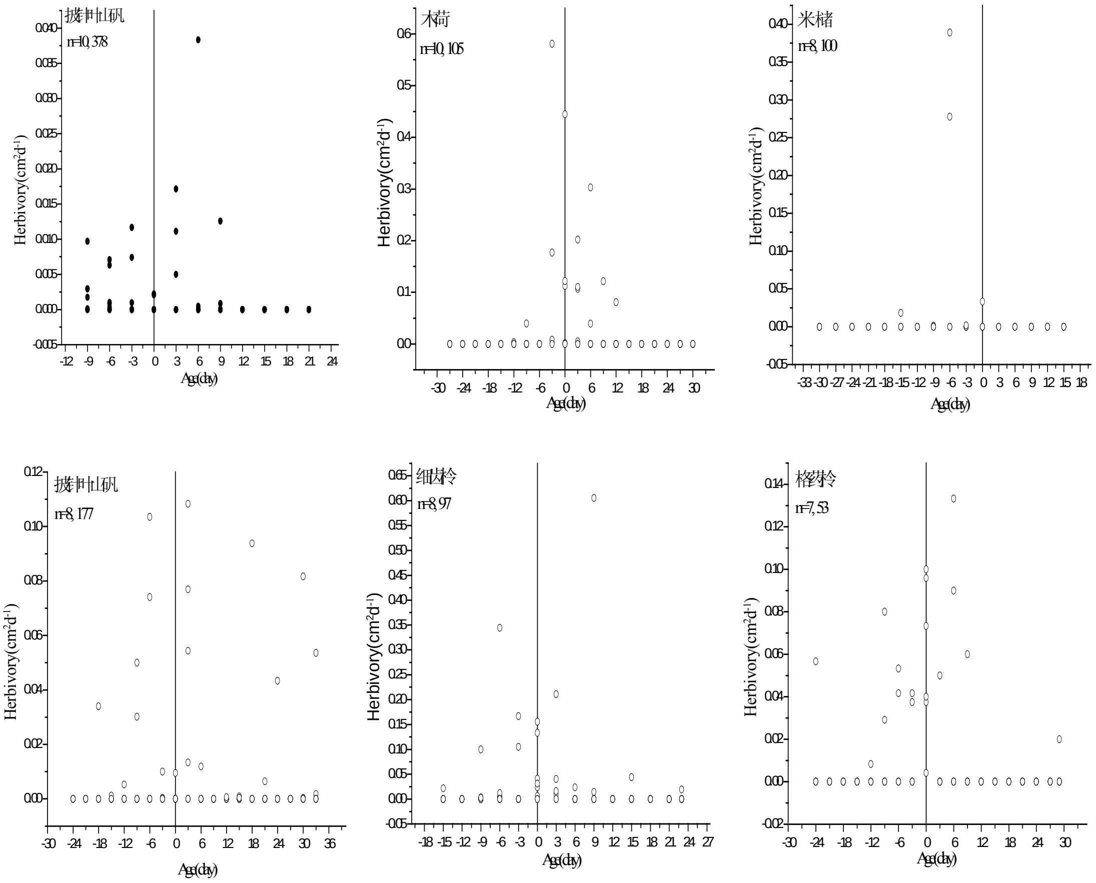


图 3 天童植物幼叶期的虫食时间格局. ●表示春季虫食动态, ○表示夏/秋季虫食动态

Fig.3 Patterns of herbivory on leaves of plants in Tiantong. ● indicates dynamics of herbivory on spring young leaves; ○ indicates dynamics of herbivory on summer/autumn young leaves.

2.3 幼虫与叶片的生长动态

木荷叶片面积在生长之初增加缓慢，随后进入快速生长期，经过一段时间的生长叶片开始缓慢生长并于 18d 后完全展开。雪毒蛾幼虫的体重在孵出之后 7d 内增加缓慢，随后快速上升并持续 18d 左右达到最大值，在幼虫体重达到最大值几天后幼虫体重快速下降，并于 2d 后进入蛹期而保持稳定。幼虫的日取食面积随幼虫体重的上升而增加，但在幼虫体重达到最大值之前 2d 达到最大值，随后快速下降并于 4d 后下降为零。因此，幼虫的生长、取食与植物叶片的生长保持同步的关系(图 4)。

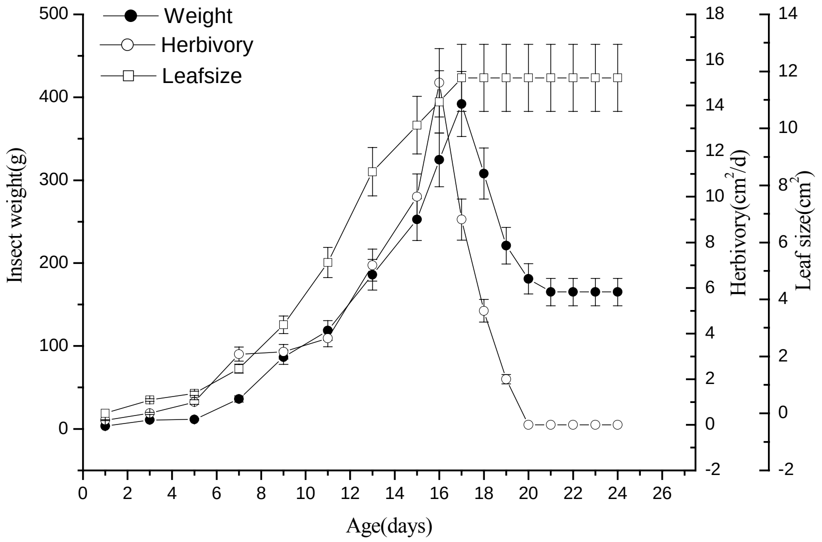


图 4 幼虫生长、取食与叶片生长动态
Fig.4 Dynamics of growth of leaf, larva and herbivory.

3 讨论

植物叶片的光合能力和营养含量随叶片年龄的增加而下降(Chabot and Hicks, 1982; Field and Mooney, 1983)，而且叶片展叶期间的虫食比成熟叶片的虫食对植株繁殖的影响更大(Krisckik and Denno, 1983; Jurik and Chabot, 1986; Mendoza, *et al.*, 1987)。不考虑昆虫对幼嫩叶片的取食所带来的影响，目前对常绿阔叶林植物叶片展叶期间的虫食动态仍知之甚少。

3.1 展叶期间叶片虫食动态

叶片发育过程中N素含量高于成熟叶片(Kursar and Coley, 2003)，高N含量的幼叶遭受更严重的虫食，因此一些植物在幼叶中含有高浓度的次生物质进行保护，但有些植物不依赖次生物质进行化学保护，而是快速的发育使叶片尽快硬化以逃避昆虫对幼嫩叶片的取食。发育过程中的叶片含有较低的次生物质、叶片硬度低且营养含量高造成叶片展开前的虫食量高，叶片完全展开后由于叶片硬度上升，给昆虫的取食和消化造成了困难，导致取食量下降，因此早食型格局的植物可能采取了逃避的策略。同时，食叶昆虫在长期的进化中，形成取食植物范围较小的狭食性或和取食范围较广的广食性昆虫 (Coley and Barone, 1996; 阎凤鸣,

2003)。专食性昆虫因为取食专化，对植物叶片所产生的次生物质具有抵抗或消化能力，而广食性昆虫则不具备这种能力，对含有较高次生物质的叶片取食较少。七种植物的叶片在展叶初期取食量高而展叶后的虫食量低，同时除深山含笑和细叶青冈以外，其他五种植物的叶片生长均非常迅速，而生长快速的植物叶片含有较高的N素营养(Kursar and Coley, 2003)，次生物质含量往往较低，因此早食型虫食格局的植物叶片可能为广食性昆虫所取食，因为昆虫对此类植物形成专食似乎没有显著的生态益处。建润楠、黄樟和黄瑞木三种植物新生叶片的展叶速度均比较慢，可能叶片的N素营养含量较低且樟科植物均有高含量的刺激性物质，因此化学防御的水平可能较高导致叶片展开前的虫食量低。随叶片的展开，叶片中的次生物质浓度下降(Coley and Aide, 1991)，叶片完全展开后虽然叶片的硬度有所增加，但次生物质的下降为昆虫的取食去除了障碍，因此形成后食型虫食格局。由后食型虫食格局可看出，在叶片展开过程中化学防御水平较高时的虫食很低，可以推测取食此类植物的昆虫并非狭食性昆虫而是广食性昆虫所为，而且后食型虫食格局的植物采取的是利用次生物质抵抗或忍耐的防御策略，这需要对植物次生物质的含量进行测定以进一步明确其含有的次生物质种类。中间型虫食格局的植物可能是处于二者之间的过渡类型，或者采取的是二者兼有的防御对策。

一些植物如木荷叶片展开时的虫食量较高不仅有植物叶片的因素，而且昆虫的发育特点也造成了叶片展开时的虫食较高。昆虫在叶片发育期间取食量逐渐增加，而且在叶片将要完全展开时进入快速生长期，取食量也达到最高，大量取食后昆虫进入老熟期，取食量急剧下降，到化蛹停止取食。在室内的饲养结果如图4所示，但是昆虫在野外的孵化和生长可能有所差异，所以在植物叶片完全展开后仍有昆虫取食，此时叶片的硬度可能是最为有效的防御方式。

浙江天童植物叶片展叶期间虫食动态同福建梅花山相似，都有前食型和中间型虫食格局，但没有发现后食型虫食格局。虫食格局是植物对昆虫取食所采取的对策结果，也是这种对策的具体反映。因此，浙江天童的植物对虫食的防御策略少于福建梅花山，虽然这可能和我们在浙江天童调查的植物种类较少有关，但也反映了浙江天童投入化学防御的植物比较少，这和浙江天童植物展叶期间的日均虫食面积小于梅花山的结果一致。本结果说明随纬度的降低，植物和昆虫的相互作用逐渐加强。

在相同群落中，叶片展叶期植物对虫食所采取的防御策略存在种间差异，这是自然选择和进化的结果，也是植物和食叶昆虫相互作用的结果，这种结果对植物和昆虫的相互关系具有重要的生态意义。常绿阔叶林植物幼叶的虫食动态与热带植物幼叶期(Kursar and Coley, 2003)相似，展叶初期虫食量低而展叶完成时的虫食量高，但常绿阔叶林植物幼叶的后食型虫食动态格局是热带植物所没有的，这可能与常绿阔叶林自然竞争弱于热带森林致使专食性昆虫较少有关，因此后食型虫食格局的植物在展叶初期利用次生物质进行了成功的防御，所以本文认为梅花山和天童的食叶昆虫均以广食性昆虫为主。

3.2 植物展叶期叶片虫食的种间差异

植物叶片展叶期的虫食存在种间差异，这种差异反映了植物对昆虫取食叶片的防御不同。因为多数虫食发生在叶片展叶期(第五章)，且叶片展叶期虫食对植物的生长和繁殖产生严重影响，所以叶片展叶期对虫食的防御对植物至关重要。植物叶片展叶期的日均虫食面积不同(表 1)，但乔木种与灌木种之间并无显著差异，表明生活型对植物的防御能力并无显著影响。低龄叶片的日均叶片损失大于高龄叶片，表明随叶片的发育植物的防御能力在逐渐增强，主要因为叶片硬化造成叶片适口性降低并使昆虫消化困难，叶片虫食损失减少(Lowman and Box, 1983; Coley, 1983; Juniper and Southwood, 1986; Kursar and Coley, 2003)。尽管植物发育过程中的防御能力有所不同，但幼嫩叶片暴露在昆虫面前的时间越长则损失的几率越大，因此展叶时间越短的植物所遭受的虫食越低。昆虫数量的多少也会对植物叶片发育期的虫食产生影响，由于昆虫的数量在生长季之初较低(Wolda, 1978; 1988)，因此早出叶的植物遭受的昆虫取食较低。前人的研究认为快速的展叶可以减少叶片暴露给昆虫的时间(Aide and Londoño, 1989; Kursar and Coley, 1991)，并因此降低叶片虫食损失。

福建梅花山植物展叶期的日均虫食面积显著高于浙江天童的植物，而且两个地区的共有种木荷、连蕊茶和格药柃的虫食也存在显著的差异，意味着在叶片展叶期间福建梅花山的植物承受的虫食压力高于浙江天童。有研究认为随纬度的降低，防御生物之间的竞争和相互关系更加激烈(Coley and Barone, 1996)，但同处于中亚热带的梅花山和天童亦表现出相似的趋势，即随纬度的降低，植物与昆虫

的相互作用更加激烈，也可能导致梅花山的植物在叶片展叶期的防御方式多于浙江天童。

总之，植物叶片展叶期的虫食动态有三种格局，这三种格局反映了植物对昆虫取食防御方式的差异。叶片展叶期是叶片一生中最脆弱的时期，且叶片表现出逃避或抵抗等防御方式，这是昆虫的选择压力所致。对于植物叶片的次生物质还需要在以后的工作中进一步测定以确定不同植物的防御策略。

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第五章 植物叶片虫食强度及季节变化

摘 要：本文研究了浙江天童常绿阔叶林中 11 种常见植物叶片的虫食及其季节变化，并比较了不同植物的虫食动态格局，研究结果如下：1）11 种植物年平均叶片虫食率为 11.87%，年平均叶片虫食频度为 50.15%；2）叶片生长的第一个月内的平均虫食率为 6.11%，占年虫食率的 56.9%，幼叶期的虫食频度为 30.81%，占年虫食频度的 62.30%；3）叶片虫食的时间动态有三种格局，叶片生长的第一个月内虫食最高的单峰格局、叶片生长的第一个月内虫食为主和 9 月虫食为辅的双峰格局以及叶片生长的第一个月内虫食为主、8 月和 10 月虫食为辅的三峰格局。以上结果表明，植物叶片的虫食具有时间动态且存在种间差异。

关键词：常绿阔叶林, 叶片, 虫食, 时间格局

前言

植物叶片虫食具有明显的高峰期，如热带雨林中有 70%的叶片虫食发生在叶片生长的第一个月内(Lowman, 1985；1992; Coley and Barone, 1996)，即叶片展叶期；热带季雨林植物叶片虫食也表现出相似的特点，即主要集中在雨季来临时，新叶大量抽生的时间(Marquis and Braker 1994; Coley and Barone, 1996; 郑征等, 2001)，这也是昆虫种群爆发的时间（Wolda, 1978；1988）。但温带森林植物叶片虫食的高峰并非在叶片展叶期，而是在叶片成熟以后，表现出了相反的趋势 Coley and Barone, 1996)。可见植物叶片虫食强度与不同地区的环境条件存在一定的关系。

亚热带常绿阔叶林可视为热带雨林与温带落叶阔叶林之间的过渡类型，其气候特点是夏季温暖湿润，冬季少雨而寒冷，植物叶片的抽生、发育和特性与热带和温带植物有着较大的差异。目前有关常绿阔叶林昆虫食叶动态的研究还很少报道，而这方面的研究是深入分析食叶昆虫与植物之间相互关系的基础，本部分是关于叶片虫食季节变化观测的结果，包括两个问题：1）常绿阔叶林植物叶片虫食的动态特征？ 2）常绿阔叶林植物叶片虫食的种间差异？

1 材料与方法

1.1 研究地点和植物

本研究在浙江天童国家森林公园(29º48´N, 121º47´E)进行，研究从2005年2月底植物萌芽前开始至11月初叶片不再有虫食后结束。公园面积349公顷，主峰太白山海拔653.3 m，一般山峰海拔300m左右，年均温度为16.2℃，年均降雨量1374.7mm。地带性土壤为山地黄红壤，质地以中壤至重壤为主，全氮和有机质含量较高。该区森林植被保存良好，地带性植被以栲树、米槠和木荷为建群种组成的常绿阔叶林(宋永昌等, 1995)。

本研究选择常绿阔叶林中较为常见的11种常绿乔灌木为研究对象，其中乔木为5种，3种为优势种，即栲树、米槠和木荷，2种为伴生种，即苦槠和青冈；灌木6种，3种为优势种即连蕊茶、格药柃和马银花，3种为伴生种，即披针叶山矾、山矾和细齿柃。为便于观测，乔木选择1~2米高的幼树叶片为观测对象。

1.2 研究方法

1.2.1 叶片的标记和采样

幼叶从叶芽萌动开始标记，为了不破坏幼嫩的叶片，用有色塑料线标记芽附近的老叶，利用叶芽上叶片的节位确定叶片的个数和位置。

1.2.2 虫食率与虫食频度的测定

展叶期间，每隔2天用带网格的透明塑料片(10格/cm^2)测量叶片虫食面积(在塑料片上依据叶片剩余部分描绘后测得)和潜在完整叶片面积(剩余面积与虫食面积之和)。虫食率%=100*叶片虫食面积/完整叶片面积；虫食频度%=100*虫食叶片个数/总叶片数。叶片成熟后则每月对所标记的叶片测量一次并记录新增加的虫食率和虫食频度。用叶片标记的方法可以避遗漏被100%虫食的叶片。考虑到实际情况，明显的由掉落的树枝或风力造成的叶片损失排除在外。森林中叶片的取食主要由昆虫造成(Coley and Barone 1996)，所以本次研究主要考虑昆虫的作用而把微生物、真菌和其它生物的影响排除在外。

1.2.3 数据分析

本文所有数据用 ORIGIN 6.0 分析处理。本研究所得虫食率为百分数，在必要时进行反正弦转换，以符合正态分布。

2 结果与分析

2.1 叶片虫食率动态

（1） 11 种植物在第一个月的幼叶期的平均虫食率为 6.11%，全年累积虫食率为 11.87%，第一个月叶片虫食率占全年累积虫食率的 56.92%(表 1)。

（2） 叶片虫食率在 11 种植物间存在明显的差异，叶片年虫食率较高的植物有栲树和苦槠，分别为 32.68%和 32.58%；木荷和米槠在 10%以上。叶片年虫食率最低的是青冈（1.85%），其他植物在 5%-10%之间。第一个月叶片的虫食率在 11 种植物间也表现出相似的趋势。(表 1，图 1)。

表 1 11 种常绿乔灌木叶片虫食率和虫食频度.

Table 1 Herbivory rate and frequency on leaves in eleven evergreen trees and shrubs

植物种 Species	虫食率(%) Herbivory Rate±SD			虫食频度(%) Herbviory Frequency±SD			样本数 Sample
	第一个月 First month	全年 Whole year	比例 First month/whole year	第一个月 First month	全年 Whole year	比例 First month/whole year	
栲树	10.28±10.00	32.68±22.69	31.44	36.67±21.00	77.88±27.04	53.82	9(188)
苦槠	18.45±14.37	32.58±22.40	56.65	45.46±33.18	84.46±24.02	47.09	10(217)
木荷	7.56±10.40	13.68±16.21	55.3	49.41±27.23	70.88±20.05	69.71	14(249)
米槠	6.98±10.50	12.51±9.56	55.86	34.35±28.57	64.06±25.33	53.62	15(411)
青冈	1.17±1.72	1.85±2.13	63.52	35.83±32.85	43.78±30.16	81.84	13(252)
连蕊茶	5.21±4.17	8.4±6.57	62.06	31.15±22.44	42.79±27.82	72.79	19(616)
披针叶山矾	3.11±4.79	6.84±6.03	45.43	14.24±12.85	34.74±23.62	40.99	10(378)
山矾	4.95±5.93	6.61±5.99	74.86	32.02±36.17	48.69±34.92	65.76	9(204)
格药柃	4.69±6.03	5.52±6.74	84.96	29.67±26.83	35.13±25.95	84.46	15(295)
马银花	2.92±3.77	5.25±7.00	55.5	22.19±20.33	30.69±24.84	72.30	14(350)
细齿柃	1.89±2.67	4.66±5.75	40.54	7.94±7.67	18.52±10.88	42.87	12(322)
平均 Average	6.11	11.87	56.92	30.81	50.15	62.29	

样本数表示植株数目(叶片数目)

（3）乔木的平均虫食率(18.66%)显著高于灌木的平均虫食率(6.21%; t=2.260, p=0.050)。优势种的平均虫食(13.00%)虽高于伴生种(10.51%)，但二者没有显著

差异(p>0.05)。

（4） 叶片虫食率的季节动态在 11 种植物间也表现出一定的差异，根据其峰值的变化分为三类，**单峰型格局**：格药柃、栲树和苦槠三种植物叶片的虫食率仅在新叶开始生长的 4 月份最高，随后虫食没有再次大规模发生，形成全年虫食的单峰型格局；**双峰型格局**：米槠、青冈、连蕊茶、马银花、披针叶山矾、山矾和细齿柃在新叶大量生长的 4 月虫食率达到最高峰，随后虫食率快速下降，8 月达到最低， 9 月和 10 月间植物叶片的虫食略有上升，形成第二个小高峰，随后虫食率快速下降至零，不同的是栲树叶片的第一次虫食率高峰发生在 7 月，第二次同样发生在 9 月到 10 月间，从而形成全年虫食的双峰型格局；**三峰型格局**：木荷叶片的第一次虫食高峰发生在新叶生长的 4 月份，随后虫食率下降，8 月份虫食略有回升形成第二次虫食的高峰，9 月虫食再次下降，10 月份虫食再次上升形成第三次虫食高峰，11 月虫食率降为零，从而形成全年虫食的三峰型格局。

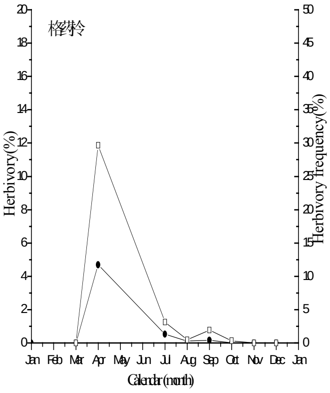
2.2 叶片虫食频度动态

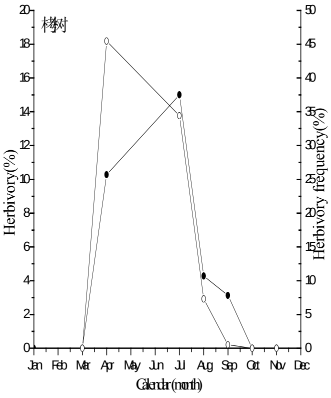
（1）11 种植物在第一个月的幼叶期的平均虫食频度为 30.81%，年平均虫食频度为 50.15%。一年中 62.29％的虫食频度发生在第一个月的幼叶期。

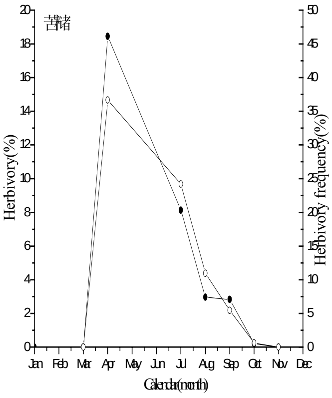
（2）虫食频度在植物间存在差异(表 1)。年叶片虫食频度最高的植物是苦槠（84.46%），栲树、米槠和木荷的虫食频度也均高于 50%，其他植物的虫食频度均低于 50%，最低的是细齿柃（18.52%）。除苦槠、披针叶山矾和细齿柃在第一个月的虫食频度占全年比例较低外，其他植物第一个月的虫食频度占全年的比例均高于 50%(表 1)。

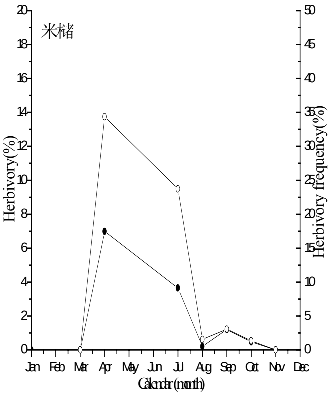
（3）乔木的平均虫食频度(68.21%)极显著高于灌木(35.09%; t=-4.213, p<0.01)。但优势种和伴生种的虫食频度并无显著差异(p>0.05)。

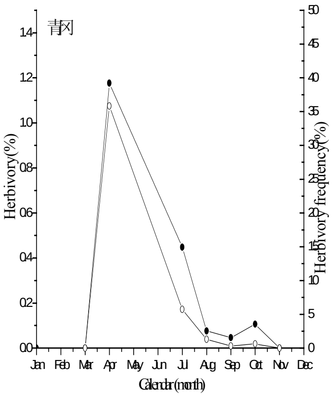
（4）叶片虫食频度的动态在 11 种植物间存在差异(图 1)，根据峰值可以区分的格局类型同虫食率的趋势一致，即可以分为单峰型、双峰型和三峰型。虫食频度与虫食率间显著正相关(r=0.854, n=11, p=0.001)。

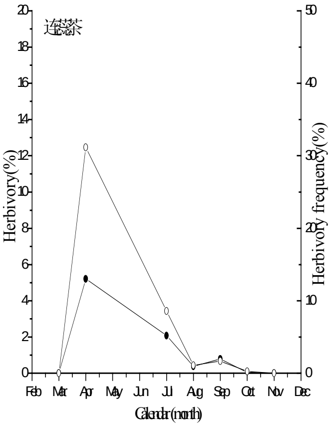

格药柃
Herbivory(%)
Herbivory frequency(%)
0 2 4 6 8 10 12 14 16 18 20
0 5 10 15 20 25 30 35 40 45 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan
Calendar (month)

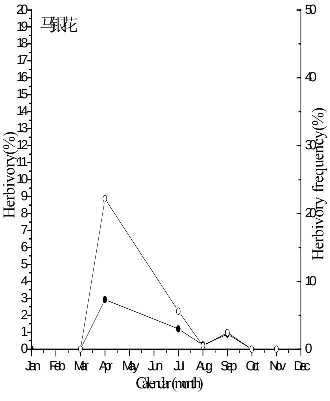

栲树
Herbivory(%)
Herbivory frequency(%)
0 2 4 6 8 10 12 14 16 18 20
0 5 10 15 20 25 30 35 40 45 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)

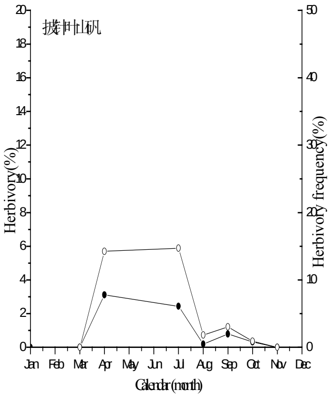

苦槠
Herbivory(%)
Herbivory frequency(%)
0 2 4 6 8 10 12 14 16 18 20
0 5 10 15 20 25 30 35 40 45 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)

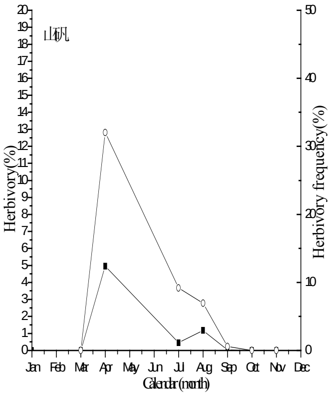

米槠
Herbivory(%)
Herbivory frequency(%)
0 2 4 6 8 10 12 14 16 18 20
0 5 10 15 20 25 30 35 40 45 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)


青冈
Herbivory(%)
Herbivory frequency(%)
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
0 5 10 15 20 25 30 35 40 45 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)


连蕊茶
Herbivory(%)
Herbivory frequency(%)
0 2 4 6 8 10 12 14 16 18 20
0 10 20 30 40 50
Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)


马银花
Herbivory(%)
Herbivory frequency(%)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
0 10 20 30 40 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)


披针叶山矾
Herbivory(%)
Herbivory frequency(%)
0 2 4 6 8 10 12 14 16 18 20
0 10 20 30 40 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)


山矾
Herbivory(%)
Herbivory frequency(%)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
0 10 20 30 40 50
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Calendar (month)

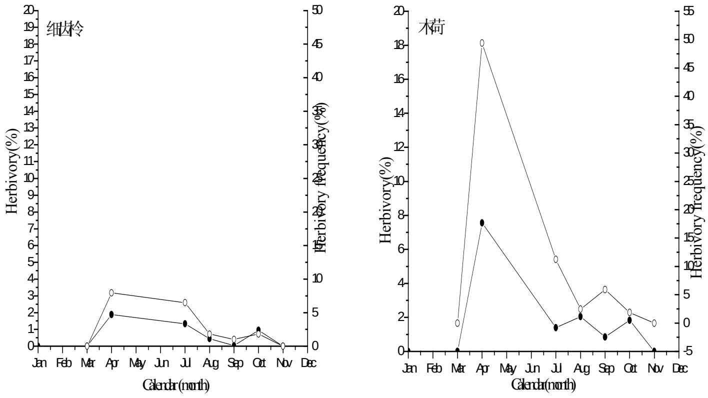


图 1 植物叶片的虫食时间动态. ●表示虫食率,○表示虫食频度.
Fig.1 Temporal dynamics of herbivory on leaves in different plants. ●indicates herbivory, ○ indicates herbivory frequency.

3 讨论

3.1 关于叶片虫食的季节动态

热带和温带地区植物叶片虫食率均具有时间动态(Aide, 1991; Lowman, 1992; Coley and Barone, 1996; 于晓东等, 2001; Kursar and Coley, 2003)。热带地区雨季是昆虫取食最多的时期，而干季则是昆虫取食最少的时期(Coley and Barone, 1996)。本研究发现叶片生长的第一个月虫食率最高，8 月份是虫食最少的时期，植物叶片的虫食时间动态在植物间存在差异。叶片虫食的时间动态(图 1)可能有以下几个成因：第一，昆虫的季节性种群变化，这与昆虫的生活史有关。昆虫种群数量在旱季显著下降，然后在雨季来临时回升直到下一个旱季来临(Janzen, 1985; Lowman, 1985; Marquis and Braker,1994; Murali and Sukumar, 1993; Wolda, 1978)，虫食率的季节性变化反映了昆虫种群的这种变化模式；第二，植物的出叶物候，植物在春季和夏末秋初可以抽生二次新叶，昆虫与植物在长期的进化中形成协同进化关系，昆虫在植物抽生新叶的时候种群数量会增加 (Wolda, 1988; Coley and Barone, 1996)；第三，叶片特性，叶片生长的第一个月内的高营养含量吸引昆虫取食，而叶片成熟以后其含水量和 N 素含量下降以及硬度的增加都给昆虫取食造成了困难，延缓了昆虫的发育，增加昆虫的死亡率，导致叶片虫食率的减少。因此昆虫的取食和植物的新叶生长保持同步，在新叶成熟以后虫食率较

低。本研究结果与南亚热带地区虫食春夏季节较低的结果有所不同(陈章和等, 1993)，陈章和等人的研究是建立在凋落物的基础上，相对而言，建立在叶片标记基础上的结果更为可信。

叶片是食叶昆虫赖以生存的食物来源(Coley and Barone, 1996)，叶片生长期间昆虫的数量大幅度增加(Wolda, 1988)，生态环境和进化的压力使昆虫的食谱变窄而形成专食性昆虫(Ehrlich and Raven, 1964; Futuyma, 1983; Jaeruke, 1990)。为提高存活率，昆虫的发育同植物叶片生长高度同步(Aide and Lodoño, 1989)，所以昆虫一年内的代数可能和植物的出叶次数有关。因此，单峰型虫食格局的植物上的昆虫则很可能为专食性昆虫且每年只繁殖一代，这种情况在天童森林公园内已有发现(个人观察)。由于多数天童植物于夏秋季节抽生二次新叶，而双峰和三峰型虫食格局植物上的昆虫则可能繁殖多代，或者第二次或第三次的取食高峰是由于昆虫即将进入秋冬季节为营养储备而进行大量取食所造成(于晓东等, 2001)。

3.2 关于叶片虫食强度的种间差异

亚热带常绿阔叶林 11 种植物的平均年虫食率高于温带阔叶林植物的平均年虫食率(7.1%, Coley and Barone, 1996)，也高于热带湿润森林的耐阴植物(11.1%)，但明显低于热带森林的喜光植物(48.0%)。但本次研究的 11 种植物中只有 4 种植物叶片的虫食率超过 10%，且只有栲树和苦槠虫食率较高，而其他 7 种植物的虫食率均较低，所以尽管 11 种植物的平均年虫食率较高，但并不能表明亚热带植物叶片虫食率高于其他地区，还需要在更多的植物上进行调查。

虫食率和虫食频度反映了昆虫与植物之间相互关系的激烈程度，本研究结果表明亚热带常绿阔叶林多数植物所面临的虫食压力低于热带植物，但高于温带阔叶林植物，即纬度越高，植物的虫食压力越低。由于植物与食叶昆虫间协同进化的关系(Futuyma and Slatkin, 1983; Pimentel, 1988; 钦俊德和王琛柱, 1998)，植物在面临昆虫食叶压力时会相应进化抵抗或逃避昆虫的取食(Kursar and Coley, 2003)，因此这种虫食率的差异也可能是植物防御昆虫取食差异的结果，这是由激烈的自然选择所致。

乔木和灌木是植物群落的重要组成成分，二者生活型不同期在群落中所处的

地位也有差异。乔木种植物多为阳生植物，叶片生长快速，植物营养含量高，有利于昆虫的幼虫迅速获得需要的能量，羽化为成虫，乔木种植物叶片的虫食率较高。而灌木种植物多生长于光照不足的林下，叶片生长缓慢，林下生长缓慢的植物叶片通常具有较高的化学防御水平(Coley *et al*., 1985)，因此降低了植物的虫食水平，表明植物虫食可能主要受到植物叶片营养和叶片防御的影响。虽然优势种的虫食率高于伴生种植物叶片，但二者没有显著差异，表明在优势种和伴生种所面临的虫食压力相似，并不因植物数量而发生改变。

虫食频度反映了植物叶片遭受昆虫取食的比例，这个问题曾受到人们的关注(于晓东等, 2001; Avila-Sakar *et al*., 2003; Wilf and Labandeira, 1999)。虫食率相同的情况下，增加虫食频度可以显著增加一种植物花粉的活力(Avila-Sakar *et al*. 2003)。在全球气温逐渐上升的过程中，或者随纬度的下降，叶片的虫食频度逐渐上升(Wilf and Labandeira, 1999)。虽然本次研究的 11 种植物叶片平均虫食频度超过 50%，但 7 种植物叶片虫食频度低于 50%，而温带地区辽东栎 90%的叶片曾遭受过昆虫的取食，虫食率却只有有 5%(于晓东, 2001)。从以上结果看似乎常绿植物的虫食频度低于温带植物，但仅仅对比一种温带植物还无法说明问题，遗憾的是目前还没有热带地区植物叶片虫食频度的相关资料，关于此问题还有待进一步调查。

乔木种植物的虫食率和虫食频度同样高于灌木种植物，虫食率和虫食频度具有显著的线形关系，表明虫食频度可以反映虫食率的情况，为今后快速调查植物虫食率提供了基础。

总之，亚热带常绿阔叶林植物叶片的虫食率低于热带部分森林而高于温带森林。叶片的虫食主要发生在叶片生长的第一个月内，其他时间段的虫食相对较少。本地区的植物叶片虫食的季节动态有三种格局，是植物与昆虫二者互相影响的结果。本研究揭示了亚热带常绿阔叶林植物叶片虫食的时间动态规律，为以后的相关研究奠定了坚实的基础。

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第六章 植物叶片虫食的空间格局

摘 要：植物叶片虫食的空间变化同生境有关，能反映昆虫与植物的相互关系。为探讨不同生境植物叶片的虫食情况，本研究以木荷林林下、林窗以及竹林林下3种不同条件下木荷幼树为研究对象，观测了其叶片虫食率与虫食频度，并分析了观测结果产生变化的可能原因。结果表明： (1) 木荷林林下木荷幼树叶片的虫食率(14.14%)显著高于竹林林下(5.71%)，木荷林林下(12.28%)低于木荷林林窗(14.72%)，但不显著；(2) 大部分受损叶片其虫食率低于10%，昆虫对叶片仅为适量取食，叶面积大量损失的情况较少；(3)木荷幼树叶片虫食频度与虫食率极显著正相关。以上结果对进一步理解昆虫取食植物叶片随生境的变化提供了有益的资料。

关键词：常绿阔叶林, 木荷, 生境, 虫食率,虫食频度

前言

植食昆虫对叶片的取食是一个植物群落的普遍特征(Cyr and Pace, 1993)，但由于植物的生存环境存在差别，昆虫对不同生境植物叶片的取食也存在明显的空间变化(Lowman, 1983; 1985; Givnish, 1988)。虫食格局的空间变化反映了植物防御策略随生境的变化，并可能对植物防御策略的自然选择方向和速度产生影响(Coley, 1983; Bazzaz, *et al.*, 1987)。植物群落类型、植物密度和光照等生境条件均会导致植物叶片的虫食在空间上产生差异(Lowman, 1983)，但目前对植物虫食空间变化的研究仍不多见(Lowman, 1983; 1985; 1992; 于晓东等, 2001)，而对常绿阔叶林虫食空间格局变化的研究还未见报道。木荷是亚热带常绿阔叶林中的关键/优势树种，可适应多种生境，是本地区研究虫食空间变化的理想植物。本项研究旨在探讨如下问题：1)不同生境条件下木荷幼树叶片虫食率和虫食频度是否具有差异；2)受损叶片上不同虫食率所占比重的特征。以上分析结果将为进一步理解常绿阔叶林昆虫与植物的关系提供有益的理论依据。

1 材料与方法

1.1 研究地点和植物

本研究于浙江省宁波市天童国家森林公园中国家生态系统野外观测定位站(29º48´N, 121º47´E)进行，公园面积 349 hm^2。主峰太白山海拔 653.3 m，一般山峰海拔 300m 左右。年均温度为 16.2℃ ，年均降雨量 1374.7mm。地带性土壤为山地黄红壤，质地以中壤至重壤为主，全氮和有机质含量较高。该区森林植被保存良好，常绿阔叶林为地带性植被类型(宋永昌和王祥荣, 1995)。由于全球气候变化和人类的经济活动，常绿阔叶林的退化日益严重，幼树的生长对森林植被的恢复具有重要作用，因此本研究分别以木荷林林窗与林下以及竹林生境下的木荷幼树(高 1-2m)为对象，对其叶片虫食进行了对比调查。

1.2 方法

1.2.1 研究区概况

木荷林位于天童生态试验站右方 300m 左右、林道上方 100m 处，海拔 163m，坡度 20 度。木荷林群落可分为三层：乔木层，主要以木荷为主，另有少量马尾松(*Pinus massoniana*)、石栎(*Lithocarpus glaber*)和苦槠(*Castanopsis sclerophylla*)，层高为 12-20m，盖度为 80%；灌木层主要以马银花(*Rhododendron ovatum*)、山矾(*Symplocos sumuntia*)和窄基红褐柃(*Eurya rybiginosa* H.T. Chang var.attenuata H.T. Chang)为主，伴有老鼠矢(*Symplocos stellaris*)、黑山山矾(*Symplocos heishanensis*)和连蕊茶(*Camellia fraterna*)等常绿灌木，层高度为 1.5-5m，盖度 60%；草本层主要为狗脊(*Cibotium barometz*)、里白(*Dicranopteris glaucum*)和一些蕨类等。

竹林位于古天童寺左方 400m 左右、海拔 110m，坡度 15 度，林木层全为毛竹。毛竹一般高 10-13m，盖度在 60-70%；林下层灌木低矮，和草本层同处于一个层次，一般都在 1m 左右，盖度 60-90%，种类大都为附近森林群落中常见树种的幼树如木荷、枫香(*Liquidambar formosana*)、青椆(*Cyclobalanopsis myrsinaefolia*)、红楠(*Machilus thunbergii*)和白栎(*Quercus fabri*)；草本植物主要为黄毛耳草(*Hedyotis chrysotricha*)和三脉叶紫苑 (*Aster ageratoides*) 等(宋永昌和王

祥荣, 1995)。

1.2.2 虫食

该地区的植物叶片在 10 月下旬基本不再遭受虫食，这时候的调查可以反映当年生叶片在本生长季节的虫食情况，于是本研究在 10 月下旬开始。分别随机调查了木荷林林下木荷幼树 24 棵、林窗木荷幼树 10 棵，竹林林下木荷幼树 66 棵，每棵随机选择 3 根当年生枝条上的所有叶片，测量叶片虫食面积和剩余面积计算出虫食率(Herbivory rate)并记录虫食频度(Herbivory frequency)。

用带网格的透明塑料片(10 格/cm^2)测量叶片虫食面积(在塑料片上依据叶片剩余部分描绘后测得)并计算完整叶片面积(剩余面积与虫食面积之和)。

虫食率%=100*叶片虫食面积/(叶片虫食面积＋叶片剩余面积)；虫食频度%=100*虫食叶片个数/总叶片数。

1.2.3 虫食率级别

为统计不同虫食率叶片的分布情况，所有受损叶片按虫食率的大小分为 0–10%(0％<叶片损失面积≤10%), 10–25%, 25–50%, 50–75%, 75–100%五个级别。

所有数据用 ORIGIN 6.0 分析处理，不同环境虫食水平用 ANOVA 进行方差分析。C.V.=标准差/平均虫食率(频度)，C.V.值越大，表明群落中不同植物的虫食差异越大。

2 结果

2. 1 不同生境木荷叶片虫食率及虫食频度的比较

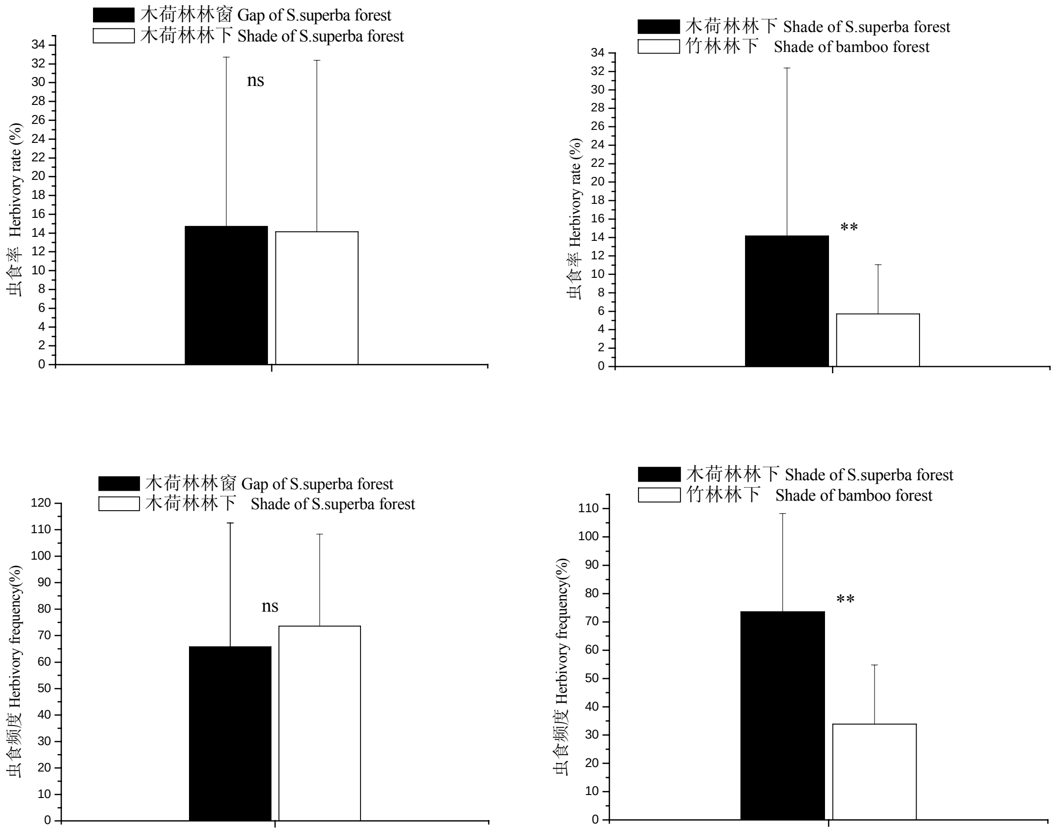
不同生境木荷叶片的虫食空间格局有很大差异 (图 1)。木荷林林下的木荷叶片虫食率是竹林林下木荷叶片虫食率的 2.5 倍，二者差异极显著 (F=10.85, df=1, 89; P=0.001)；木荷林林下的木荷叶片虫食频度也极显著高于竹林林下木荷叶片虫食频度 (F=11.47, df=1, 89; P=0.001)。木荷林林下叶片虫食率低于林窗而虫食频度高于林窗，但差异均不显著(F = 3.45, df=1, 33; P = 0.072; F = 1.54, df=1, 33; P = 0.223)，表明在木荷林中光照条件对虫食水平没有显著影响。

木荷林中木荷叶片虫食率在各植株间变异较大(CV>1)，竹林中木荷叶片虫食率与虫食频度在各植株间变异均较小(CV<1)，两种生境下木荷叶片虫食率的变异都大于虫食频度，表明同一生境下植物叶片受昆虫攻击的机会差异不大，而

虫食面积损失则有较大差异。

图 1 不同生境木荷叶片的虫食格局

Fig. 1 Patterns of insect herbivory on leaves of *Schima superba* in habitats



采样株数及叶片数如下：林窗(10 株, 140 片),木荷林林下(24 株,354 片), 竹林(66 株,1455 片).**表示 0.01 水平上差异极显著.

Sample sizes of plants and leaves are as follows: Light gap of *Schima superba* forest (10plants, 140 leaves), Shade of *Schima superba* forest (24plants, 354 leaves), Shade of bamboo forest (66plants, 1455 leaves). ** indicate significantly difference at 0.01 levels.

2.2 不同级别的叶片虫食率与虫食频度的变化

木荷林林下木荷叶片上不同级别的虫食率占木荷叶片总虫食率的比例差异较大，比例随虫食率级别的增加先上升后下降而后又上升（图 2)。虫食率在 25%～50%间的叶片其虫食率占总虫食率的比例最高，在 50%～75%间的叶片其虫食率所占比例最低。叶片数比例随虫食率级别的增加先下降后上升（图 2)，叶面积损失在 0～10%之间的叶片数最多，叶面积损失在 50～75％之间的叶片数最少，表明大多数叶片由虫食造成的叶面积损失并不高。

竹林林下各级别虫食率的比例随虫食率级别的增加先增加后下降(图 2)，虫食率在 25%～50%间的叶片其虫食率占总虫食率比例最高，虫食率在 50%～75%间的叶片其虫食率所占比例最低。叶片数比例随虫食率级别的增加先下降后上升，同木荷林林下木荷叶片的规律相似。

木荷林林下与竹林林下大部分的木荷受损叶片其虫食率均低于 10%，虫食主要发生在虫食率为 10%~50%之间的叶片上。木荷林林下虫食率低于 10%和超过 75%的叶片比例均高于竹林，即木荷林叶片虫食率分布相比竹林更为分散。木荷林林窗与林下则没有显著差异。

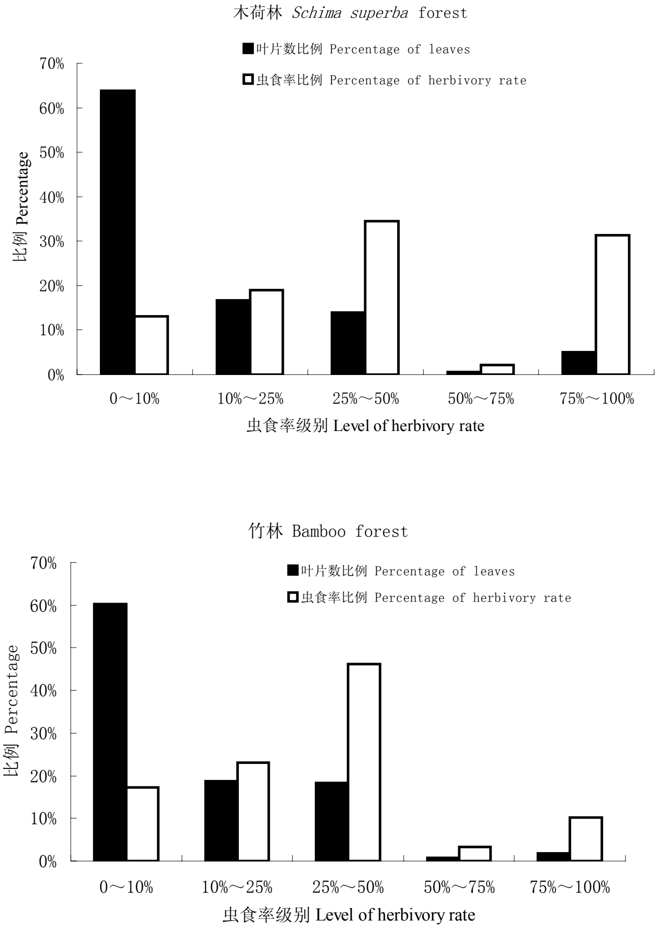


图 2 木荷林林下与竹林林下不同虫食水平叶片的分布

Fig.2 Distribution of leaves on different herbivory levels in shade of *Schima superba* forest and bamboo forest.

2.3 虫食率与虫食频度的关系

木荷林林下叶片虫食频度较高，虫食率也较高，二者存在极显著线性关系(图

3)。同样的关系存在与竹林林下的木荷叶片上(图 3)，表明在林下环境中受昆虫攻击的叶片数目越多，叶片损失越大。

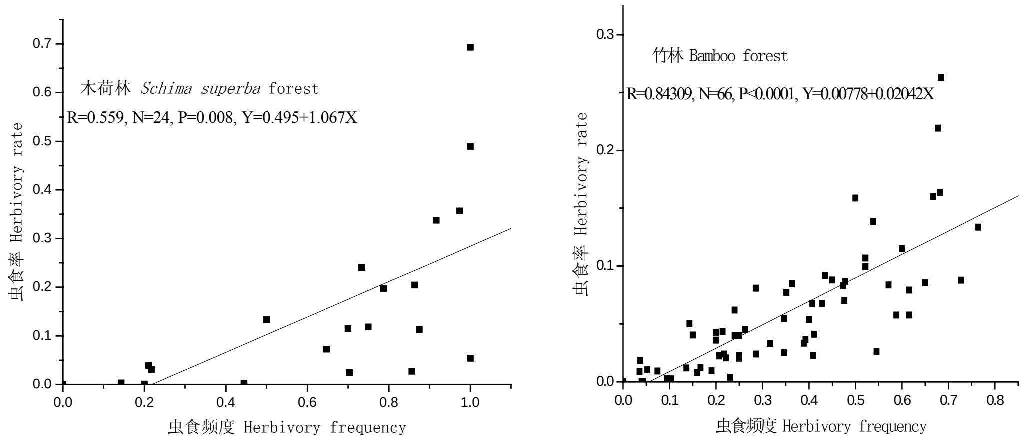


图 3 不同生境林下叶片虫食率与虫食频度的关系.

Fig. 3 Herbivory rate versus herbivory frequency of shade leaves in habitats.

3 讨论

3.1 林窗与林下的虫食

在生物群落中，昆虫对寄主植物的选择亦即对小生境的选择，由此影响昆虫在一定范围的空间分布和数量。植物本身对生境有选择性，它们所处的环境必然也影响昆虫与植物的关系。木荷幼树叶片虫食率和虫食频度的差异正是植物和昆虫在不同生境相互作用的体现。木荷林林窗虫食率高于木荷林林下而虫食频度却低于后者，但均无显著差异，说明光照条件对昆虫取食行为没有显著影响，但表明昆虫在林窗内的活动相对林下有运动量少而取食量大的特点。有研究表明遮光后小麦的茎硬厚度下降时其抗虫性消失(Roberts and Tyrrell, 1961)，遮光使玉米对玉米螟的抗性减弱(Loomis, *et al.*, 1957)，温度下降使植物的抗虫性趋于不明显(Dahms and Painter, 1940; Wood and Starks, 1972)，那么遮光的林下环境应该更适合昆虫的活动，但本研究的结果表明木荷叶片上的昆虫更喜欢活动于林窗内，据观察该地区木荷叶片主要为鳞翅目的一些蛾类幼虫所取食，本研究结果可能和这些昆虫的习性有关。

3.2 木荷林与竹林的虫食

木荷林林下叶片虫食率极显著高于竹林林下，表明植物群落结构的变化造成的环境差异可对植食性昆虫的取食活动产生明显的影响。竹林生物量较木荷林低很多，土壤也较木荷林瘠薄(宋永昌和王祥荣, 1995)，营养瘠薄的群落植物叶片寿命较长且叶片营养周转率低，叶片的防御水平也较好(Coley, 1985)。竹林中木荷的成年植株比较少，竹林植物多样性及昆虫多样性均低于木荷林，虫口密度也小于竹林(李恺未发表数据)，Janzen-connell 理论(Janzen, 1970; Connell, 1971)指出母株较少的生境对幼树更为有利，受以同种植物为生的昆虫和病原物的影响较小，这些可能是竹林中木荷幼树虫食率较低的原因。昆虫与植物的作用是相互的，昆虫对叶片的取食并非只产生负面的影响，适量的取食可以加快地上部分和地下部分的物质和能量循环(Wardle, *et al.*, 2004)，而低的虫食水平会降低群落中土壤物质和能量循环速度，考虑到毛竹的强烈竞争，竹林中木荷幼树的生长应非常缓慢。

3.3 虫食率与虫食频度的关系

昆虫有选择的对所发现的植物叶片进行取食，而不是攻击所有的叶片。木荷林中超过 60%的叶片受到植食昆虫的攻击，竹林中只有超过 30%的叶片曾被昆虫攻击，而且两个生境中被昆虫取食的叶片其虫食率多低于 10%，虫食率多集中发生于 10~50%面积损失的叶片上，表明昆虫在食物充足的情况下，对叶片不是浅尝则止而是适量的，过量取食叶片的情况较少发生。有研究表明植物叶片可以对适量的面积损失进行光合等方面的超补偿以弥补损失(Morrison, 1995)，适量的虫食可以诱导植物产生化学防御并显著增加植物的适合度(Agrawal, 1998)，且可以促进营养循环并提高植物的产量(Belovsky and Slade, 2000)。昆虫适量取食植物是长期进化的结果还是偶然为之，还需要我们更长时间的观察。虫食频度与虫食率间显著线性相关，虫食频度可以有效反映虫食强弱程度，这一结果为我们以后快速了解植物的虫食情况提供了参考。相同虫食率下，虫食相对集中可以显著提高花粉活力(Gelman, 2003)，因此损失相同比例的叶面积，受攻击的叶片数目越多，植物受到的影响越大，这一结果也说明木荷林中幼树受到昆虫的影响大于竹林。

总之，取食木荷叶片的昆虫受植物群落类型的影响较大，而受光照条件的影响则不显著，深入了解这些因子对昆虫行为的影响对揭示昆虫和植物关系具有重要的生态学意义，同时也对了解全球环境变化下的昆虫与植物群落动态产生积极作用。

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第七章 植物出叶物候及其与虫食的关系

摘要：为研究植物的出叶物候与叶片虫食的关系，对梅花山 14 科 38 种植物的出叶时间、展叶速度、展叶期以及出叶格局进行了调查，同时调查了植物出叶期的叶片虫食。分析了植物出叶物候与叶片虫食的相互关系，结果如下：1)植物叶片展叶期的平均虫食率为 8.59%，虫食频度为 33.29%，乔木和灌木之间的虫食没有显著差异；2）82%的植物于 4 月份抽生新叶，乔木与灌木的出叶时间差异不显著。出叶时间对展叶期叶片虫食率的影响不显著。3）展叶速度与出叶时间显著正相关(R=0.38, p<0.05)，出叶越早的植物展叶越慢，出叶越晚的植物展叶越快。乔木的展叶速度显著快于灌木(t=2.196, p<0.05)。展叶速度对展叶期叶片虫食有显著影响(R=0.35, p=0.039)，展叶速度越快的植物幼叶期虫食率越高，反之越低。4）乔木的出叶同步性低于灌木，但二者差异不显著，植物的出叶同步性与虫食率无显著关系，但同虫食频度显著正相关(R=0.35, p=0.030)，即出叶同步性越高，被昆虫攻击的叶片越多。5）展叶期最短的植物是鹿角杜鹃(16d)，而展叶期最长的植物是深山含笑(77d)，二者相差近 5 倍。展叶期与展叶速度极显著负相关(R=-0.423, p=0.008)，但展叶期同虫食率无显著相关性。

关键词：常绿阔叶林, 出叶时间, 展叶速度, 展叶期, 出叶格局, 叶片虫食

前言

第四、五章的研究结果表明，亚热带常绿阔叶林植物叶片展叶期是遭受虫食最多的时期。叶片展叶期遭受虫食对植物的影响显著高于叶片成熟后(Jurik and Chabot, 1986; Mendoza, *et al.*, 1987; Coley and Barone, 1996; Kursar and Coley, 2003)。为减少幼叶的损失，植物在进化中发展出多种对策防御昆虫的取食，如物候、物理和生物等防御对策，其中叶片物候被认为是植物防御虫食的有效对策之一(Aide, 1991; Aide and Lodoño, 1989; Sun, *et al.*, 2006)。

叶片物候防御有三种可能的方式，即通过早抽生、同步生长以及快速展叶来逃避昆虫取食。在热带雨林中，雨季来临之前昆虫的数量较低(Wolda, 1978; Lowman, 1982)，叶片较早抽生不仅有利于植物延长其光合时间，还可以避开昆

虫种群的高峰期以减少虫食(Murali and Sukumar, 1993; Coley and Barone, 1996; Moles and Westoby, 2000)。此外，叶片通过同步抽生在较短时间内产生大量新叶使昆虫饱食，达到减少虫食的目的(Feeny, 1976; Mckey, 1979; Coley, 1983; Aide, 1988; Clark and Clark, 1991; Aide, 1993; Murali and Sukumar, 1993)。最后，快速展叶可以缩短叶片脆弱的展叶期，较早使用成熟叶片的硬度等防御方式降低昆虫的成活率，进而减少虫食(Hay, *et al.*, 1988; Aide and Londoño, 1989)。Aide(1993)认为在热带雨林中虫食同展叶速度之间不具有相关性，而 Kursar(2003) 则认为展叶越快的植物叶片中营养含量高其虫食率也越高，因此展叶速度同虫食的关系还有待于进一步验证。

叶片物候与虫食关系的研究多在热带进行，但对亚热带常绿阔叶林中植物出叶物候与昆虫食叶的关系还知之甚少。本研究的目的是通过研究福建梅花山地区常绿阔叶林中常见植物的出叶时间、展叶速度、出叶的同步性以及展叶期间的叶片虫食率，探讨亚热带常绿阔叶林中的植物出叶物候与虫食的关系。

1 材料与方法

1.1 研究区概况

本研究在中国福建梅花山国家级自然保护区内(N25º25′, E116º50′)进行，详细描述见第二章。

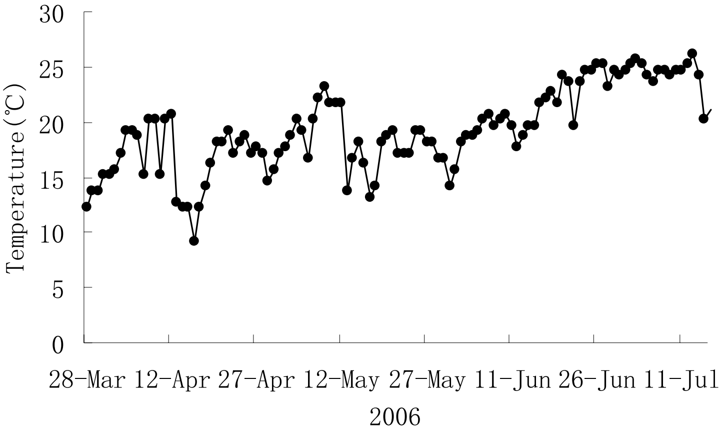

图 1 梅花山地区 2006 年 3 月 28 日到 7 月 15 日期间的日均温度, 涵盖了所有研究植物的出叶及展叶时间.

Fig.1 Daily average temperature from March 28th to July 15th, covering the period of leaf emergence and expansion of the species in the forest in Mt. MeiHuaShan of eastern China.

2006 年从 3 月底到 7 月初，所研究植物的出叶和展叶期间的日均温度总体呈上升趋势(图 1)，但 3 月底到 5 月初期间的温度波动较大，特别是 4 月中旬温度降低到 8℃左右，此时恰恰为大部分植物抽叶和展叶的时间。

1. 2 研究材料

本文研究了 14 个科的 38 种植物，包括 16 种乔木和 22 种灌木（表 1）。为便于调查，所选择的植株均为生长于林下的高 1~2 米的植株。调查了不同植物种叶片的出叶时间、展叶速度、展叶期、叶片大小及叶片的出叶格局。

1. 3 研究方法

1.3.1 样本标记

每种植物选择 6~10 棵健壮植株，每株于阳面随机选择三根枝条。每三天调查一次每根枝条上所抽生的叶片数，同时选择枝条中部的 3 片记录其每次的叶面积，直至叶片面积在连续三次的观测中不再增加为止，即认定该叶片展叶结束。为避免破坏幼嫩的叶片，用有色塑料线标记在芽附近的老叶上，利用叶芽上叶片的节位确定叶片的个数和位置。

1.3.2 出叶物候

本次研究的植物种其叶片抽生均发生在 3 月 1 日以后，故规定 3 月 1 日为第 1 天，每种植物有 10％的叶片抽出的时间距离 3 月 1 日的天数记做该种植物抽叶开始的时间。

叶片展叶速度是叶片展叶期物候窗对食叶昆虫能开放多久的关键特征。展叶期每 3 天测量一次叶面积。用以下公式(kursar and Coley 2003)计算叶片每天的展叶速度(Leaf expansion rate per day, LER)：

$$LER\ (\%/d) = 100*[e^{(\ln(area2/area1)/time)}-1]$$

area1 和 area2 是两次测量时的叶片面积，time 为两次测量的间隔天数。展叶速度为 100%指叶片面积每天增加一倍。

出叶格局用每种植物每次观察到的出叶百分比的变异系数(C.V.)来表示，C.V.值越大表明植物出叶在某一时段越集中，即出叶的同步性越强。每一个点的数据为每次观察到的新生叶片数占该种植株春季所产生总叶片数的百分比。

1.3.3 虫食率与虫食频度的测定

展叶期间，每 3 天用带网格的透明塑料片(10 格/cm^2)测量叶片虫食面积(在塑料片上依据叶片剩余部分描绘后测得)和潜在完整叶片面积(剩余面积与虫食面积之和)。叶片虫食状包括缘食、孔状、潜叶以及由昆虫造成的任何形状的叶片损失(王宏伟等 2006)。森林中叶片的损失主要由昆虫造成(Coley and Kursar, 1996)，因此主要考虑昆虫的作用而排除了微生物和真菌的影响，本次调查了 38 种植物 320 棵植株共 2684 片叶。*虫食率%=100*叶片损失面积/完整叶片面积；虫食频度%=100*虫食叶片个数/总叶片数*，本文所有数据用 ORIGIN 6.0 分析处理。

1.3.4 昆虫数量的调查

在本次研究所标记的植物上记录昆虫数量，由于本项研究主要涉及食叶昆虫且以鳞翅目昆虫为主，故不取食植物叶片的昆虫种类并不计算在内。为配合植物的出叶物候，本次调查从 3 月中旬开始持续到 7 月下旬结束，每 3 天调查一次。昆虫密度以平均每株植物上的昆虫数目表示。

2 结果与分析

2.1 植物叶片的虫食强度

(1) 乔木幼叶的平均虫食率(7.46%)低于灌木幼叶的平均虫食率(9.40%)，但二者没有显著差异。同虫食率相似，乔木的平均虫食频度(32.69%)低于灌木的虫食频度(33.73%)，但二者同样没有显著差异。梅花山植物叶片发育期间的平均叶片虫食率为 8.59%，平均虫食频度为 33.29%，且生活型并不对虫食产生显著影响。
(2) 植物叶片虫食率存在种间差异，叶片虫食率较高的是三花冬青、冬青和石笔木，均超过了 20%；叶片虫食率较低的植物是单耳柃、细叶青冈、红楠和绒毛润楠，四种植物的叶片虫食率均在 1%-2%之间，而大多数植物的虫食率低于 10%。

表 1 38 种常绿植物的出叶物候与虫食

Table 1 Leaf phenology and herbivory on leaves of 38 evergreen broad-leaved forest species

植物种 Species	生活型 LF	出叶时间 TLE	展叶速度 LER	展叶期 DLE	出叶格局 PLE(C.V.)	虫食率 H(%)	虫食频度 HF(%)
细叶青冈	T	36	9.73	54	1.01	1.29	12.03
红楠	T	55	9.92	28	0.98	1.48	16.41
水团花	T	25	12.08	45	1.05	3.29	11.31
建润楠	T	40	10.06	40	1.55	3.70	61.9
深山含笑	T	81	6.41	77	1.04	4.38	8.33
黄樟	T	32	8.85	43	1.20	6.95	37.41
甜槠	T	39	17.53	25	0.96	7.60	43.4
木荷	T	54	14.43	27	0.81	7.90	50.8
罗浮锥	T	33	10.94	27	0.70	7.97	41.32
厚皮香	T	39	11.28	35	0.63	8.97	50.00
栲树	T	36	10.28	50	1.92	9.00	50.11
上杭锥	T	101	22.00	18	0.72	9.70	49.10
杨梅	T	62	14.85	32	1.41	9.78	20.96
少叶黄杞	T	76	20.26	25	0.79	12.11	16.67
乳源木莲	T	41	10.52	28	0.90	12.50	16.66
猴欢喜	T	43	16.59	34	0.69	12.81	36.66
单耳柃	S	36	6.00	32	0.80	1.06	14.29
绒毛润楠	S	65	9.20	44	0.34	1.92	9.76
黄瑞木	S	24	8.43	26	1.57	2.36	32.34
交让木	S	70	14.19	28	1.41	2.67	19.47
辣汁树	S	42	8.95	26	0.87	3.37	16.98
鹿角杜鹃	S	36	13.98	16	1.21	4.56	20.37
狗骨材	S	40	9.89	63	1.52	5.75	75.00
油茶	S	43	6.67	27	0.58	6.51	38.93
山矾	S	34	15.12	33	0.61	6.67	20.00
赤楠	S	30	9.79	51	0.99	6.95	11.46
格药柃	S	30	11.6	31	1.54	7.67	29.18
毛冬青	S	65	8.10	58	1.09	7.72	20.99
小叶乌饭树	S	33	11.31	22	0.60	8.2	20.44
黄栀子	S	43	10.28	49	1.22	9.74	15.56
大萼两广黄瑞木	S	44	8.30	38	1.39	9.90	49.60
乌饭树	S	36	9.00	25	0.61	11.43	31.23
连蕊茶	S	27	7.64	24	1.28	11.59	60.24
老鼠矢	S	33	13.00	36	1.24	13.8	52.77
石斑木	S	54	11.86	30	1.42	14.64	51.67
石笔木	S	36	12.8	35	0.77	21.71	45.44
冬青	S	57	10.00	39	1.10	22.71	51.55
三花冬青	S	30	12.78	40	1.50	25.87	54.80

注：以虫食率大小排序. Note: Species are ranked by herbivory.

2.2 出叶时间及其与虫食的关系

(1) 从 3 月下旬到 6 月中旬均有植物抽生叶片，但 82%的植物在 4 月份(30-60)抽叶(表 1)，表明 4 月是植物的出叶高峰期。乔木的平均出叶时间 (49)晚于灌木的平均出叶时间 (41)，但二者差异并不显著 ($p=0.14$)。植物的出叶时间存在种间差异，出叶最早的植物是黄瑞木(24)，出叶最晚的植物是上杭锥(101)，两种植物出叶时间跨度达 77 天。

(2) 线性回归分析表明植物的出叶时间同展叶期间叶片的虫食率没有显著相关性($p>0.05$, 图 1)，表明出叶早的植物并不能有效降低其虫食率而出叶晚的植物其虫食率并不高。

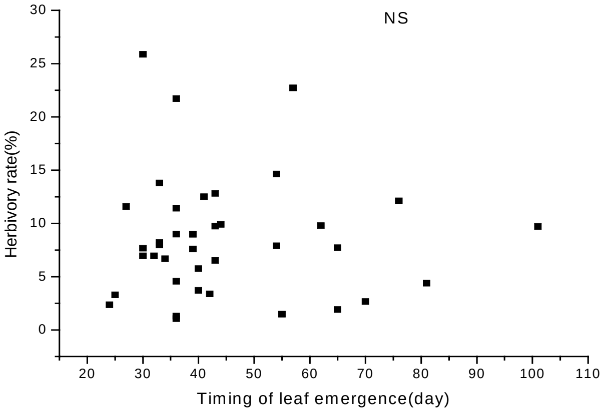

图 1 出叶时间同虫食率的关系

Fig. 1 Herbivory rate vs timing of leaf emergence

2.3 展叶速度及其与虫食的关系

(1) 植物的展叶速度存在种间差异，展叶较快的植物是上杭锥 (22.00%d^{-1})、少叶黄杞(20.26%d^{-1})和甜槠(17.53%d^{-1})，而展叶较慢的植物是单耳柃(6.00%d^{-1})、深山含笑(6.41%d^{-1}) 和油茶(6.67%d^{-1})，大部分植物的展叶速度在 7%d^{-1}-15%d^{-1} 之间。乔木与灌木的平均展叶速度存在显著差异($t=2.196$, $p<0.05$)。乔木的平均展叶速度为 12.85%d^{-1}，显著大于灌木 10.40%d^{-1} 的平均展叶速度。

(2) 展叶速度同虫食率极显著正相关(图 2)，即展叶越快的植物其虫食率越高，而展叶速度越慢的植物其虫食率越低(图 2)。展叶速度与虫食频度没有显著相关性(图 2)。展叶速度与出叶时间显著正相关($r=0.38$, $p<0.05$)，即出叶越晚展叶速度越快。

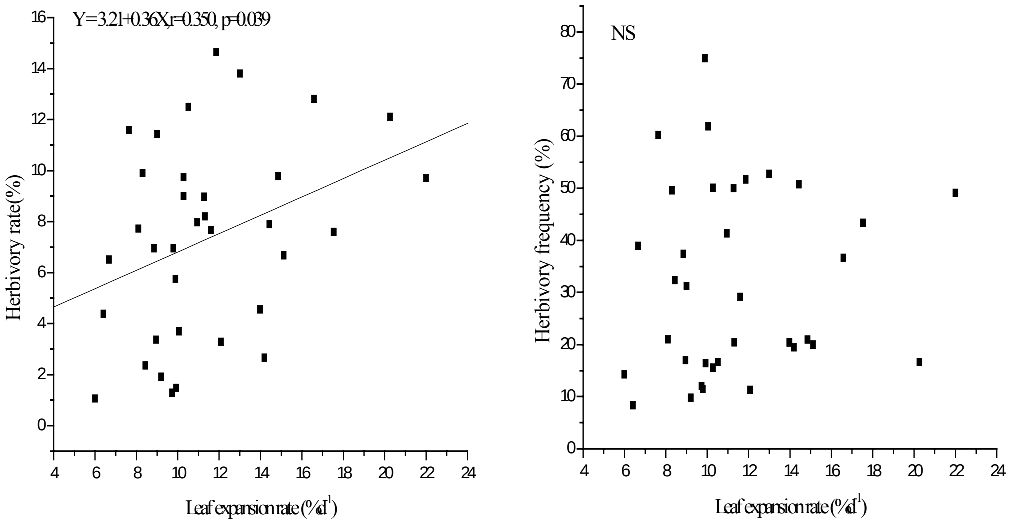

图 2 展叶速度与虫食率和虫食频度的关系

Fig.2 Herbivory rate and herbivory frequency in relating to leaf expansion rate

2.4 出叶同步性及其与虫食的关系

(1) 植物的出叶同步性存在种间差异，栲树所有的叶片几乎在同一时间抽出，叶片抽生同步性最高(1.92)；而绒毛润楠的叶片却逐个的抽出，其叶片抽生同步性最低(0.34)，其他植物的出叶同步性介于两者之间。乔木出叶的同步性(1.02)低于灌木(1.07)，但二者差异并不显著(t=-0.44, p>0.05)。

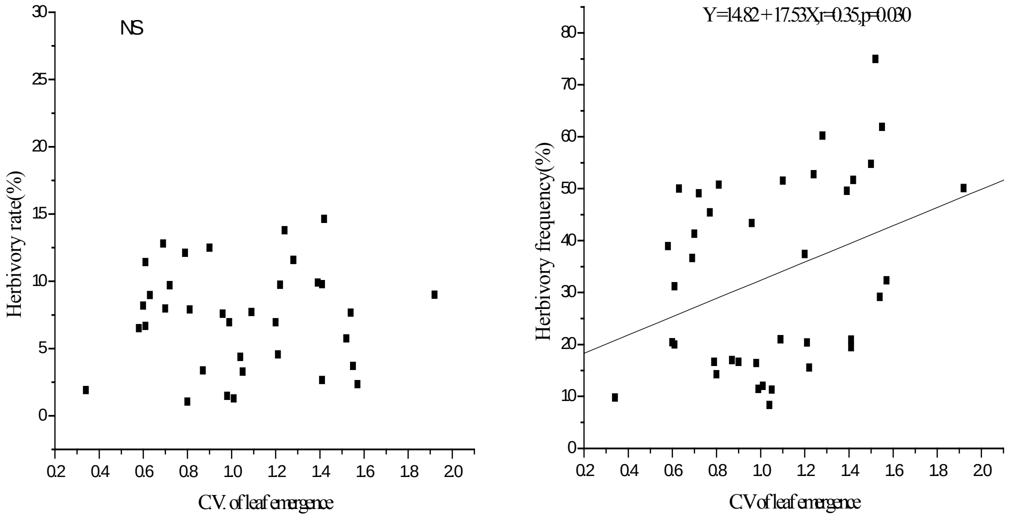

图 3 出叶同步性与虫食频度的关系.

Fig.3 Herbivory frequency in relating to C.V. of leaf production.

(2) 出叶同步性与虫食频度显著正相关(图 3)，出叶同步性越高的植物，其被昆虫所取食过的叶片数目比例越高，反之则越低。线性回归分析表明出叶格局同虫食率并无显著相关性(图 3)。

2.5 展叶期及其与虫食的关系

(1) 植物叶片展叶期种间存在较大差异(见表 1)。展叶期最短的是鹿角杜鹃(16d)，展叶期最长的是深山含笑(77d)。39%的植物在 30d 内完成展叶过程，57%的植物在 30-60d 内完成展叶过程，仅有狗骨材和深山含笑两种植物需要 60d 以上的时间完成展叶过程。乔木的平均展叶期(36.75d)与灌木的平均展叶期(35.13d)没有显著差异(t = -0.374, p = 0.710)。

(2) Pearson 相关分析表明展叶期同出叶时间相关性不显著(p=0.692)，而同展叶速度极显著负相关(R=-0.423, N=38, p=0.008)，表明展叶速度越快，完成展叶的时间越短。展叶期同虫食率和虫食频度负相关，但均不显著(R=-0.093, p=0.579; R=-0.082, p=0.624)。

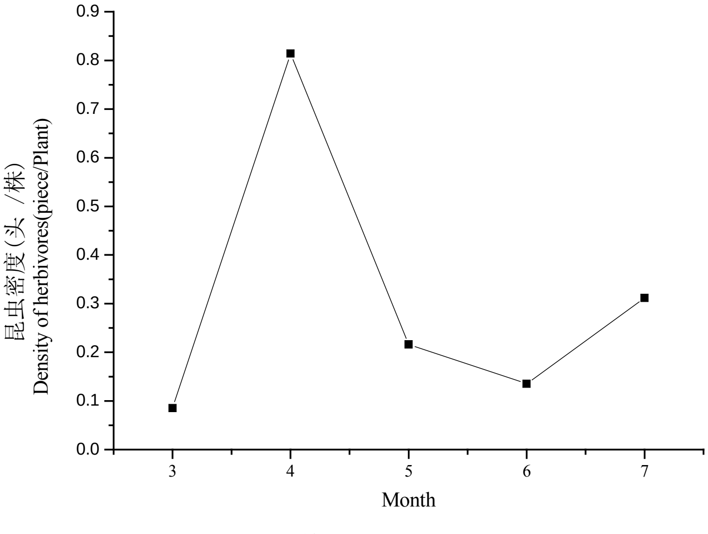

图 4 2006 年梅花山昆虫数量动态

Fig.4 Dynamics of insect population in Mt. MeiHuaShan in 2006.

2.6 昆虫数量动态

梅花山地区昆虫的数量从 3 月到 7 月间一直处于变化之中(图 4)。3 月份昆虫数量比较低，在 4 月份急剧增加并达到高峰；五月份昆虫数量显著低于 4 月份，但仍高于 3 月份，6 月份昆虫数量继续下降至 7 月昆虫数量开始回升。因此，本

地区昆虫数量在生长季节之初的 3 月最低，植物出叶高峰期的 4 月最高，而 7 月昆虫数量有所回升。

3 讨论

梅花山常绿阔叶林植物展叶期叶片平均虫食率为 8.59%，低于澳大利亚亚热带雨林幼叶期的虫食(11.3%, Lowman, 1983)和热带植物展叶期的虫食率(27%, Aide, 1993; 11.5%, Coley and Barone, 1996)。热带植物幼叶期的虫食受到出叶时间、展叶速度和出叶格局等出叶物候的影响(Aide and Lodoño, 1989; Aide, 1993; Kursar and Coley, 2003)，对亚热带常绿阔叶林植物的出叶物候与虫食关系的讨论如下：

3. 1 植物出叶时间与虫食

早出叶被认为是植物逃避昆虫取食的一种对策(Aide, 1988; Coley and Barone, 1996; Moles and Westoby, 2000)。在印度南部的森林中发现旱季抽生的叶片虫食率显著低于雨季抽生的叶片(Marali and Sukumar, 1993)，因为在雨季开始之前或者雨季之初，森林中的昆虫数量较少(Wolda, 1978; Lowman, 1982)，所以植物在昆虫数量爆发之前出叶，虫食率较低(Finke and Scriber, 1988)，而晚出叶的植物则遭受较严重的虫食(Washburn and Cornell, 1981)。以上结果似乎表明早出叶的植物可逃避昆虫的取食，但本次研究发现植物出叶时间同虫食率并无显著相关性，虽然水团花和黄瑞木出叶较早其虫食率也较低，但连蕊茶出叶早其虫食率仍较高，而且植物出叶高峰和昆虫数量高峰同时出现在4月(表1, 图4)，说明植物在群落水平上集中出叶并不能有效降低其虫食，因此虫食并不是植物出叶时间的主要选择因素。

植物出叶除受到昆虫等生物的因素影响外，还受到温度、降水和光照的影响(van Schaik, 1993；周云龙, 1999)。但对于旱季较短或不明显的森林，温度和光照可能是影响植物出叶的关键因素。昆虫的活动虽然同植物一样也受到环境因素的影响，但昆虫要经历蛹、产卵和幼虫阶段才能对植物叶片进行取食，因此早出叶的植物可能有利于逃避昆虫取食。本研究中植物出叶时正值雨季即将来临，为避开雨季阳光短缺的劣势，多数植物选择在雨季之初展开，而此时气温也达到了植

物出叶的要求(图1)。虽然叶片大量生长时昆虫数量快速增加(图4)，但相对于阳光的限制，此时出叶对植物最为有利，这也是80%以上的植物于4月份出叶的原因。较晚出叶的植物则避开了雨季阳光不足的劣势，且此时林中昆虫数量下降，植物叶片的虫食率并不高，与早出叶植物相比并无劣势，但其优势仍让人费解。乔木和灌木出叶的平均时间并无显著差异，表明不同生活型的植物其出叶限制因子相同，也可能与本研究所选择植物同为生长于林下的植株有关。

3.2 展叶速度和展叶期与虫食

展叶期是虫食发生的主要时期，亚热带热带植物近60%的叶片损失发生在这一时期(见第四章)。硬度被认为是叶片抵御昆虫取食的有效方式(Lowman and Box, 1983; Coley, 1983; Juniper and Southwood, 1986; Kursar and Coley, 2003)。由于展叶期幼叶营养含量高且无法利用硬度防御虫食，为更早的利用硬度防御虫食，提高展叶速度缩短幼叶期是许多植物的选择(Hay *et al*., 1988, Moles and Westoby, 2000; Kursar and Coley, 2003)。提高展叶速度意味着植物将在短时间内投入大量的营养物质以支持叶肉细胞的快速分裂和生长，而高营养的幼叶是吸引昆虫取食的重要因素，这使植物在遭受虫食时面临损失更多能量的风险，因此植物可能在是否提高展叶速度方面存在权衡(Kursar and Coley, 1991)。正因植物在提高展叶速度与资源投入方面存在权衡，所以关于展叶期及展叶速度是否对虫食有影响的研究结果有不同(Hay, *et al*., 1988; Aide and Londoño, 1989; Aide, 1993; Kursar and Coley, 2003)。

尽管前人的研究结果有所不同，但本研究发现植物的展叶速度同虫食率显著正相关(图2)，即展叶速度越快的植物其叶片虫食率越高，而展叶速度越慢的植物其虫食率越低。展叶速度受温度的影响(Van Volkenburgh, 1999)，展叶越晚气温越高则植物展叶速度越快。温度也是影响昆虫发育的重要因素，随温度的升高，昆虫的数量增加，此时展叶的植物所面临的虫食压力越大，而且展叶较快的植物叶片营养含量高(Kursar and Coley, 2003)，也是吸引昆虫的重要因素。出叶较早的植物因为此时温度低，虽然不利于叶片的扩展，但低温同样限制了昆虫的发育导致昆虫数量较少，同时展叶慢的植物通常投入较多的化学物质进行防御（Kursar and Coley, 2003），这也是展叶慢的植物虫食率低的可能原因。

3.3 出叶同步性与虫食

同步出叶让昆虫饱食被认为是植物降低虫食的有效对策(Aide, 1988; Mckey, 1989; Clark and Clark, 1991; Aide, 1993; Murali and Sukumar, 1993; Coley and Barone, 1996)。在热带和温带的研究中均发现这种对策的存在(Aide, 1993; Coley and Barone, 1996; Feeny, 1976)，无论在植物群落的整体水平上还是在单个植物的水平上均为如此。但以往研究均为出叶高峰期与非高峰期的对比，对出叶高峰期植物出叶同步性的关注则没有引起重视。

本次研究发现同步出叶与虫食间关系并不显著，表明虫食不是植物同步出叶的关键选择因素。植物群落中的昆虫可以分为广食性和狭食性，如果植物叶片的大部分虫食为广食性昆虫所为，则植物会倾向于在群落水平上同步出叶，就如本次研究所发现82%的植物集中在4月间出叶，这可能是广食性昆虫为多数的群落的选择。出叶高峰期之外出叶的植物，如上杭锥、深山含笑、少叶黄杞、交让木、毛冬青、绒毛润楠和杨梅可能是寡食性昆虫选择的结果，因为同其他植物同步出叶并没有特别的生态优势，而出叶较晚则可能由于气温高而加快展叶缩短幼叶期以减少虫食。尤其是深山含笑、交让木、毛冬青和杨梅四种植物的出叶同步性均较高。虽然出叶同步性同虫食率没有直接相关，但出叶同步性与虫食频度正相关，即出叶同步性越高的植物被昆虫取食的几率越大，也说明这种同步性部分来自于虫食的压力。尽管虫食率与出叶同步性相关性并不显著，但本研究发现出叶同步性高的植物平均虫食率高于出叶同步性低的植物，说明这种较高的同步性部分来自于虫食的压力。

总之，亚热带常绿阔叶林中的昆虫取食与植物的出叶时间和出叶同步性没有显著关系，而同叶片展叶速度相关，并且昆虫与植物叶片的生长保持较高的同步性。

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第八章 植物叶片发育及其与虫食的关系

摘要：植物叶片特性是影响虫食的重要因素，为揭示亚热带常绿阔叶林植物叶片发育过程中叶片特性与虫食的关系，测定了亚热带地区 41 种常绿植物幼叶期叶片的叶绿素含量、叶片含水量、比叶重、叶片硬度及幼叶期间的叶片虫食率和虫食频度，分析了叶片发育对虫食的影响，结果发现：1）叶绿素含量与比叶重极显著负相关($p<0.001$)，同叶片硬度显著负相关($p=0.012$)，比叶重同叶片硬度极显著正相关($p<0.001$)；2）植物叶片虫食率与叶片含水量显著正相关($p=0.034$)，而同叶绿素含量、比叶重和叶片硬度没有显著相关性；3）77%的植物发育中的叶片虫食与含水量正相关，而且 5 种植物 (两广石栎、苦槠、木荷、甜槠和连蕊茶)达显著水平；73%的植物发育中的叶片虫食与比叶重负相关，3 种植物(两广石栎、苦槠和木荷)达显著水平。68%的植物发育中的叶片虫食与叶片硬度负相关，4 种植物(两广石栎、米槠、青冈和木荷)达显著水平，但建润楠发育中的叶片与叶片硬度显著正相关。叶绿素含量对发育中叶片虫食的影响不明确。4）叶片硬度对所有植物成熟叶片的虫食均没有显著影响；比叶重与成熟叶片的虫食负相关，但只有马银花和连蕊茶达显著水平；叶片含水量与成熟叶片的虫食率正相关，但只有格药柃和细齿柃达显著水平；叶绿素含量与成熟叶片的虫食率负相关，且青冈、木荷和连蕊茶达到显著水平。5）虫食率与虫食频度极显著正相关($p=0.004$)，虫食频度反映了虫食率的大小。以上结果表明，叶片特性不仅影响植物间虫食的差异，还影响了植物发育中叶片的虫食动态，而且对成熟叶片依然具有较大影响，其中叶片含水量是影响虫食的重要因素，而叶绿素含量、比叶重和叶片硬度对叶片虫食的影响在植物种间具有很大差异。

关键词：常绿阔叶林, 幼叶, 叶绿素, 含水量, 比叶重, 叶片硬度, 虫食

前言

植物叶片虫食与叶片发育密切相关(Loman and Box, 1983; Coley and Barone, 1996)，由于不同植物叶片发育期间其叶片理化特性有较大差异，即使同种植物的叶片特性也存在时间动态，这有季节变化的原因(Feeny, 1970; Mattson, 1980;

Schultz, *et al.*, 1982; Bryant, *et al.*, 1983; Rossiter, *et al.*, 1988; Mauffettee and Oechel, 1989)，也有昆虫与植物相互影响带来的结果(Baldwin and Schultz, 1983; Haukioja and Neuvonen, 1985; Schultz, 1988; Mauffettee and Oechel, 1989; Haukioja, 1990)。不同植物种的叶片硬度更具有很大差异(Lowman and Box, 1983)，也导致了植物叶片虫食的种间差异(Gaku Kudo, 2003)。

同种植物其生境的改变将会引起叶片特性的变化，这种叶片特性的改变可能影响昆虫的取食行为(Schultz, et al., 1982; Rossiter, *et al.*, 1988; Hemming and Lindroth, 1995)。目前有关叶片特性对虫食影响的研究多在单一植物种上进行，且证明叶绿素含量、叶片的硬度、含水量、比叶重以及次生物质等叶片特性影响了昆虫的取食行为，生长发育以及繁殖能力(Lowman and Box, 1983; Basset, 1991; Coley and Barone, 1996; Natalia, *et al.*, 2003; Gaku Kudo, 2003; Kursar and Coley, 2003)。群落中植物与昆虫种类繁多，关系复杂，前人关于植物叶片特性与虫食的研究多在热带地区进行，对亚热带地区的植物叶片特性、叶片特性之间的关系及其与叶片虫食关系的研究还未见报道。

中国常绿阔叶林分布最广、面积最大，类型最为复杂多样，是全球常绿阔叶林的主体(宋永昌, 2005)，对常绿阔叶林植物的叶片特性和虫食特征的研究，将有助于揭示亚热带常绿阔叶林植物与昆虫相互作用的机制。浙江天童和福建梅花山的植被均保护良好，植物种类复杂多样，分别代表了中亚热带中部和中亚热带南缘的植被特征，故本项研究在两地进行。

本文有两个目的：1)植物叶片特性的种间差异及其关系；2)植物叶片特性与叶片虫食的关系。

1 材料与方法

1.1 研究地点和植物

本研究分别于2005和2006年在浙江天童国家森林公园和福建梅花山中国虎园内和进行。研究地区详细资料参见第二章。

本研究分别选择了浙江天童4科10种常见植物(5种为乔木，5种为灌木种)和梅花山常绿阔叶林中12科31种常见植物(14种为乔木种，17种为灌木种)为研究对象。为避免生境条件对植物及昆虫的影响，所选植物均为林下生长的1~2m

高的植株。

1.2 叶片的标记和采样

幼叶从叶芽萌动开始标记，为了不破坏幼嫩的叶片，用有色塑料线标记芽附近的老叶，利用叶芽上叶片的节位确定叶片的个数和位置。每种植物标记 6~15 株幼树，每株于阳面随机选择 3 根枝条，每根枝条选择 10 片叶左右。做硬度、含水量和叶绿素测定的叶片样本来自被标记植株，统一采取阳面枝条叶片。采样从幼叶面积达到成熟叶片 20~30%大小时开始。为防止幼叶失水，将采集的样本放置在冰袋中，及时带回实验室进行测定，每三天测定一次至叶片完全展开后 18 天左右叶片基本脱离幼叶状态为止。

成熟叶片分别在 7、8、9 和 10 月下旬各采样一次，进行叶片特性的测定。

1.3 叶片理化特性测定

本项研究选择了硬度、叶片含水量、比叶重及叶绿素含量来反映叶片特征。

1) 叶片硬度

叶片硬度用自制硬度计(制作方法参照 Feeny, 1970)测定。叶片硬度用将叶片(避免叶脉)打穿的时候缓慢添加到一定叶面积(ø=5mm)上的物重(g)表示。

2) 叶片含水量及比叶重

通过对比鲜叶和干叶(70℃烘箱中烘烤 24 小时)的重量计算得到叶片含水量及比叶重(Leaf mass per area, LMA)。

3) 叶绿素含量

叶绿素含量为叶绿素 a 与叶绿素 b 之和，用 7200 型分光光度计分别在 663nm 和 645nm 处测量叶片丙酮提取液光吸收值后计算得出，具体实验方法和计算方法见朱广廉等(1990)。

1.4 虫食率与虫食频度的测定

展叶期间，每 3 天用带网格的透明塑料片(10 格/cm^2)测量叶片虫食面积(在塑料片上依据叶片剩余部分描绘后测得)和潜在完整叶片面积(剩余面积与虫食面积之和)。虫食率%=100*叶片虫食面积/完整叶片面积；虫食频度%=100*虫食

叶片个数/总叶片数，测量至叶片脱离幼叶状态为止。

展叶完成后的成熟叶片，分别于 7、8、9 和 10 月下旬测量一次叶片新增加的虫食率和虫食频度。

本文所有数据用 SPSS11.3 和 ORIGIN 6.0 分析处理。

表 1　植物叶片特性及虫食

Table 1 Leaf traits and herbivory during leaf expansion

种 Species	生活型 LF	叶绿素(mg/g) C±sd	含水量(%) W±sd	比叶重(mg/cm^2) LMA±sd	硬度(g) T±sd	虫食率(%) H±sd	虫食频度(%) HF±sd
细叶青冈	T	0.73±0.25	59.46±6.84	6.87±2.12	317.09±177.68	1.29±2.02	12.03±48.09
红楠	T	1.28±0.17	73.36±1.87	4.55±1.56	273.98±177.06	1.48±2.46	16.41±18.03
水团花	T	1.91±0.38	73.00±4.45	3.53±0.66	433.71±150.58	3.29±3.13	11.31±10.76
建润楠	T	1.10±0.34	63.28±17.87	3.89±1.49	323.39±153.73	3.70±4.73	61.9±54.77
黄樟	T	0.64±0.15	72.22±4.22	4.90±0.88	227.60±100.98	6.95±9.67	37.41±32.08
甜槠	T	0.87±0.36	61.52±7.41	7.62±2.02	470.96±243.65	7.60±13.56	43.4±36.67
木荷	T	1.25±0.17	69.80±5.82	5.35±1.41	375.97±172.81	7.90±7.6	50.8±32.9
罗浮锥	T	1.00±0.21	68.35±7.14	5.35±1.15	405.60±198.60	7.97±9.28	41.32±40.91
厚皮香	T	0.56±0.11	77.16±5.86	7.71±1.65	510.16±180.45	8.97±12.43	50.00±27.89
栲树	T	1.21±0.08	73.07±4.22	4.33±0.78	267.88±49.59	9.00±9.8	50.11±33.2
上杭锥	T	1.02±0.08	66.96±4.56	6.73±1.23	313.25±199.25	9.70±9.4	49.10±38.8
杨梅	T	1.31±0.13	69.55±4.15	3.68±0.84	207.74±101.43	9.78±11.74	20.96±21.29
乳源木莲	T	1.55±0.35	74.67±11.25	4.37±2.02	345.12±131.57	12.50±12.01	16.66±16.67
猴欢喜	T	0.79±0.15	71.75±4.67	4.28±1.07	226.22±104.75	12.81±16.35	36.66±23.09
单耳柃	S	0.48±0.15	67.46±5.40	6.41±0.86	507.12±231.30	1.06±2.49	14.29±24.61
黄瑞木	S	0.94±0.21	74.76±4.59	5.36±1.20	417.88±162.87	2.36±2.21	32.34±25.87
辣汁树	S	0.85±0.14	65.97±9.30	4.92±1.69	242.90±134.97	3.37±7.52	16.98±24.22
鹿角杜鹃	S	0.48±0.08	73.12±6.67	6.98±2.72	437.29±195.04	4.56±7.47	20.37±24.05
油茶	S	0.55±0.09	70.36±4.16	8.02±1.86	485.11±235.15	6.51±7.09	38.93±40.48
山矾	S	0.37±0.12	78.72±5.38	3.56±1.11	406.90±127.20	6.67±7.64	20.00±20
赤楠	S	0.62±0.10	65.54±2.88	6.46±0.84	255.93±95.69	6.95±19.41	11.46±28.81
格药柃	S	0.72±0.18	72.41±6.22	4.99±1.46	476.00±229.99	7.67±16.18	29.18±38.66
毛冬青	S	2.46±0.53	73.27±3.03	2.55±0.34	177.60±50.73	7.72±11.65	20.99±20.57
小叶乌饭树	S	0.60±0.11	72.43±8.09	5.05±2.00	265.43±156.52	8.2±12.02	20.44±14.56
黄栀子	S	2.47±2.92	72.54±3.73	3.91±0.49	184.97±35.86	9.74±20	15.56±21.26
乌饭树	S	0.83±0.13	72.31±6.36	5.30±1.75	323.06±132.34	11.43±14.78	31.23±15.72
连蕊茶	S	1.66±0.65	70.66±7.06	3.42±0.93	241.57±43.96	11.59±12.27	60.24±60.44
老鼠矢	S	0.83±0.27	74.68±6.31	6.30±2.07	533.89±166.74	13.8±15.3	52.77±41.11
石斑木	S	0.80±0.18	68.27±3.97	5.78±1.65	219.43±43.26	14.64±18.89	51.67±33.58
石笔木	S	0.69±0.15	77.72±4.21	5.53±1.84	421.92±236.62	21.71±35.69	45.44±33.81
三花冬青	S	0.72±0.10	74.27±5.32	4.18±1.12	275.89±89.29	25.87±31.28	54.80±44.38
平均 mean	--	1.01	70.9	5.22	341.02	--	--

注：植物以虫食率大小排序. Note: Species are ranked by herbivory.

2 结果与分析

2.1 植物叶片理化特性的比较

(1) 植物幼叶的叶绿素含量种间差异较大，叶绿素含量较高的植物有黄栀子(2.47mg/g)、毛冬青(2.46mg/g)、水团花(1.91mg/g)和连蕊茶(1.66mg/g)，含量较低的植物有山矾(0.37mg/g)、单耳柃及鹿角杜鹃(0.48mg/g)和，其他植物的叶绿素含量处于 0.5-1.5mg/g 之间。乔木种植物的叶绿素含量高于灌木种植物的叶绿素含量，但二者差异并不显著(表 2)。

(2) 植物叶片发育期的含水量存在种间差异，叶片含水量较高的植物有山矾(78.72%)、石笔木(77.72%)和厚皮香(77.16%)，叶片含水量最低的植物有细叶青冈(59.46%)，其他植物叶片含水量均高于 60%。灌木种植物叶片的含水量高于乔木种植物，但二者差异并不显著(表 2)。

(3) 植物叶片发育期的比叶重种间差别较大，比叶重范围在 2.55~8.02mg.cm^{-2} 之间，比叶重较高的是油茶(8.02mg/cm^2)、厚皮香(7.71mg/cm^2)和甜槠(7.62mg/cm^2)，比叶重较低的是毛冬青(2.55mg/cm^2)和水团花(3.53mg/cm^2)。乔木种植物的比叶重稍高于灌木种植物的比叶重，二者差异并不显著(表 2)。

(4) 植物叶片发育期的叶片硬度种间差异较大，叶片硬度较小的植物有毛冬青(177.60g)和黄栀子(184.97g)，硬度较大的有老鼠矢(533.89g)、厚皮香(510.16g)和单耳柃(507.12g)，其他植物的叶片硬度均在 200g-500g 之间。乔木种植物的叶片硬度低于灌木种植物的叶片硬度，但二者没有显著差异(表 2)。

表 2 乔木与灌木的叶片特性比较

Table 2 Comparison of leaf traits between trees and shrubs

	乔木 Trees	灌木 Shrubs	t 值	*p*
	平均值 Mean±SD	平均值 Mean±SD		
叶绿素 C (mg/g)	1.09±0.37	0.94±0.63	-0.736	0.467
含水量 WAC (%)	69.58±5.18	72.03±3.69	1.533	0.136
比叶重 LMA (mg/cm^2)	5.23±1.44	5.22±1.41	-0.013	0.989
硬度 T (g)	335.62±93.80	345.46±120.51	0.249	0.805

2.2 植物叶片发育期间叶片理化特性的变化

(1) 植物叶片发育期的叶片特性在展叶前后均发生变化，但叶片特性的变化在植物种间有较大差异(图 7)。一些植物的叶片硬度和比叶重在叶片将要完全展开之前便开始快速增加而含水量则快速下降(如木荷、辣汁树、细齿柃和格药柃)，而有些植物的叶片特性是在展叶完成后才快速变化(如苦槠、米槠、甜槠、连蕊茶和石笔木)，另外一些植物的叶片特性在展叶完成前后并没有快速变化(如马银花、鹿角杜鹃、乌饭、小叶乌饭和黄樟)。叶绿素含量的变化同含水量、比叶重和叶片硬度的变化趋势并不一致，几乎所有植物的叶绿素含量均在叶片完全展开后才缓慢的增加，但幅度并不大(见图 7)。

(2) 成熟叶片的叶片特性也随时间而变化(见图 8)，除苦槠和披针叶山矾的硬度在 7 月下降外，其余植物叶片硬度均继续增加。除苦槠和山矾的叶绿素含量在 7 月达到最高值随后开始下降外，所有植物的比叶重和叶绿素含量均持续增加。所有植物的叶片含水量均持续下降并在 7－8 月间达到最低，但 9－10 月间叶片含水量略有回升(见图 8)。

2.3 叶片特性之间的关系

叶绿素含量同比叶重极显著负相关(表 3, 图 1)，叶片的叶绿素含量越低，比叶重越高。而比叶重同硬度极显著正相关(表 3, 图 2)，即比叶重越高的植物其叶片的硬度越大。因此，叶绿素含量同叶片硬度显著负相关，即叶绿素含量越低，叶片硬度越高(表 3, 图 3)。但也有例外，如水团花，水团花的叶绿素含量较高，但比叶重和硬度也较高，这降低了叶绿素和这两种特性之间的相关系数。

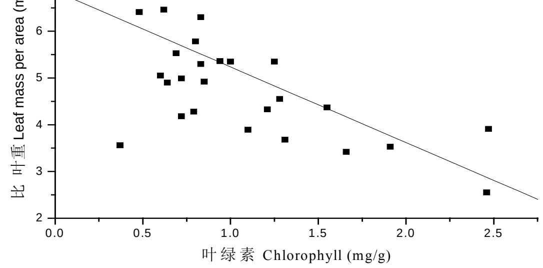


图 1 叶绿素和比叶重的关系, N＝31.

Fig.1 Relationship between chlorophyll and leaf mass per area, N=31.

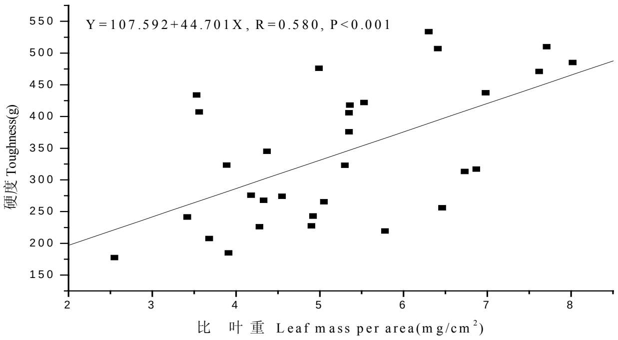


图 2 比叶重与叶片硬度的关系, N=31.

Fig.2 Relationship between leaf mass per area and toughness, N=31.

表3 叶片特性和虫食的相关性分析

Table 3 Pearson Correlations among leaf traits and herbivory in evergreen broad-leaved forest.

	含水量 WAC	比叶重 LMA	硬度 T	虫食率 H	虫食频度 HF
叶绿素C	0.059 ^{ns}	-0.614**	-0.442*	-0.022 ^{ns}	-0.135 ^{ns}
含水量WAC		-0.307 ^{ns}	0.145 ^{ns}	0.381*	0.025 ^{ns}
比叶重LMA			0.580**	-0.129 ^{ns}	0.111 ^{ns}
硬度T				-0.144 ^{ns}	0.114 ^{ns}
虫食率H					0.499**

** Correlation is significant at the 0.01 level.* Correlation is significant at the 0.05 level.

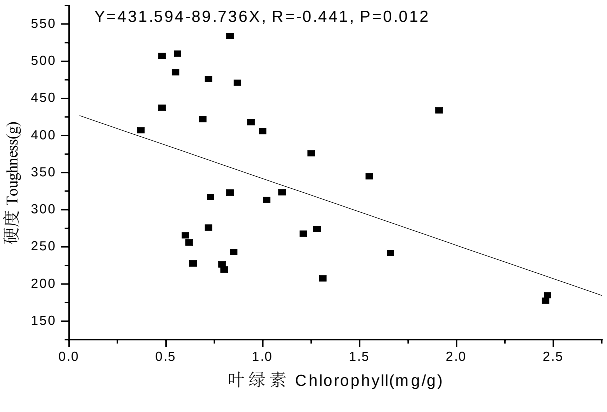


图 3 叶绿素和硬度的关系. 图中的点包括本次调查的乔木与灌木,N=31.

Fig.3 Relationship between chlorophyll and toughness. The regression analyses were conducted for all tree and shrub species.N=31.

2.4 叶片特性对虫食的影响

叶片含水量同植物虫食率显著正相关，即植物叶片含水量越高，植物在幼叶期间的虫食率越高(表 3, 图 4)。虫食率与叶片硬度负相关，但并不显著。植物的虫食率同虫食频度有关，虫食频度越高的植物其虫食率也越高(表 3, 图 5)。虫食率以及虫食频度同比叶重和叶绿素含量并没有显著的相关性(表 3)，表明并非所有叶片特性都是造成植物种间虫食差异的显著因素。

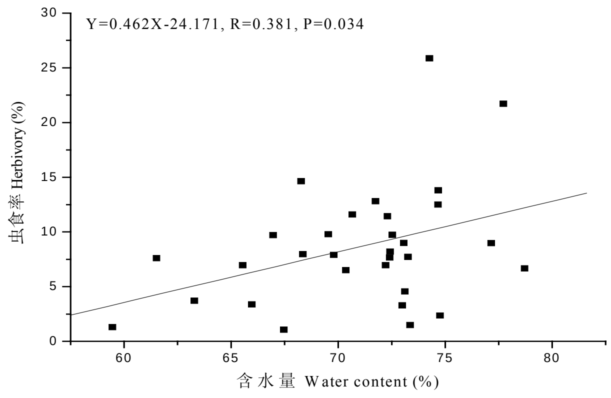


图 4 含水量与虫食率的关系. 图中的点包括本次调查的乔木与灌木, N=31.
Fig.4 Relationship between herbivory and water content. The regression analyses were conducted for all tree and shrub species.N=31.

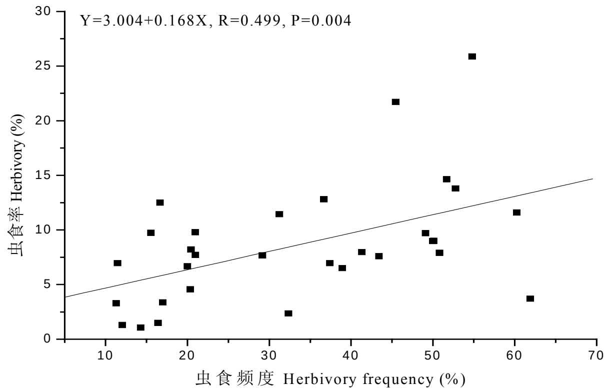


图 5 虫食频度与虫食的关系. 图中的点包括本次调查的乔木与灌木, N=31.
Fig.5 Relationship between herbivory and herbivory frequency. The regression analyses were conducted for all tree and shrub species.

植物叶片发育期间的虫食面积同叶绿素含量的关系在植物种间差异较大(图 6)，22 种植物中，10 种植物日均虫食面积同叶绿素正相关，但只有梅花山地区

的连蕊茶与建润楠相关性显著；其他植物虫食面积同叶绿素负相关，只有青冈达显著水平； 22 种植物中有 17 种植物幼叶的虫食面积同含水量正相关，且两广石栎、甜槠、苦槠、木荷和连蕊茶达到显著水平； 22 种植物中有 16 种植物幼叶虫食面积同比叶重负相关，且两广石栎、苦槠和木荷达到显著水平，但例外的是建润楠虫食面积同比叶重显著正相关； 22 种植物中 15 种植物幼叶日虫食面积同叶片硬度负相关，但只有两广石栎、米槠、青冈和木荷达到显著水平，而建润楠日虫食面积与叶片硬度显著正相关。

成熟叶片的叶片特性继续影响叶片的虫食，其中成熟叶片的虫食率与叶绿素含量均为负相关，且青冈、木荷和连蕊茶达到极显著水平。成熟叶片虫食率同含水量正相关，且格药柃和细齿柃达显著水平。马银花和连蕊茶的成熟叶片虫食面积同比叶重显著负相关。叶片成熟后，叶片硬度对虫食的影响并不确定，且在植物种间存在很大差异(图6)。

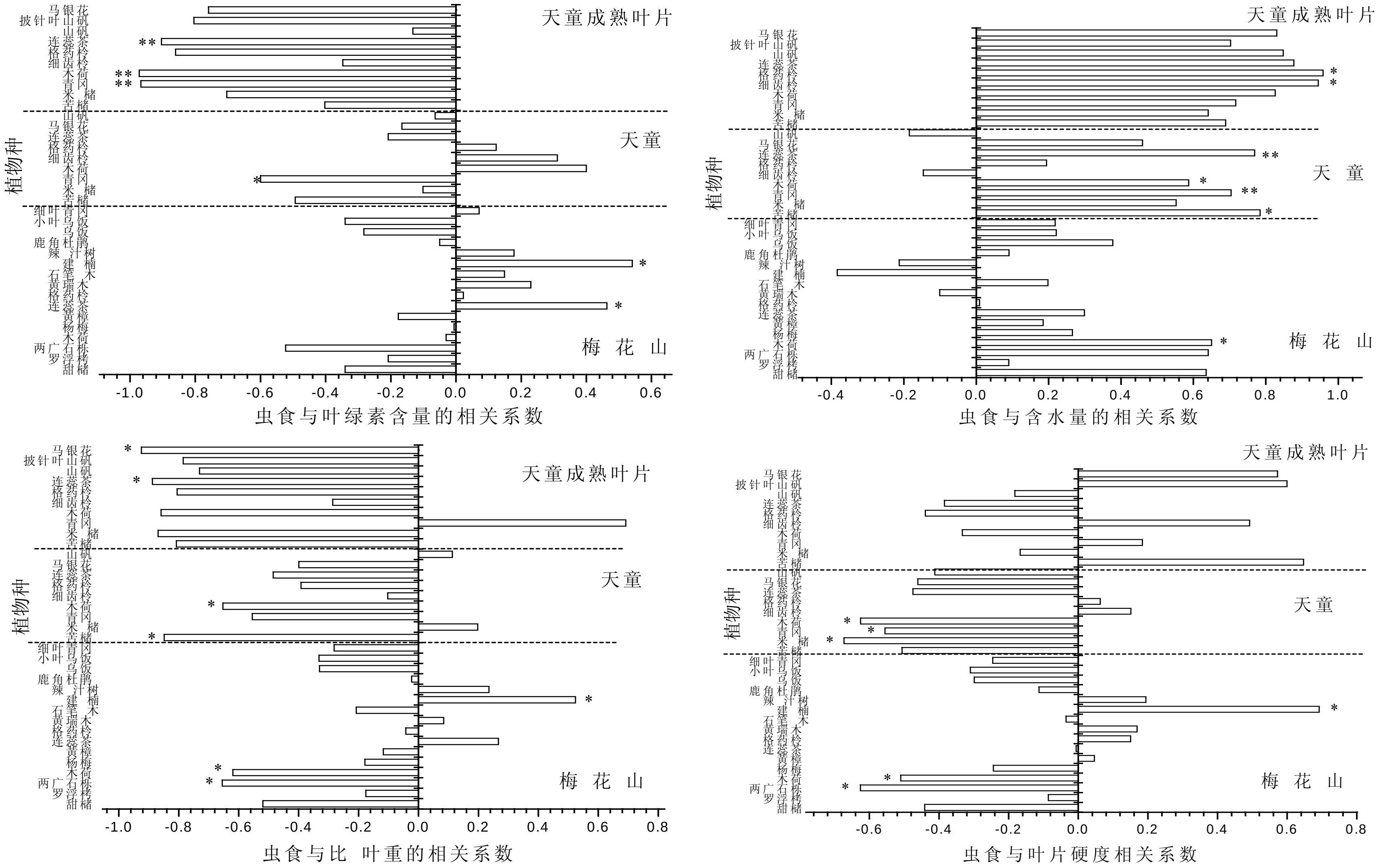


图 6 叶片虫食与叶片特性的相关性.*,**分别表示在 0.05 和 0.01 水平上相关性显著.

Fig.6 Correlation between herbivory and leaf traits. *, ** indicate significant correlation in 0.05 and 0.01 level individually.

3 讨论

3.1 叶绿素与虫食

植物叶片是食叶昆虫的主要食物来源，叶绿素含量、叶片硬度和 N 素含量均对叶片虫食产生影响(Kursar and Coley, 2003)，植物通过调节叶片的资源投入降低叶片损失对植物带来的负面影响(Coley and Barone, 1996)。热带植物通过延缓变绿或叶绿体发育的方法降低幼叶中 N 素和营养含量，以达到减少虫食负面影响的目的(Kursar and Coley, 1991; 1992)，但本地区植物叶片展叶期的叶绿素含量普遍高于延迟变绿的水平(叶绿素<0.5mg/dm^{-2})(蔡志全和曹坤芳, 2002)。因为在一定虫食率下，延迟变绿虽然可以降低负面影响，但代价是在叶发育过程中减少了光合收益，只有在光照强度低和虫食率高的环境下延缓变绿的植物才会有优势，而这种环境在热带的低山雨林中则比较多见(Kursar and Coley, 1991)，因此本地区植物并不依靠延缓叶绿体发育的方式降低虫食影响。本地区植物叶绿素含量的种间差异并不是导致植物叶片虫食率种间差异的原因所在，而且梅花山植物出叶时正值雨季，导致光照不足且虫食率不高，较高的叶绿素含量有利于植物在早春的生长竞争中占优势。虽然建润楠和连蕊茶的虫食同叶绿素含量均显著正相关以及青冈的虫食同叶绿素显著负相关，但这并不能说明叶绿素同虫食具有直接的关系，因为叶绿素含量同叶片其他特性密切相关(表 3)。

叶绿素含量同植物展叶速度负相关(Kursar and Coley, 2003)，叶绿素含量越高，则植物叶片投入细胞分裂促使生长的资源就越低，植物叶片生长就越缓慢，导致叶片的比叶重越低。同时，生长缓慢的植物细胞壁生长较慢，而细胞壁以及纤维素是植物叶片硬化的主要因素。因此，叶绿素含量越高的植物，比叶重和硬度越低。比叶重同植物的出叶时间有关(Sun, *et al.*, 2006)，植物出叶越早，比叶重越高。植物叶片特性之间的关系在许多生态系统及植物种上得到了证明(Reich, *et al.*, 1991, 1992; Reich, 1993; Reich, *et al.*, 1999; Wright *et al.*, 2004)。

3.2 叶片硬度与虫食

展叶期是植物叶片一生中较为脆弱的时期，不同植物的幼叶硬度存在较大差

异(表 1)。硬度高的叶片，由于细胞壁更大程度的硬化而展叶缓慢，幼叶的硬度对食叶昆虫有影响，但对体形较大的植食昆虫影响却很小，因此，硬化防卫有其局限性，幼叶必须依赖其他的防卫方式。Kouki 和 Manetas(2002)认为植物发育期的虫食受叶片硬度的影响很小，起决定作用的是叶片中含有的化学物质，如丹宁和酚类化合物，Lowman 和 Box(1983)也持有相同观点。幼叶期的虫食不仅受到叶片硬度以及化学物质含量的影响还受到 N 素营养含量的影响，叶片硬度越小、N 素含量越高，则虫食率越高，但需要明确的是植物叶片中的化学物质是一个总的含量而不是某种具体的物质影响了虫食(Kursar and Coley, 2003)。本次研究发现，多数植物随叶片硬度的增加，叶片的虫食率下降，叶片硬度是影响虫食的重要因素(图 6, 图 7, 图 8)。乔木种植物更多的依赖叶片硬度来防御昆虫的取食，如青冈、米槠、木荷和两广石栎，乔木叶片生长速度较快(见第七章)，可以快速的利用叶片硬度降低虫食。相反，那些含有刺激性气味的樟科植物，如润楠、辣汁树和黄樟随叶片硬度的增加虫食却逐渐上升，这可能是随叶片的成熟，幼叶中的次生物质含量下降导致。虽然叶片硬度是导致植物叶片虫食下降的重要因素，但并不是所有植物都依赖这种防御方式，而且叶片成熟以后叶片硬度对虫食的影响并不显著(图 6)。

3.3 含水量与虫食

水是昆虫维持生命活动的介质，也是影响昆虫种群数量动态的重要因素。昆虫主要从食物中获得水分，虫体含水量与所取食植物的含水量正相关(牟吉元等, 1996)。本研究发现含水量是影响叶片虫食的重要因素(表 3, 图 4)。多数植物的叶片含水量随叶片的展开而上升，完全展开后含水量下降直至稳定(图 7)，叶片虫食率同叶片含水量显著正相关，含水量高的植物比含水量低的植物更受到昆虫的青睐。以含水量低的叶片为食的昆虫其消化吸收营养物质缓慢且生长缓慢(Scriber, 1977)，延长了幼虫期，并可能因此提高了昆虫的死亡率，因此叶片含水量是影响植物间虫食差异的关键因素之一。不仅叶片含水量高的植物易遭受昆虫取食，而且多数植物的叶片虫食率同含水量正相关(图 6)，即随叶片含水量的下降，虫食面积减少。苦槠、青冈、木荷和连蕊茶叶片虫食面积同叶片含水量显著相关，但其他植物的叶片含水量同虫食面积相关性并不显著。

植物的叶片含水量不仅影响了种间虫食面积的差异，还影响了植物叶片的虫食动态，只是对有些植物显著，而对大部分植物并不显著，这可能和植物所处环境以及生活史对策有关。在热带雨林的雨季，由于水分含量不是植物的限制因素，因此发育期的叶片含水量对昆虫没有显著影响(Basset, 1991)。本研究发现天童的植物比梅花山的植物叶片虫食率受叶片含水量的影响更普遍(图 6)，天童植物出叶时正值旱季末，而梅花山地区植物抽生叶片正值雨季之初，所以这种季节差别可能是天童植物叶片虫食率与含水量相关性更普遍的原因。

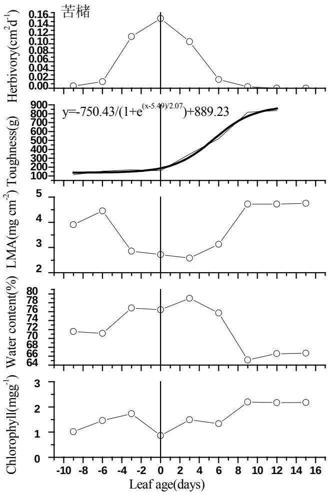
天童植物叶片成熟以后的虫食率与叶片含水量相关性更高，且木荷和细齿柃的叶片含水量对虫食率有显著影响，表明植物叶片含水量对昆虫食叶具有长期影响。

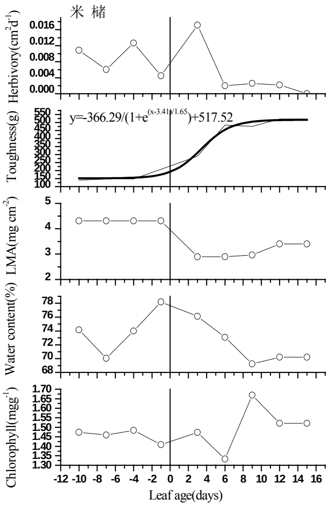
3.4 比叶重与虫食

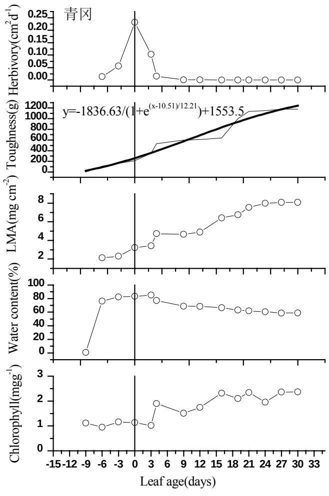
比叶重与多数植物的虫食负相关(图 6)，并且比叶重与叶绿素含量和叶片硬度均极显著正相关(表 3, 图 1, 图 2)。随叶片成熟，叶绿素含量和叶片硬度均增加且比叶重上升，叶片含水量和虫食开始下降，两广石栎、木荷以及苦槠的叶片变化最为显著。然而，建润楠的虫食面积同比叶重显著正相关。相关分析表明比叶重不是叶片虫食种间差异的显著因素(表 3)，比叶重对虫食并不产生直接的影响，而是与比叶重相关的其他叶片特性共同影响了虫食。植物 N 素营养、水分及其他营养物质是昆虫追求的资源，比叶重增加意味着 N 素营养和水分含量的降低，取食营养含量低的食物使昆虫生长缓慢甚至患病(邹钟琳, 1980)，增加死亡几率，因此昆虫较少取食比叶重较高的食物。同时，在漫长的进化过程中，昆虫同植物的物候期趋于一致，比叶重和硬度增加时也是昆虫幼虫阶段结束的时间(钦俊德, 1987; Coley and Barone, 1996)，二者的这种一致也是导致叶片比叶重上升虫食下降的原因。因此，尽管比叶重对虫食有影响，但比叶重并不是影响植物间虫食差异以及植物叶片虫食动态的关键因素。

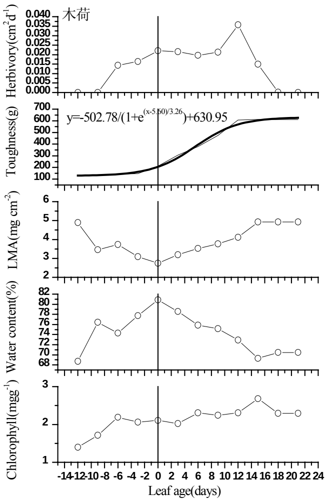
总之，叶片特性对发育期叶片虫食具有影响，但不同植物的生活史策略以及营养分配策略等的差异，叶片特性在植物之间的差别较大，且植物叶片特性的动态变化趋于多样。本研究只是发现叶片含水量同叶片发育期虫食率显著相关，叶绿素含量、比叶重以及叶片硬度对虫食率均有影响，但在不同植物间差异很大。

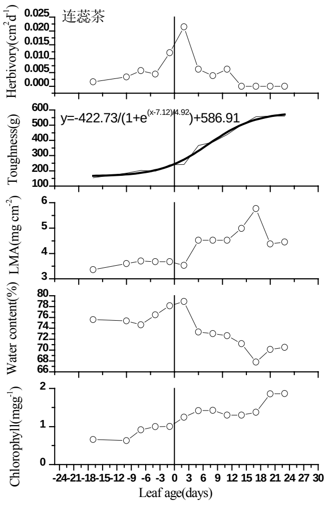
因此，高含水量、低硬度和低比叶重的植物其叶片虫食率较高，而低含水量、高硬度和高比叶重的植物叶片虫食率较低，也意味着快速从高含水量、低硬度和低比叶重的状态过渡到低含水量、高硬度和高比叶重的植物将能更有效的防御昆虫的取食。

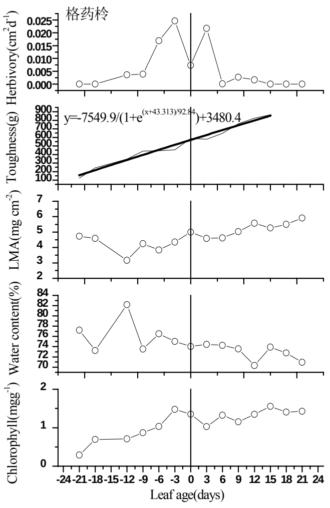

苦槠
Herbivory(cm²d⁻¹)
y=-750.43/(1+e^(x-5.49)/2.07)+889.23
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-10 -8 -6 -4 -2 0 2 4 6 8 10 12 14 16
Leaf age(days)

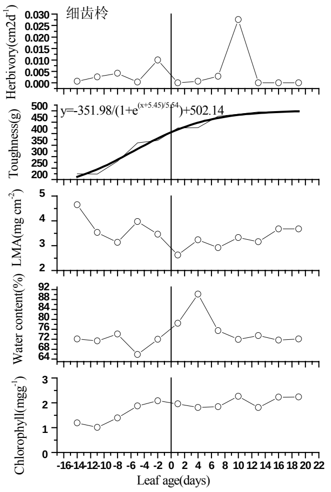

米 槠
Herbivory(cm²d⁻¹)
y=-366.29/(1+e^(x-3.41)/1.65)+517.52
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14 16
Leaf age(days)

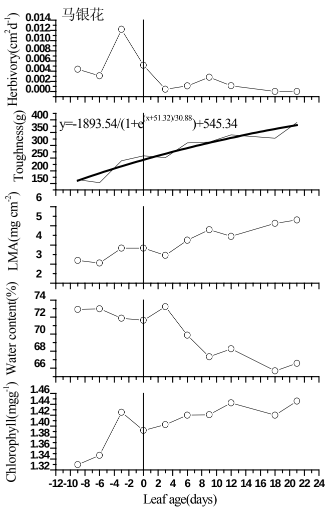

青冈
Herbivory(cm²d⁻¹)
y=-1836.63/(1+e^(x-10.51)/12.21)+1553.5
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-15 -12 -9 -6 -3 0 3 6 9 12 15 18 21 24 27 30 33
Leaf age(days)

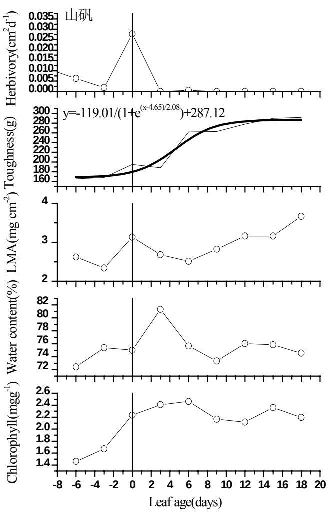

木荷
Herbivory(cm²d⁻¹)
y=-502.78/(1+e^(x-5.60)/3.26)+630.95
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14 16 18 20 22 24
Leaf age(days)

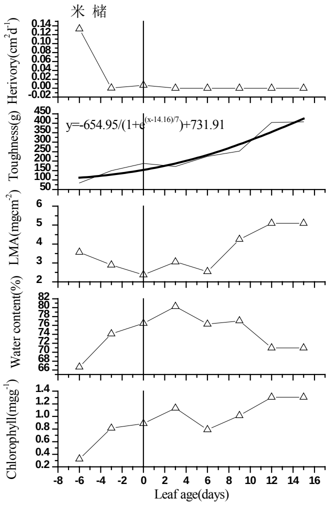

连蕊茶
Herbivory(cm²d⁻¹)
y=-422.73/(1+e^(x-7.12)/4.92)+586.91
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-24 -21 -18 -15 -12 -9 -6 -3 0 3 6 9 12 15 18 21 24 27 30
Leaf age(days)

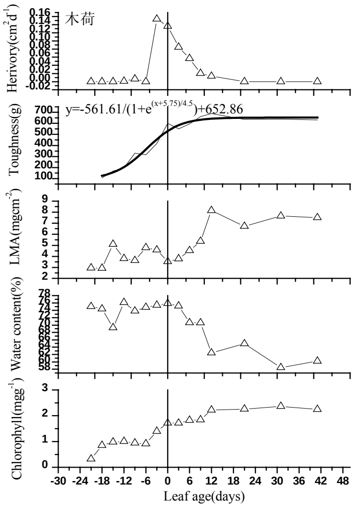

格药柃
Herbivory(cm²d⁻¹)
y=-7549.9/(1+e^(x+43.313)/92.84)+3480.4
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-24 -21 -18 -15 -12 -9 -6 -3 0 3 6 9 12 15 18 21 24
Leaf age(days)

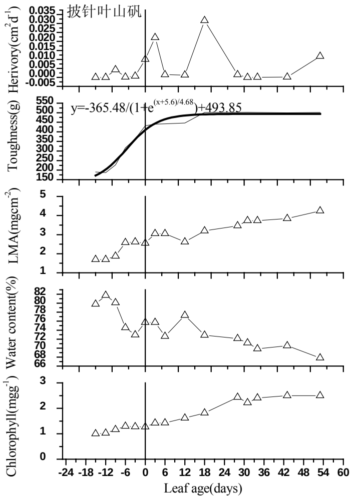

细齿柃
Herbivory(cm2d-1)
y=-351.98/(1+e^(x+5.45)/5.54)+502.14
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-16 -14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14 16 18 20 22
Leaf age(days)

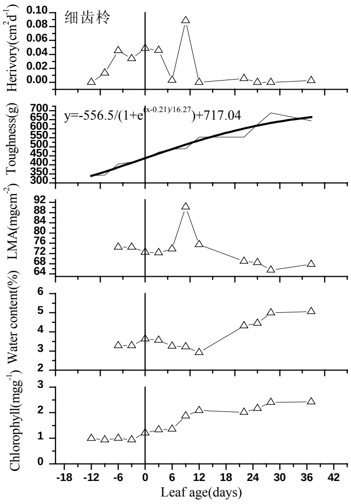

马银花
Herbivory(cm²d⁻¹)
y=-1893.54/(1+e^(x+51.32)/30.88)+545.34
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14 16 18 20 22 24
Leaf age(days)

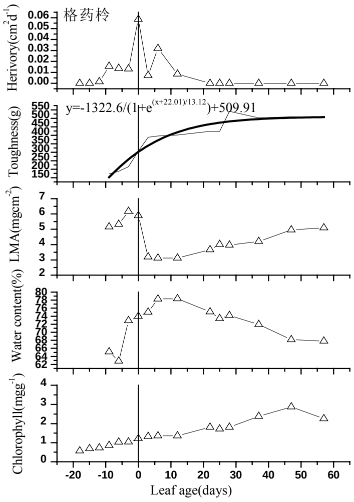

山矾
Herbivory(cm²d⁻¹)
y=-119.01/(1+e^(x-4.65)/2.08)+287.12
Toughness(g)
LMA(mg cm⁻²)
Water content(%)
Chlorophyll(mgg⁻¹)
-8 -6 -4 -2 0 2 4 6 8 10 12 14 16 18 20
Leaf age(days)

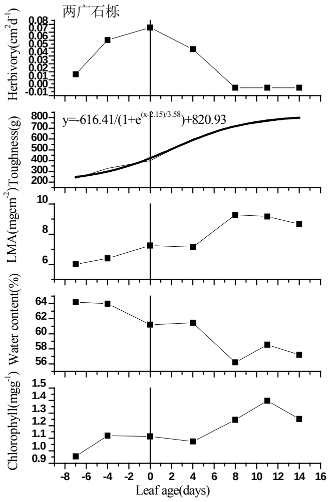

米 槠
Herivory(cm^{2}d^{-1})
Toughness(g)
y=-654.95/(1+e$^{(x-14.16)/7}$)+731.91
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

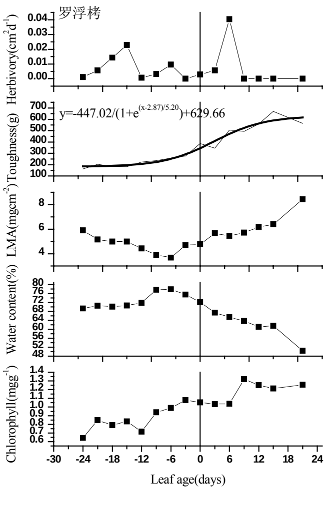

木荷
Herivory(cm^{2}d^{-1})
Toughness(g)
y=-561.61/(1+e$^{(x+5.75)/4.5}$)+652.86
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

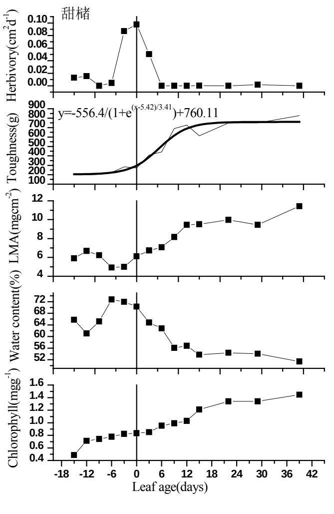

披针叶山矾
Herivory(cm^{2}d^{-1})
Toughness(g)
y=-365.48/(1+e$^{(x+5.6)/4.68}$)+493.85
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

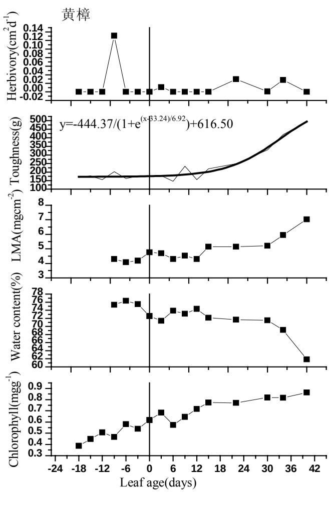

细齿柃
Herivory(cm^{2}d^{-1})
Toughness(g)
y=-556.5/(1+e$^{(x-0.21)/16.27}$)+717.04
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

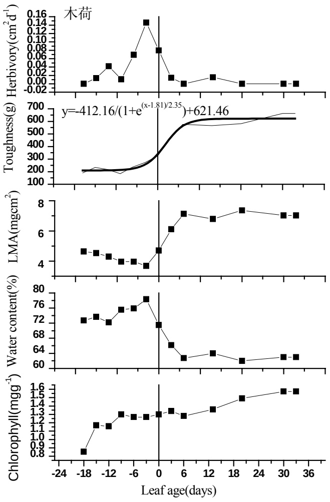

格药柃
Herivory(cm^{2}d^{-1})
Toughness(g)
y=-1322.6/(1+e$^{(x+22.01)/13.12}$)+509.91
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

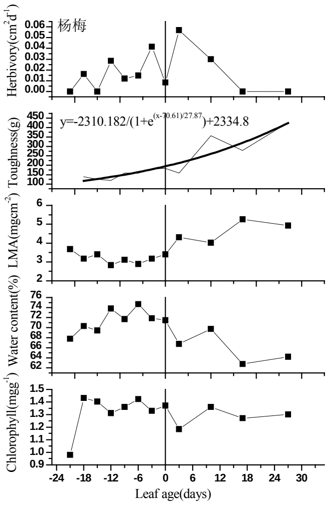

两广石栎
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-616.41/(1+e$^{(x-2.15)/3.58}$)+820.93
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

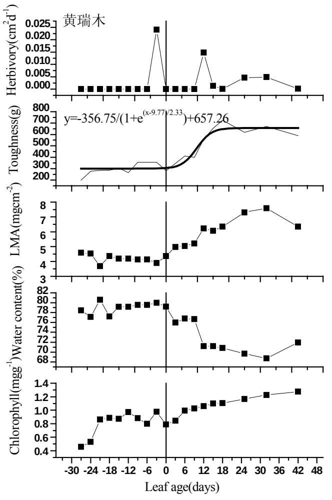

罗浮栲
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-447.02/(1+e$^{(x-2.87)/5.20}$)+629.66
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

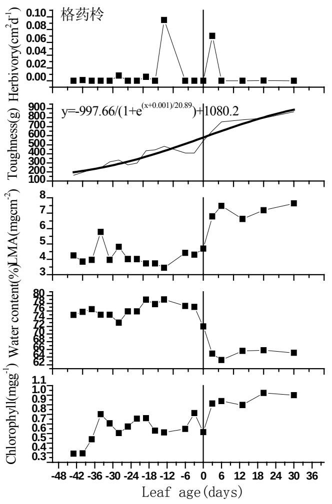

甜槠
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-556.4/(1+e$^{(x-5.42)/3.41}$)+760.11
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

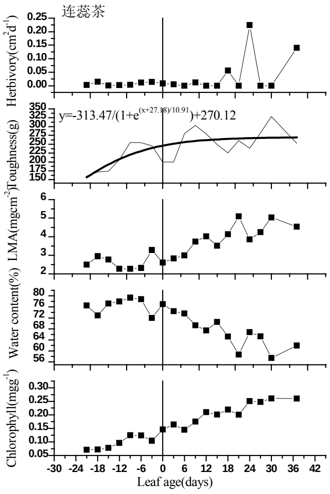

黄樟
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-444.37/(1+e$^{(x-33.24)/6.92}$)+616.50
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

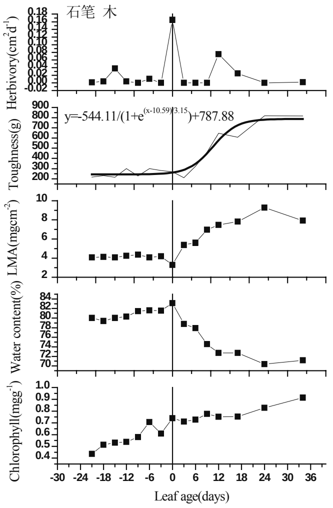

木荷
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-412.16/(1+e$^{(x-1.81)/2.35}$)+621.46
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

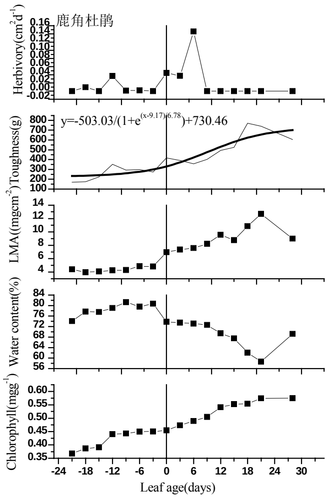

杨梅
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-2310.182/(1+e$^{(x-70.61)/27.87}$)+2334.8
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

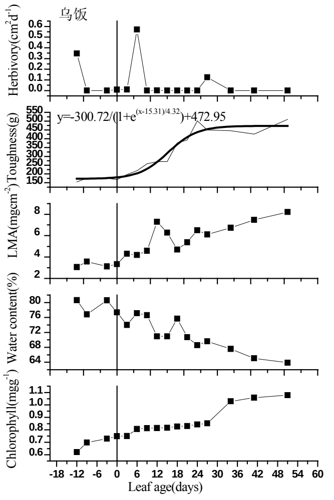

黄瑞木
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-356.75/(1+e$^{(x-9.77)/2.33}$)+657.26
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

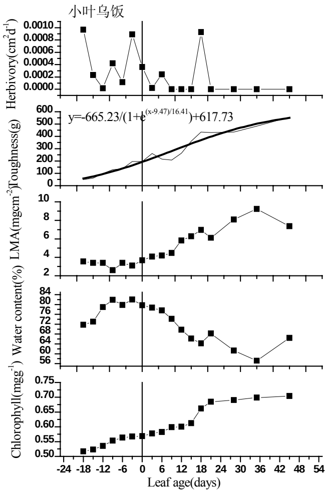

格药柃
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-997.66/(1+e$^{(x+0.001)/20.89}$)+1080.2
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)


连蕊茶
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-313.47/(1+e$^{(x+27.18)/10.91}$)+270.12
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)


石笔 木
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-544.11/(1+e$^{(x-10.59)/3.15}$)+787.88
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)


鹿角杜鹃
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-503.03/(1+e$^{(x-9.17)/6.78}$)+730.46
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)


乌饭
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-300.72/(1+e$^{(x-15.31)/4.32}$)+472.95
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)


小叶乌饭
Herbivory(cm^{2}d^{-1})
Toughness(g)
y=-665.23/(1+e$^{(x-9.47)/16.41}$)+617.73
LMA(mgcm^{-2})
Water content(%)
Chlorophyll(mgg^{-1})
Leaf age(days)

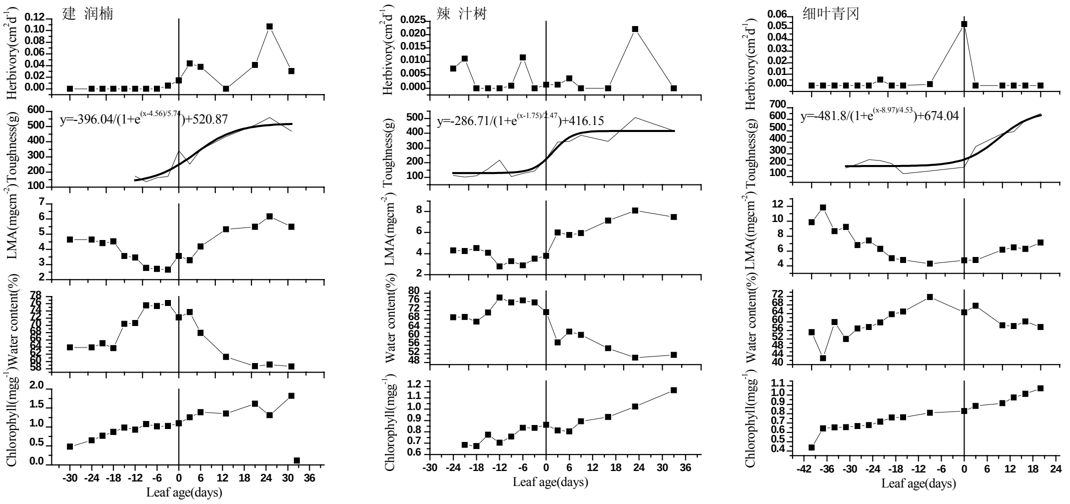
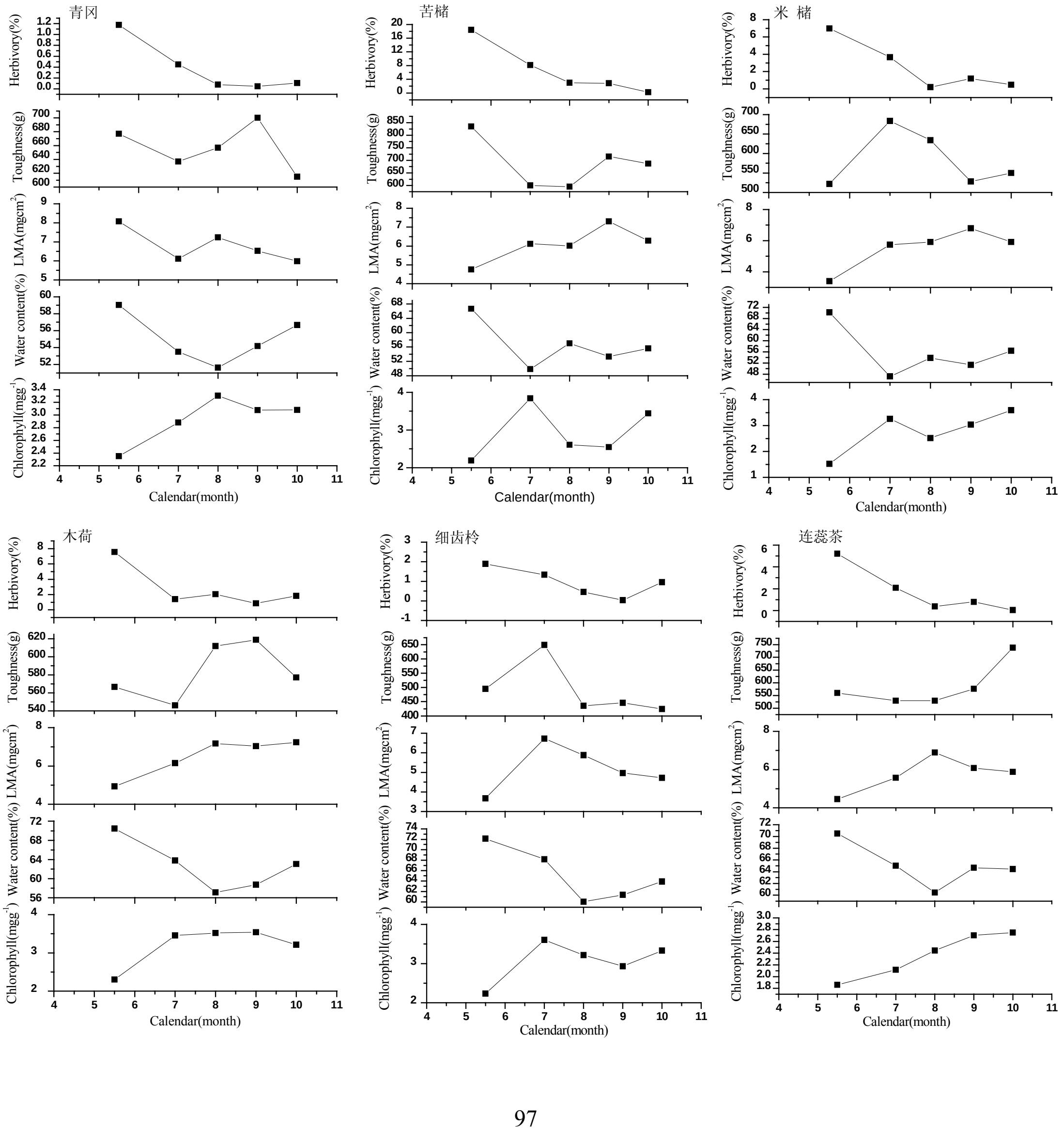


图 7 植物幼叶特性与虫食时间动态.“○”表示浙江天童春季的植物, △表示天童夏/秋季节植物, ■表示福建梅花山春季的植物.

Fig. 7 Dynamics of herbivory and leaf traits of young leaves. ‘○’ indicates plants in spring in Tiantong,; ‘△’ indicates summer/autumn in Tiantong, ‘■’ indicates plans in spring in Mt. MeiHuaShan.



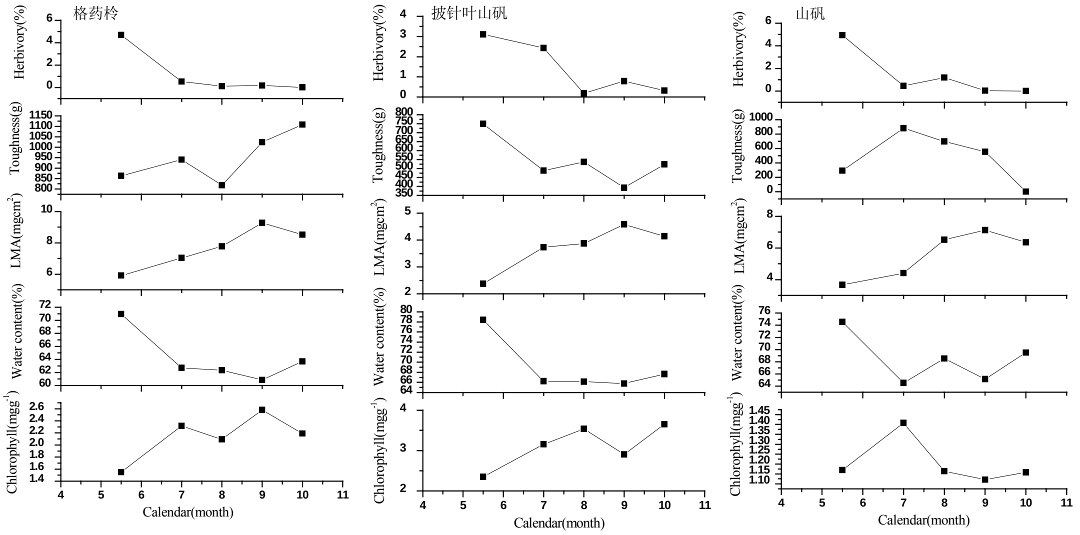


图 8 浙江天童植物叶片虫食和叶片特性的季节动态

Fig. 8 Seasonal dynamics of leaf traits and herbivory on leaves

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总结与讨论

通过对常绿阔叶林植物出叶物候、叶片特性以及叶片虫食时空动态的分析研究，探讨了出叶物候、叶片特性与叶片虫食的关系，揭示了植物出叶物候和叶片特性对叶片虫食的影响，以及植物对虫食采取的对策。经过对以上研究内容的汇总分析，在回答本研究开始时所提出问题的同时，结合本文的目的和目标得到如下结论并进行讨论：

1 关于叶片虫食特征及种间差异

1.1 展叶期叶片虫食特征及种间差异

展叶期是叶片遭受虫食最严重的时期，但展叶期的虫食随叶片的发生和发育处于动态之中，叶片完全展开时的虫食较高。叶片在展叶期的虫食格局可以分为三种：1）虫食在展叶之初的虫食较高，而叶片完全展开后的虫食急剧下降，虫食主要发生在叶片完全展开之前，称之为前食型虫食格局；2）虫食在展叶之初比较低而随着叶片的展开则出现了虫食，虫食主要发生在叶片完全展开之后，称之为后食型虫食格局；3）在叶片展开前后均有虫食发生，只是在叶片完全展开时较高，形成不同于前食型和后食型的中间型虫食格局。

展叶期的三种虫食格局形成原因可能有以下几个方面：(1) 前食型虫食格局的植物叶片含水量高但硬度低，其出叶时间晚但展叶速度快，由于快速展叶的需求此类植物叶片营养含量高，但又局限于资源的配置可能导致化学防御物质投入不够，所以此类植物倾向于快速的生长以逃避昆虫的取食，如壳斗科植物青冈、两广石栎和甜槠以及山茶科植物木荷。但植物逃避昆虫的取食并不仅仅依靠快速的展叶以缩短幼叶期，植物可在昆虫数量较少的旱季末或雨季之初展叶，如连蕊茶、格药柃、单耳柃以及赤楠等小叶片的植物出叶比其他植物早；(2) 后食型虫食格局的植物叶片含水量低但硬度大，生长缓慢，此类植物叶片中营养含量通常较低，但可能化学物质含量高且出叶时间早，此时森林中昆虫数量较少，此类植物以抵抗的方式防御昆虫的取食，如樟科的植物辣汁树、建润楠和黄樟；(3) 中间型虫食格局的植物可能是前两者之间的过渡类型，但目前对此类植物叶片虫食

的对策仍不明确，可能采取既抵抗又逃避的对策，也不排除采取其他对策的可能。

1.2 虫食季节特征及种间差异

常绿阔叶林植物一个生长季节的平均虫食率为 11.87%，但 11 种植物中只有 4 种植物虫食率高于 10%，且 56.9%的虫食发生在展叶期。乔木种植物的虫食率显著高于灌木种植物的虫食率($p=0.050$)。植物叶片在一个生长季中的虫食动态可以分为三类：1）虫食只是在展叶期比较高，而其他时期的虫食均较低，形成单峰型虫食格局；2）虫食除了在展叶期出现一次高峰外，夏末秋初又出现一次小高峰，形成双峰型虫食格局；3）虫食在展叶期、夏季和秋季各出现一次高峰，形成三峰型虫食格局。

三种虫食季节动态的出现不仅与植物物候有关，也与昆虫的种群数量有关。虽然本文没有调查天童的昆虫数量动态，但对梅花山昆虫数量动态的调查表明第一次昆虫取食高峰和昆虫数量较多有关。而其他虫食高峰期可能和植物二次抽生叶片以及昆虫一年繁殖的代数有关，因为昆虫总是在追求幼嫩的植物资源。

1.3 虫食空间变化

木荷林中木荷幼树叶片的虫食率显著高于竹林($p<0.05$)，但林下与林窗中木荷叶片虫食率没有显著差异。木荷林处于该常绿阔叶林的顶级群落，生物多样性高于竹林，从本研究结果看，生物多样性高的植物群落的虫食率高于生物多样性低的植物群落，这可能是由于顶级群落支持的昆虫数量和种类更多的缘故。而对于同一植物群落，光照环境对叶片虫食率没有显著影响，说明昆虫习性不因光照环境而改变，也可能和天童木荷林中鸟类数量较少有关。

由于昆虫与其宿主的协同进化，二者关系复杂，但又能达到协调统一，多数受损叶片其虫食率低于 10%表明昆虫对叶片仅为适量取食，而叶面积大量损失的情况较少发生。为何昆虫不对植物叶片个体过量取食呢？是植物叶片的原因还是昆虫取食习性所致？其中机制还有待进一步研究。

梅花山植物展叶期叶片虫食高于浙江天童，梅花山在地理位置上纬度更低，昆虫与植物的作用更为强烈，排除两地气候因素的影响，随纬度的降低叶片虫食有增加的趋势。目前还没有相同纬度不同海拔的植物叶片的虫食数据，这将在以

后的工作中进行。

1.4 植物叶片虫食状类型及种间差异

虽然在天童 11 种植物叶片上共发现了 16 种虫食状类型，但植物叶片上的虫食状类型存在种间差异，且虫食状多样性在植物种间差异也较大。缘食状在植物叶片上最为常见，虫瘿在植物叶片上则不常见。叶片虫食状在植物上的分布格局可分为 3 种类型，即一种虫食状占绝对优势的单优格局，两种虫食状共占优势的双优格局，三种及三种以上虫食状占优势的多优格局。

虫食状是昆虫食叶后在叶片上留下的痕迹，是昆虫食叶过程及结果的记录，可对植物与昆虫的相互作用起指示作用。虽然虫食状多样性与植物－昆虫的相互作用有关，但遗憾的是本文没有涉及虫食状与昆虫的对应关系，需要在以后的研究中进行昆虫饲养方面的工作。

2 关于植物展叶期叶片虫食的影响因素

2.1 叶片的出叶物候对虫食的影响

植物的出叶物候是影响幼叶虫食的重要因素。叶片的展叶速度与幼叶期虫食显著正相关($p<0.05$)，即展叶速度快的植物虫食率高，展叶速度慢的植物虫食率低。出叶时间、展叶期与出叶格局对幼叶期虫食率均没有显著影响。出叶时间与展叶速度显著正相关($p<0.05$)，展叶期与展叶速度极显著负相关($P<0.01$)。

出叶物候对虫食有重要影响，是植物对虫食防御对策物候方面的体现。抵抗(defense)和逃避(escape)是植物常见的两种防御对策(Coley and Barone, 1996, Kursar and Coley, 2003)，逃避还是抵抗是植物面对虫食压力的生活史对策。逃避意味着快速生长和防御减弱从而面临严峻的虫食压力，甚至导致植株的死亡；抵抗意味着生长缓慢，从而在激烈的种间竞争中处于劣势。因此，展叶速度快，展叶期短的植物采取的是逃避的策略，而展叶速度慢，展叶期长的植物采取的是抵抗的策略，对昆虫的取食造成困难。但每一种对策都有其利弊，植物在权衡利弊得失之后作出的选择，将可能是植物的最佳生活史对策。

2.2 展叶期的叶片理化特性对虫食的影响

叶绿素含量、叶片硬度和比叶重对幼叶期植物虫食均有影响，但只有含水量同虫食率显著正相关($p<0.05$)，是幼叶期虫食率种间差异的原因之一，而且含水量对成熟叶片的虫食依然有重要影响。不同植物对叶片虫食动态的影响因素不同，叶片含水量与虫食动态普遍正相关，吸引昆虫取食；而叶片硬度与虫食动态普遍负相关，对昆虫取食造成障碍。叶绿素含量和比叶重对植物叶片的虫食动态影响不显著。

植物对昆虫食叶的影响，最理想的方式是植物叶片快速生长缩短展叶期、降低含水量和含N量，降低叶片的适口性且次生物质含量高以提高抵抗能力。但是植物叶片的快速生长必须有高N含量的支持，以及来自次生物质和叶绿素合成所需的资源，在资源有限的情况下，这显然是不可能达到的。资源限制是植物无法逾越的生理障碍，因为植物对资源投入进行权衡，只有在获利大于投入的情况下才可能选择一种防御方式。植物生理特性之间的联系导致无法简单的从某种植物特性得出植物的防御对策，最常见的是若干种特性的组合，以实现植物在生长和防御之间的权衡，这也是本研究中并不是所有植物虫食都同含水量及硬度有关的原因所在。

3 关于植物对昆虫食叶防御的潜在机制

展叶期是植物叶片最脆弱的时期，也是昆虫大量取食的时期，因此植物展叶期的防御尤为重要。尽管植物的防御存在种间差异，而且植物的防御在不同时期可能会发生变化，但本研究认为常绿阔叶林植物对昆虫食叶主要有以下三种防御对策(见表1)。

显然，采取抵抗对策的植物其叶片损失低于采取逃避对策的植物，但为何植物不都采用抵抗的方式降低昆虫的取食呢？这可能和资源的分配有关。虫食会显著降低植物的适合度，所以减少资源损失应该是植物的首选，但植物在生长、繁殖和抵抗方面的资源投入是有限的，以快速生长逃避虫食的方式可能是抵抗失败时的选择。快速生长逃避昆虫取食的植物叶片寿命均较短，显然投入过多的资源在寿命短的叶片上对植物不利，而对于叶寿命长的植物则有利于资源的保存。由于昆虫与植物的协同进化，昆虫在进化中逐渐适应了植物的化学防御，使化学防御失去作用，植物迫于虫食压力选择了逃避对策。所以，植物与昆虫的攻防关系

总是处于变化之中，一种植物不可能应用所有对策防御虫食，而只能应用部分防御对策。因此，本文认为采取逃避对策的植物有：格药柃、鹿角杜鹃、两广石栎、甜槠、上杭锥、苦槠、米槠、细叶青冈、山矾等植物，其中多数植物属于壳斗科植物和山茶科植物，此类植物在群落中占有优势地位，其特征见表 1。而采取抵抗对策的植物有建润楠、辣汁树和黄瑞木等植物，这类植物在群落常为伴生物种，其特征见表 1。但多数植物应对虫食的对策并不明确或者二种对策兼有，根据现有的研究结果，亚热带常绿阔叶林植物采取逃避对策的较多，而采取抵抗的植物较少，这反映了亚热带地区昆虫与植物关系的特点。

如果植物对昆虫食叶首先采取的是保存资源的抵抗对策，那么随植物群落的演替和昆虫的适应，这种抵抗对策会否失去作用？植物是否转向逃避对策呢？因此，顶级群落中的植物以及优势植物可能采取的是逃避对策，而群落演替前期的植物或伴生种可能采取的是防御对策，希望以后对不同演替阶段植物群落的虫食及应对对策的研究能为此提供答案。

表 1 不同防御对策植物的叶片理化特性和出叶物候特征

Table 1 Young leaf characteristics of species with different defense strategies.

	抵抗 Defense	逃避 Escape	抵抗/逃避 Defense/escape
虫食率 HR	低	高	中
虫食频度 HF	低	高	中
虫食动态 DH	后食型	前食型	中间型
出叶时间 TLE	早	晚	中
出叶格局 PLE	分散	集中	中
展叶速度 LER	慢	快	中
展叶期 DLE	长	短	中
叶寿命 LL	长	短	中
叶片硬度 LT	高	低	中
含水量 W	低	高	中
比叶重 LMA	高	低	中

HR-Herbivory rate; HF- Herbivory frequency; DH- Dynamics of herbivory; TLE- Timing of leaf emergence; PLE- Patterns of leaf emergence; LER- Leaf expansion rate; DLE- During of leaf expansion; LL- Life longevity; LT- Leaf toughness; W- Water content; C- Chlorophyll content; LMA- Leaf mass per area.

附录 1：本论文所涉及的植物名录

冬青科	Aquifoliaceae
冬青	*Ilex purpurea*
三花冬青	*Ilex triflora*
毛冬青	*Ilex pubescens*
杜鹃花科	Ericaceae
马银花	*Rhododendron ovatum*
鹿角杜鹃	*Rhododendron latoucheae*
乌饭树	*Vaccinium bracteatum Thunb*
小叶乌饭树	*Vaccinium bracteatum*
杜英科	Elaeocarpaceae
杜英	*Elaeocarpus decipidns*
猴欢喜	*Sloanea sinensis*
胡桃科	Juglandaceae
少叶黄杞	*Engelhardtia*
交让木科	Daphniphyllaceae
虎皮楠	*Daphniphyllum oldhamii*
交让木	*Daphniphyllum macropadum*
壳斗科	Fagaceae
苦槠	Castanopsis sclerophylla
米槠	*Castanopsis carlesii*
罗浮锥	*Castanopisis fabric*
上杭锥	*Castanopsis lamontii*
栲树	*Castanopsis fargesii*
甜槠	*Castanopisis eyrei*
两广石栎	*Lithocarpus synbalanus*
石栎	*Lithocarpus glaber*

青冈	*Cyclobalanopsis glauca*
细叶青冈	*Cyclobalanopsis myrsinaefolia*
木兰科	Magnoliaceae
乳源木莲	*Manglietia yuyuanensis*
深山含笑	*Michelia maudiae*
野含笑	Michelia shinneriana
茜草科	Rubhceae
狗骨材	*Tricalysia dubia*
黄栀子	*Gardenia jasminoides*
水团花	*Adina pilulifera*
蔷薇科	Rosaceae
石斑木	*Rhaphiolepis indica*
山茶科	Theaceae
细齿柃	*Eurya nitida*
细枝柃	*Eurya nitida*
单耳柃	*Eurya weissiae*
格药柃	*Eurya muricala*
大萼两广黄瑞木	*Adinandra glischroloma*
黄瑞木	*Adinandra millettii*
厚皮香	*Tenstriemia gymnanthera*
连蕊茶	*Camellia fraterna*
油茶	*Camellia oleifera*
木荷	*Schima superba*
石笔木	*Tutcheria spectabilis*
山矾科	Symplocaceae
老鼠矢	*Symplocos stellaris*
山矾	*Symplocos sumuntia*
披针叶山矾	*Symplocos ancilimba*
桃金娘科	Myrtaceae
赤楠	*Syzygium buxifolium*

五加科	Araliaceae
树参	*Dendropanax dentigera*a
杨梅科	Myricaceae
杨梅	*Myrica rubra*
樟科	Laturaceae
建润楠	*Machilus oreophila*
绒毛润楠	*Machilus velutina*
浙江润楠	*Machilus chekiangensis*
红楠	*Machilus thunbergii*
黄樟	*Cinnamomum porrectum*
辣汁树	*Cinnamomum tsangii*
金缕梅科	Hamamelidaceae
檵木	*Loropetalum chinense*

附录 2：本论文所涉及的部分植物与昆虫图片

天童林相

梅花山林相

石栎幼叶抽生

黄樟幼叶抽生

连蕊茶鳞翅目昆虫取食

披针叶山矾鞘翅目昆虫取食

苦槠鞘翅目昆虫取食

披针叶山矾鳞翅目昆虫取食

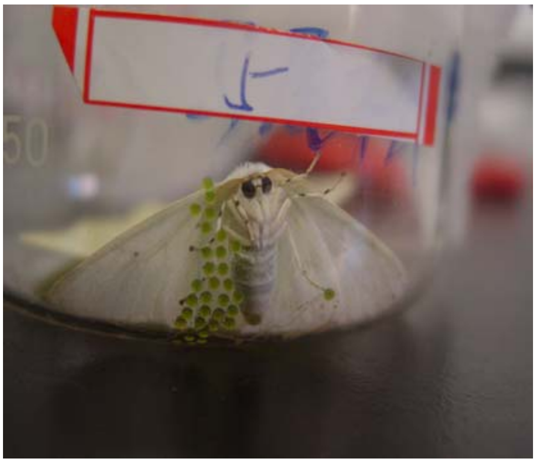
檫木鳞翅目昆虫取食

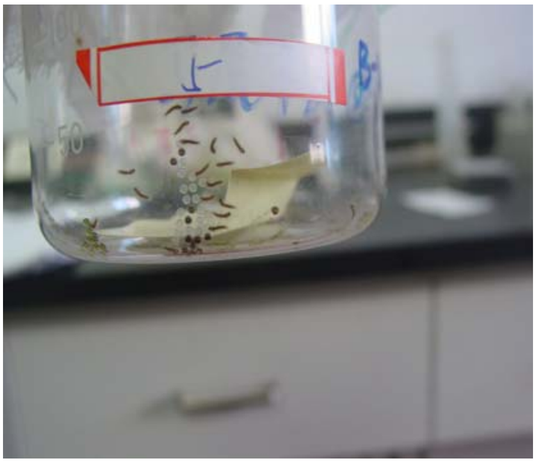
白花野木瓜直翅目昆虫取食

大萼两广黄瑞木鳞翅目昆虫取食


栲树鳞翅目昆虫取食


栲树上半翅目昆虫蝽


饲养的鳞翅目昆虫虫卵和成虫


鳞翅目幼虫的孵出


鳞翅目昆虫的一龄幼虫取食木荷幼叶


鳞翅目高龄幼虫取食木荷叶片

附录 3：相关文章

Leaf Phenology and Herbivory in Juveniles of *Schima superba* (Theaceae) in East-Chinese Evergreen Broad-leaved Forest

Abstract: Leaf phenology can play an important role in plant/herbivore interactions. To research the effect of leaf phenology on plant/herbivore interactions in evergreen broad-leaved forest, dynamics of herbivory on young leaves were measured from March to September of 2005 for Schima superba (Theaceae) juveniles in understory. Levels of herbivory on leaves produced in spring and summer were compared. Phenology, Water content, leaf mass per area (LMA), chlorophyll content and toughness of leaves were determined during leaf expansion of the species in Eastern Chinese subtropical evergreen forests. The results were as follows. (1) Leaves that flushed in spring expanded faster than those did in summer. Water content and chlorophyll content of young spring leaves were higher than those of summer leaves, and LMA of spring leaves was lower than that of summer leaves. But toughness was not significantly different between leaves occurred in two seasons; (2) During leaf expansion, leaves produced in spring suffered lower rates of herbivory than in summer. Herbivory was low in the beginning of leaf expansion, slightly higher with expansion, peaks when leaves reached full size, and dropping rapidly after full expansion; (3) Levels of herbivory were associated with timing of leaf emergence and rate of leaf expansion. Herbivory was strong negatively correlated with leaf toughness and LMA. Positive relationship was found between herbivory and leaf water content, but no correlation was found between herbivory and chlorophyll content. (4) Strategy of escape was used by S. superba juveniles to reduce herbivory in spring by synchronous leaf production and rapid leaf expansion. However, strategy of endurance was used by the species to reduce energy loss in summer by decreasing leaf quality. This indicates that a given species may only invest in a subset of defenses under different conditions in the subtropical evergreen broad-leaved forest.

Keywords: Subtropical evergreen broad-leaved forest, Schima superba, Leaf phenology, Leaf traits, Herbivory

INTRODUCTION

Most plants suffer loss of leaf tissue to herbivores all the time (Cyr and Pace 1993), with most damage being due to insect herbivores (Coley and Barone 1996). This has selected for a wide variety of chemical, mechanical and phenological defenses in plants (Coley and Barone 1996). Many studies suggested that leaf phenology (e.g. timing of leaf emergence and abscission, leaf life span, and leaf expansion duration) evolved to minimize leaf loss in addition to maximizing leaf photosynthetic assimilation (Reich et al. 1999, Kikuzawa 1995, 1996, Ackerly and Reich 1999, Westoby et al. 2002, Wright et al. 2004, Seiwa et al. 2006). In addition to defense, another strategy used by tropical species is an escape by fast expansion and synchrony of leaf production (Kursar and Coley 2003). Previous studies have shown that different species can alter strategies of escape and/or defense to reduce herbivory and a given species only invests in a subset of defenses (Coley and Kursar 1996). However, up to now, it has not been known whether a given species adopts either escape or defense to reduce herbivory.

Many studies have shown that herbivory on leaves is strongly correlated with development of leaves (Aide and Londoño 1989, Coley and Barone 1996, Kursar and Coley 2003). For tropical shade-tolerant species, 68% of the lifetime damage occurs during the small window of leaf expansion when tender young leaves contain high levels of water and nitrogen (Coley 1983, Coley and Aide 1991, Lowman 1992). Indeed the proportion of herbivory on young leaves of young trees was 73% in seasonal rain forest of XiShuangBanNa, China (Zheng et al. 2001). This it is in marked contrast to the temperate zone where only 27% of the lifetime damage accumulates while the leaf is expanding (Coley and Barone 1996). Therefore, herbivory on young leaves of tropical plants is significantly higher than that of temperate plants. Why is there this difference between them? Is there also a difference between herbivory of subtropical plants and tropical plants or temperate plants?

In addition, leaf phenology and leafing type of plants play the important role in mapping the pattern of herbivory (Lowman 1983, 1992, Aide 1991, Coley and Barone 1996). In tropical forests species that produced leaves during the dry season, a period of relatively low insect abundance, suffered less damage than leaves produced during the wet season. Leaves produced during synchronous flushing received less damage than those produced out of synchrony (Aide 1993). Similar effects of leaf phenology and leafing pattern on herbivory were demonstrated in temperate forests (Sun 2003, Sun et al. 2006). Thus, leaf phenology and leafing types can play an important role in reducing herbivore damage either by the seasonality or the synchrony of leaf production. However, there are very few studies examining such a effect of leaf phenology and leafing type on herbivory in subtropical evergreen broad-leaved forest at present.

Here we report results on herbivory and strategies for young leaves of *S. superba* in two seasons in a subtropical evergreen broad-leaved forest that is distinctly different in many features such as species composition, community structure and leaf phenology from tropical or temperate forests (Li 2000). Therefore relationships between leaf phenology or leaf traits and herbivory character in the zone may differ with those of tropical or temperate forests. At our study site, most species produce leaves twice a year; in spring (March) and summer (August). Moreover, timing and the type of leaf emergence are different between the two seasons. In this study, three major questions concerning herbivory were addressed 1) What are the differences in the development of leaves produced in early spring versus late summer? 2) Is the dynamics of herbivory during leaf expansion different between the two seasons? (3) Does herbivory vary with leaf traits during leaf expansion?

METERIAL AND METHODS

Study site and species

The study was conducted in 2005 in TianTong National Forest Park (29º48•N, 121º47•E) of ZheJiang Province, East China, a field site administered by the Ecological Station of East China Normal University. The forest is a subtropical evergreen broad-leaved forest at 300 m above sea level and receives 1374.7 mm of rainfall per year, most of which occurs in June and September. The mean annual temperature is about 16.2°C, with extremes of monthly means being 4.1°C in the coldest January and

28.1°C in the warmest July (Wang et al. 2006). Descriptions of the vegetation can be found in Song (1995).

Of the 271 evergreen species in the Park, *Schima superba* (Theaceae) dominates the forest in terms of individuals and biomass and its leaves are produced twice annually in spring (April) and in late summer (August). This means that young leaves of *S. superba* will open two distinctly different "phenological windows" (Marquis 1991, Marquis and Braker 1994, Coley and Kursar 1996) to herbivores at different times of the year. Thus, *S. superba* may be one of the best materials for studying the interaction between plants and herbivores in a subtropical evergreen broad-leaved forest. Leaves of *S. superba* were damaged mainly by larvae of Geometridae and Lymantriidae in the forest park (private observation), but the dynamics of herbivory and defenses of *S. superba* against herbivores are still unknown. Here we collected data on individual plants between 1-2m tall growing in the shaded understory in spring and summer.

Leaf marking and sampling

Young leaves were marked as they emerged from the bud by placing plastic wire on a mature leaf near the flush at a known number of nodes distal to the target leaf. Sample size of plants and leaves were as follows: spring (14 plants, 249 leaves), summer (10 plants, 105 leaves), and the 10 plants used in summer were different as those used in spring.. For chlorophyll, toughness and water content analysis, young leaves (between 20-100% full size) were placed in bags of ice to prevent desiccation and measured within a few hours of collection.

Leaf traits

Toughness

Leaf toughness was measured by using a device that was constructed according to Feeny (1970). The leaf was clamped between a 2 cm thick and a 1 cm thick wooden board with a 6 mm diameter hole drilled through them that were jointed by two hinges. The number of grams of weight it was necessary place on a 10 cm^2 wooden platform mounted on a 5 mm diameter rod in order to punch its tip through the leaf blade away from major veins gives an index of toughness.

Water content and special leaf weight

Water content and leaf mass per area (LMA) were calculated from the weight of fresh leaves (FW) compared with dried leaves (DW) after 48 hrs in a 70°C oven. Water content = 100*(FW-DW)/FW. LMA was calculated by dividing leaf dry mass by leaf area.

Chlorophyll

Chlorophyll content provides an excellent measure of chloroplast development. Fresh leaves were extracted in 100% acetone, centrifuged for 10 min, adjusted to 80% acetone and absorbance measured at 663 and 645 nm and corrected for light-scattering by 80% acetone. Chlorophyll concentrations were determined using the equation of Zhu et al. (1990).

Leaf expansion

We measured leaf expansion rate, a critical trait that determines how long the window of young leaves is open to herbivores. Leaf area was measured every 3 days from approximately 20% full size to full expansion. Leaves were considered to have ceased to expand when their length and width had remained unchanged for three successive observation days. We calculated the daily percent increase in size during the expansion phase using the following equation (Kursar and Coley 2003):

$$\text{Leaf expansion rate as percent per day} = 100*[e^{(\ln(area2/area1)/time)}-1]$$

Where ‘area1’ and ‘area2’ are leaf areas at two different measurements and ‘time’ is the number of days between measurements. Values of 100% per day indicate that the leaves doubled in size daily.

Herbivory

Actual leaf area and leaf loss areas were measured every 3 days with a plastic grid (10grids/cm2) to determine herbivory rate of leaf area eaten while the leaf was expanding.

Herbivory rate (%) =100*leaf loss area/(actual leaf area + leaf loss area); Herbivory frequency (%) =100*number of damaged leaf/sample size.

Data analysis

One-way ANOVA for independent variables was employed to test the different in leaf traits and herbivory between young leaves in spring and summer. We applied linear regression analysis to determine the relationship between herbivory and leaf traits of young leaves both in spring and summer. Because leaves were not produced synchronously in a cohort, we selected leaves that leafed out earlier from each cohort to determine the curve of leaf area with leaf expansion. The average multiple curve was applied to present the dynamics of the species leaf area during leaf expansion. All data were analyzed with software of ORIGIN 6.0.

RESULTS

Leaf phenology

S. superba produced leaves twice respectively in early spring and late summer in a year. Leaves that flushed synchronously in early April needed 18 days to reach full size after bud break (Table 1, Fig.1A).

Table 1 Phenology of leaves produced in spring and summer respectively.

	Bud break	Full expansion	Expansion (days) ±SD	LER (%/d) ±SD
Spring	11–15 Apr.	28 –30 Apr.	18±3.2	24.12±6.64
Summer	6–16 Aug.	1–12 Sep.	27±1.96	15.69±4.70

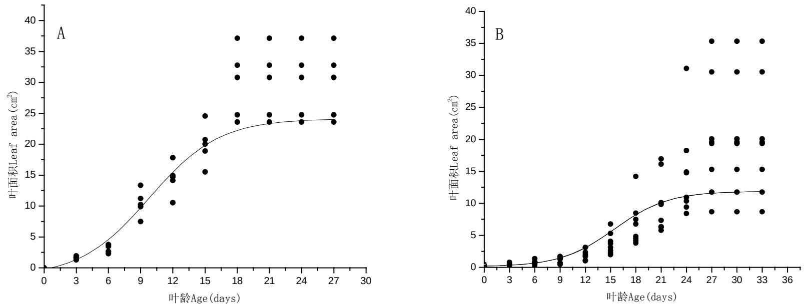
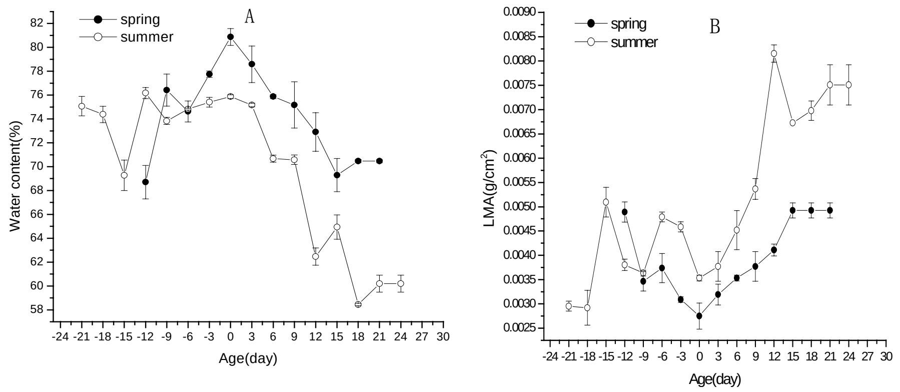


Fig.1 Curves of leaf growth that produced in spring and summer. Age zero is the day at which leaves reach full size. Negative ages are during expansion of young leaves.

Leaves produced in early August required 27 days for full expansion (Table 1, Fig.1B). Mean rate of leaf expansion in spring was 24.12%, significantly higher than the 15.96% in summer (F = 9.921, df=1, 12, p = 0.005).

Although dynamics of leaf development were similar, there were differences in leaf traits between leaves produced in two seasons (Fig.2). For leaves produced in spring, water content increased gradually with leaf expansion and reached a peak when the leaf was fully expanded then dropped rapidly over a few days after full expansion. Leaves produced in summer showed less variation in water content during leaf expansion but it dropped dramatically after the leaf reached full size (Fig.2A). LMA and toughness of leaves flushed in spring showed the opposite dynamics to that of water content (Fig.2B, Fig.2C). Chlorophyll content increased continuously with leaf development (Fig.2D). Chlorophyll content and water content of leaves flushed in spring were significantly higher than of those in summer (Table 2, F =8.419, df=1, 22, p=0.007) but LMA was lower (F=11.829, df=1, 22, p<0.0001). No significant difference was found between toughness of leaves flushed in two seasons (F=2.299, df=1, 24, p=0.143).



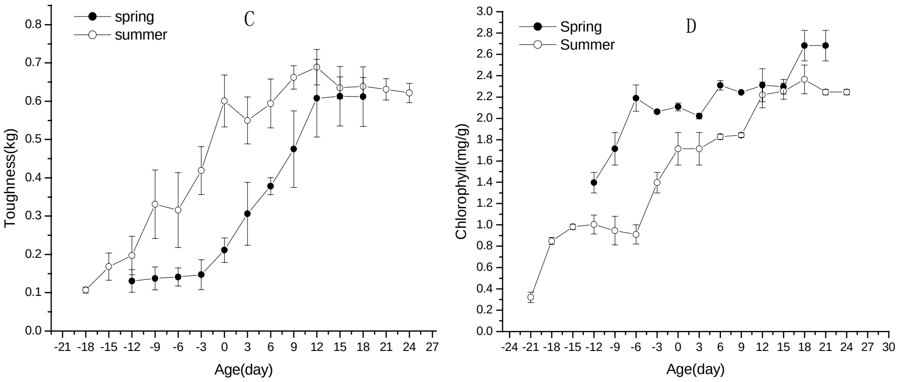


Fig.2 Dynamic of leaf traits during leaf expansion. Leaf traits here include chlorophyll content, water content, toughness and LMA.

Herbivory

For leaves flushed in spring, herbivory (cm^{2}d^{-1}) increased gradually with leaf expansion and reached a peak when leaves were fully expanded then dropped rapidly over a few days (Fig.3, Table 2). Similarly, herbivory (cm^{2}d^{-1}) in summer was greatest when leaves reached full size and dropped dramatically a few days later (Fig.3, Table 2).

Table 2 Comparison of traits of leaves produced in two seasons. ** indicate significant differences between the mean leaf traits of leaves produced in two seasons during leaf expansion.

	Chlorophyll (mg/g)±SD	Water content (%)±SD	Toughness (kg)±SD	LMA (g/cm^2)±SD	Herbivory rate (%)±SD	Herbivory frequency (%)±SD	Herbivory (cm^{2}d^{-1}) ±SD
Spring	2.12±0. 338	74.6±3.9	0.342±0. 205	0.004±0. 001	7.56±10. 0	43.06±32	0.016±0. 012
Summer	1.51±0. 638	70.5±6. 1	0.467±0. 205	0.005±0. 002	18.97±24. 91	80.48±13. 01	0.156±0. 154
P-value	0.007**	<0.0001**	0.143	<0.0001**	0.156	0.012	0.016

Dynamics of herbivory on leaves during leaf expansion was similar in the two seasons though herbivory in summer was more synchronous on the day when the leaf reached full size as compared to spring. Overall herbivory (cm2d-1) was higher in summer than in spring (F=7.339, p=0.016). Thus, herbivory occurred in a short time during leaf expansion and resulted in high damage rate.

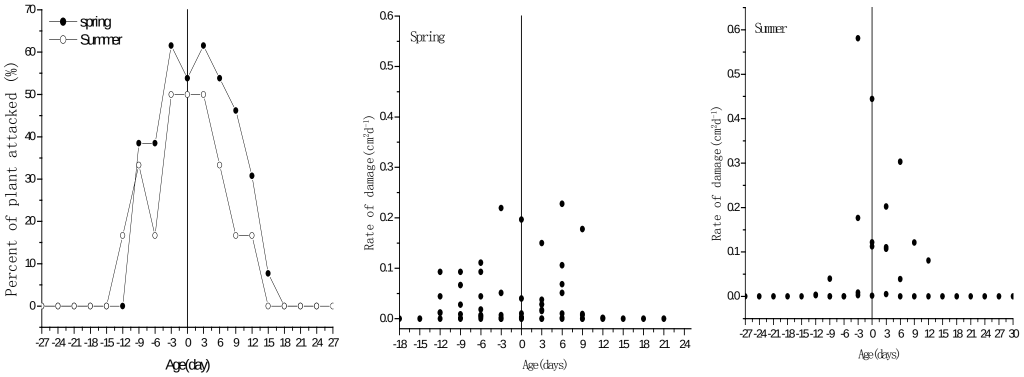


Fig.3 Dynamic of rates of damage to leaves and percent of plant damaged by herbivore during leaf expansion in two seasons.

Relationships between herbivory and leaf phenology and leaf traits

Herbivory was correlated with leaf phenology and leaf expansion rate. For leaves produced in spring, herbivory rate and herbivory frequency were both lower than in summer (Table 2). S. superba produced leaves synchronously in spring and that expanded faster than in summer. Thus, synchronous leaf production and leaf fast expansion may reduce damage from herbivores.

Herbivory (cm^2d^{-1}) was correlated with water content, LMA and toughness of leaves during leaf expansion (Fig.4). Although leaf phenology and leaf expansion rate were both different for leaves produced in the two seasons, water content decreased rapidly while LMA and leaf toughness increased quickly over a few days after leaves reached full size. In spring herbivory was positively correlated with LMA (r=-0.65, p=0.02, n=12) and leaf toughness (r=-0.63, p=0.03, n=12) and negatively correlated with leaf water content (r=0.59, p=0.04, n=12), whereas no significant correlation was found with and leaf chlorophyll content (r=-0.42, p=0.17, n=12). In summer, in contrast no significant correlations were found between leaf traits and herbivory.

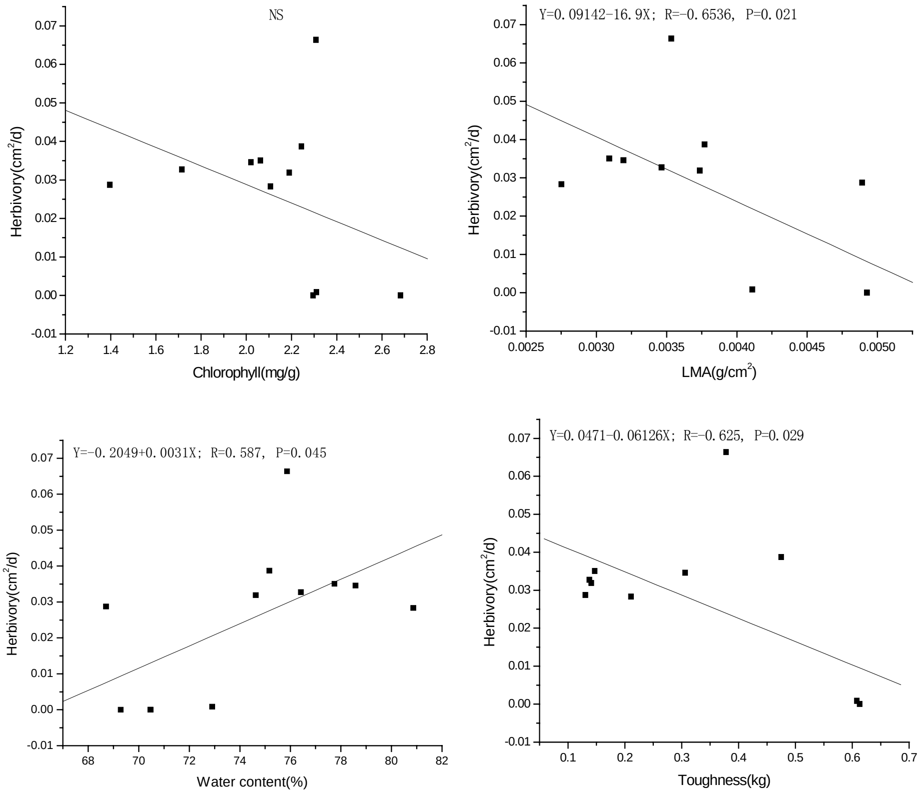


Fig.4 Relationships of herbivory (cm^2d^{-1}) and leaf traits during development of leaves (N=12). The regression analyses were conducted for leaves produced in spring only because no correlations were found between leaf traits and herbivory on leaves produced in summer.

Discussion

In this study, *S. superba* produced leaves twice annually (in spring and in summer), and there were major differences between young leaves produced in the two season. *S. superba* produced leaves synchronously in spring, but continuously in summer (Table 1).Young leaves produced in spring expanded faster than those in summer. Leaf phenology of *S. superba* may be affected by both extrinsic abiotic (i.e. temperature, light, and water; Chabot and Hicks 1982, Wright et al. 2002, Van Volkenburgh 1999) and biotic factors (such as herbivory pressure and plants traits) (Kikuzawa 1983, Aide 1988, Coley and Barone 1996, Sun 2006). In spring, plants often begin to produce leaves with increasing temperature and rainfall. The ephemeral light resource in spring would select for synchronous leaf production and rapid leaf expansion in *S. superba* to take advantage of high light levels before canopy closure. Moreover, synchronous rapid leaf production and expansion may effectively avoid herbivore damage on young leaves because herbivory to young leaves was lowest at the start of the wet season (Lieberman and Lieberman 1984). However, there would be no particular advantage for flushing simultaneously with fast leaf expansion in summer under a closed canopy. Investing energy to fast leaf growth when insect populations are high in summer may be very costly for *S. superba*. Thus, we think leaf phenology of *S. superba* may result from many ecological factors and reflect different life history strategies of the species under different stresses.

Leaf quality changed during leaf expansion in overall similar ways for young leaves produced in spring and in summer, though there were also some significant differences. Chlorophyll content and water content in young spring leaves were higher than those in summer while LMA and toughness of young leaves in spring were lower than those in summer, indicating that young leaves produced in spring had higher quality and photosynthetic capacity than those in summer. High leaf quality may result from higher nutrient allocation to vegetation growth in spring. The primary function of plant leaves is energy gain in addition to photo-sensing (Ackerly 1999, Sun 2006). Therefore, higher chlorophyll content of spring young leaves could be competitive strategy to increase photosynthetic capacity of the species in shaded conditions. More nutrient allocation to reproduction than vegetative growth in summer (Zhou 1999) may result in the low leaf quality of young leaves in summer. In addition, low investment of nitrogen and energy to young leaves in summer can reduce the negative impacts of a given amount of herbivory (Kursar and Coley 1991, 1992), especially when herbivores are abundant. Hence the different leaf traits of young leaves between spring and summer might be strategies of *S. superba* to compete efficiently with others in the forest.

Many studies have shown that the majority of herbivory occurs during the short window when leaves are young and expanding (Marquis 1991, Marquis and Braker 1994, Coley and Barone 1996). In this study, as well as others, young leaves suffered serious damage from herbivores during leaf expansion (Aide 1991, 1993, Coley and Barone 1996). Furthermore, there was no significant difference between herbivory rates on young leaves produced in spring versus summer. The rate of herbivory on young leaves of *S. superba* was higher than mean herbivory rates of trees in temperate forests but lower than that in the tropics during leaf expansion (Coley and Barone 1996). The pattern of herbivory is dynamic during leaf expansion due to nutritional changes in the leaves (Stamp and Casey 1993, Kursar and Coley 2003). We found that rate of herbivory (cm^2d^{-1}) was very dynamic, increasing exponentially during development and then dropping precipitously within a few days as soon as leaves reached full size and become tough (Fig.2, Fig.3). The patterns of herbivory on young leaves of *S. superba* are similar to those of tropical species with poor-defended young leaves (Kursar and Coley 2003). Although the changes of herbivory during leaf expansion were similar in spring and summer, rates of herbivory (cm^2d^{-1}) on summer young leaves were significantly higher than in spring (Table 2), probably because herbivores are more abundant in summer than in spring (Wolda 1988, Coley and Barong 1996).

In addition to phenological defence, leaf traits affect herbivore performance and development (Aide and Londoño, 1989, Coley and Barone1996, Kursar and Coley 2003). Toughness is a particularly effective defence that reduces nutritional value of the leaf and presents mechanical problems for chewing insects (Lowman and Box 1983, Coley 1983, Juniper and Southwood 1986). However, young leaves cannot toughen until leaves have reached full size and cells are no longer expanding. Furthermore, thin primary cell walls and absence of secondary cell walls result in higher nitrogen and water content of young leaves. Herbivory decreased as soon as water content of leaves declined after leaves reached full size (Fig.2B, Fig.3). Thus, both water content and toughness contribute to the dynamic of herbivory during leaf development. Regression analysis showed that herbivory on young leaves was significantly positively correlated with water content but negatively correlated with LMA and leaf toughness in spring, consistent with our suggestions mentioned above. It means that leaf traits are key factors to influence herbivory patterns during leaf expansion. However, no significant relationships were found between herbivory and young leaf traits in summer.

The differences of young leaves in leaf phenology and leaf traits reflected the variation of leaf quality in spring and in summer because rapidly expanding leaves often have more nitrogen than slow expanding ones (Kursar and Coley 2003), indicating young leaves in summer are lower in nutritional quality than those in spring.

High leaf quality enhances the attractiveness of young leaves to herbivores. Hence, synchrony leaf production and fast leaf expansion may be strategies promoting escape from herbivores used by *S. superba* in spring. However, lower quality leaves produced in summer indicate that plants invest less nitrogen to leaf growth. Moreover, secondary metabolites not investigated here may contribute to the low leaf quality in summer. This phenomenon is a feature that lowers the nutrition and energy content of young leaves in summer, thereby reducing the negative impacts of a given amount of herbivory, an idea analogous to delayed greening as a way to decreasing energy losses (Kursar and Coley 1991, 1992). Thus, reducing nutrition investment may be strategy of endurance for *S. superba* to minimize energy loss in disadvantageous conditions.

In general, the young leaves of *S. superba* can escape herbivory effectively by synchronous leaf production and rapid leaf expansion in spring. Endurance was employed by young leaves of the species to decrease energy loss in summer (Table 3). Herbivory on young leaves was affected by leaf phenology and leaf traits such as toughness, water content and LMA. The alternation of strategies of young leaves may result from evolutionary and ecological interactions between plants and herbivores in subtropical evergreen broad-leaved forest. In the subtropical evergreen broad-leaved forest, many other species as well as *S. superba* produce leaves twice annually. Do they employ the same life history strategies to avoid herbivory? Clearly this issue needs a great deal more attention.

Table 3 Young leaf characteristics for leaves in two seasons with ‘escape’ and ‘endurance’ strategies

	Spring	Summer
Herbivory	Low	High
Toughness	Low	High
Leaf expansion rate	High	Low
Chlorophyll content	High	Low
Water content	High	Low
Synchrony of leaf production	High	Low

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Herbivory in Relation to Leaf Development in Juveniles of *Schima superba* (Theaceae) in Evergreen Broad-leaved Forest of Mt. MeiHuaShan

Abstract: Leaf traits can play important role in plant/herbivore interaction. To explore the effects of leaf traits on herbivory and dynamics of herbivory during leaf expansion, leaf production, leaf expansion rate, chlorophyll content, water content, leaf toughness and leaf mass per area (LMA) were measured. Rates of herbivory on young leaves were determined on juveniles of *Schima superba* in subtropical evergreen broad-leaved forest, in Mountain MeiHuaShan of eastern China. The results are as follows: (1) Leaves were produced out of synchronously and leaf expansion rate was 14.43%, with 27 days for leaves from bud break to full size. (2) Chlorophyll content and leaf toughness both increased early in expansion and enhanced rapidly over a few days after leaf reached full size. Water content increased smoothly with leaf expansion and reached peak value (78.3%) when leaf reached full size then dropped quickly several days later. (3) Rates of herbivory (cm^2d^{-1}) increased gradually with leaf development and got peak value (0.9 cm^2d^{-1}) when leaf reached full size then dropped rapidly within a few days after leaf fully expansion. Herbivory rate and herbivory frequency were 7.9% and 50.8% during leaf development (4) Rates of herbivory (cm^2d^{-1}) were positively correlated with water content. There were negative correlations between herbiovry and LMA and leaf toughness. However, no correlation was found between herbivory and chlorophyll content. (5) *S. superba* may be a poorly defended species in the forest.

Key words: Subtropical evergreen broad-leaved forest · *Schima superba* · Leaf expansion rate · Water content · Leaf mass per unit area · Leaf toughness · Herbivory

Introduction

For most plants, loss of leaf tissue to herbivores is a constant feature of the environment (Cyr and Pace 1993). Young leaves of shade-tolerant tropical species suffer much higher rates of herbivory than mature leaves (Marquis and Braker 1994; Coley and Barone 1996; Kursar and Coley 2003). For tropical shade-tolerant species, 68% of the lifetime damage occurs during the small window of leaf expansion for high levels of water and nitrogen and low leaf toughness (Coley 1983; Coley and Aide 1991; Lowman 1992), and the proportion of herbivory on young leaves of young trees was 73% in seasonal rain forest of XiShuangBanNa, China (Zheng et al. 2001). But it is in marked contrast to the temperate zone where only 27% of the lifetime damage accumulates while the leaf is expanding (Coley and Barone 1996).

High levels of water and nitrogen and low leaf toughness result in greater herbivore pressure (Coley and Aide 1991). Effective defenses of mature leaves, such as toughness or high fiber content, are not viable if a leaf is still in the expansion stage. Thus, herbivory pressure has led to the evolution of physiological defenses in plants (Coley and Barone 1996). Several researches suggested that herbivory on leaves was strong correlated with leaf traits (such as chlorophyll content, water content, LMA and leaf toughness) (Aide 1991; kursar and Coley 2003; Sun 2006). Leaves can delay chloroplast development to reduce negative impacts of herbivory and toughness is an effective defense for leaves to reduce herbivory in tropical forests (Lowman and Box 1983, Coley 1983, Juniper and Southwood 1986, kursar and Coley 1991; Coley and Barone 1996).

Although herbivory was correlated with leaf traits, temporal patterns of herbivory were dynamic with leaf traits changes and the dynamics was varied among different life history species in the tropics (Kursar and Coley 2003). However, no other data that have followed damage through leaf development and correlated it with leaf traits changes in the leaves. Furthermore, little was known about effects of leaf traits on herbivory during leaf expansion in subtropical evergreen broad-leaved forest.

Evergreen broad-leaved forest is regional vegetation in eastern China (song et al. 2005) and it is different from tropical and temperate forest in climate, community and species (Li 2000), but the relationships between herbivores and plants are not clear yet. In order to explore the interaction of herbivores and plants in evergreen broad-leaved forest, three major questions concerning herbivory were addressed: (1) What are dynamics of leaf traits during leaf expansion? (2) What are the levels of herbivory and its dynamics during leaf expansion? (3) What are the relationships between herbivory and dynamics of leaf traits?

METERIAL AND METHODS

Study site and species

The study were conducted in 2006 in southern China tiger Park (N25º25′, E116º50′) of Mt. MeiHuaShan of Fujian province, a field site in natural conservation area of Meihuashan, China. The forest is subtropical evergreen broad-leaved forest which altitude is 1200m above sea level. The mean annual precipitation is about 1700～2200mm, approximately 70% of which occurs from March to June. The mean annual temperature is 13～18℃, with extremes of monthly means being 7.5～8.3℃ in the coldest January and 22.9～23.8℃ in the warmest July. The soil type in the site is a forest brown soil.

From April to May of 2006, i.e. during leaf emergence and development of the study species, daily average temperature showed a general increasing pattern (Fig. 1), ranging between about 8℃and 22℃. A large fluctuation in temperature was found in the spring (From late March to early May).

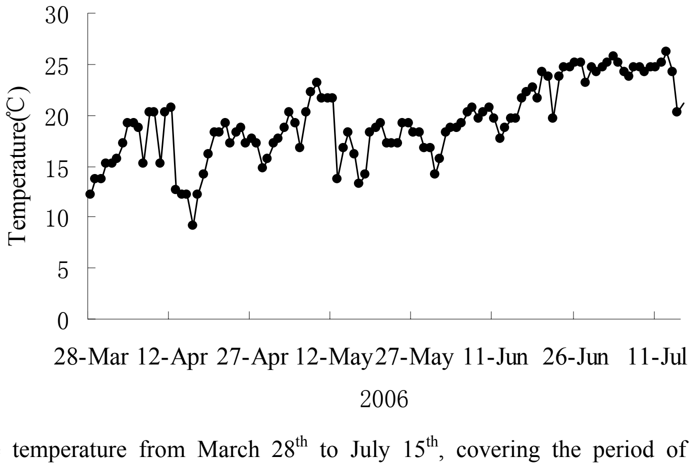

Fig. 1 Daily average temperature from March 28th to July 15th, covering the period of leaf emergence and expansion of the species in the forest in Mt. MeiHuaShan of eastern China.

There are about 1628 plant species in the natural conservation area of MeiHuaShan. *Schima superba* dominates the forest in terms of individuals and biomass. Thus, S. *superba* may be one of the best materials for studying the interaction of plant/herbivore in subtropical evergreen broad-leaved forest. *S. superba* leaves were damaged mainly by the larvae of *Lepidoptera* in the park (private observation). In order to studying the dynamics of herbivory on young leaves, we collected data on juveniles of *S. superba* between 1-2m tall growing in the shaded understory.

Leaf mark and sample

Young leaves were marked as they emerged from the bud. So as not to damage the tender leaf, we placed plastic wire on a mature leaf near the flush, and identified young leaves by the number of nodes distal to the marked leaf. 15 individual plants and 137 leaves totally were selected for long- term observation (from leaf emergence to leaf fully expanded). For chlorophyll, toughness, leaf mass per area (LMA) and water content analysis, young leaves (between 20–100% full size) were placed in ice bags to prevent desiccation and measured within a few hours of collection.

Toughness

Leaf toughness was measured by using a device that was constructed according to Feeny (1970). The leaf was clamped between two wood plates that were jointed by two hinges. Thickness of one plate is 1 cm and another one is 2 cm, each drilled with a 6 mm diameter hole. The number of grams of weight necessary to punch a 5 mm diameter rod with area wood plate (10 cm^2) on its tip through the leaf blades outside major veins gives an index of toughness.

Water content and LMA

Water content and LMA were calculated by the weight of fresh leaves (FW) and dry ones (DW) roasted about 48 hrs in 70 ℃ oven. Water content (%) =100*(FW-DW)/FW; LMA was calculated by dividing leaf dry mass by leaf area.

Chlorophyll

Chlorophyll content provides an excellent measure of chloroplast development. Fresh leaves were extracted in 100% acetone, centrifuged for 10 min, adjusted to 80% acetone and absorbance measured at 663 and 645 nm and corrected for light-scattering by 80% acetone. Chlorophyll concentrations were determined using the equation of Zhu et al. (1990).

Leaf expansion

We measured leaf expansion rate, a critical trait that determines how long the window of young leaves is open to herbivores. Leaves area was measured every 3 days from approximately 20% full size to full expansion. Leaves were considered to have ceased to expand when their length and width had remained unchanged for three successive observation days. We calculated the daily percent increase in size during the expansion phase using the following equation (kursar and Coley 2003):

$$\textit{Leaf expansion rate as percent per day} = 100*[e^{(\ln(area2/area1)/time)}-1]$$

Where ‘area1’ and ‘area2’ are leaf areas at two different measurements and ‘time’ is the number of days between measurements. Values of 100% per day indicate that the leaves doubled in size daily.

Herbivory

Actual leaf area and leaf loss areas were measured every 3 days with a plastic grid (10grids/cm^2) to determine herbivory rate of leaf area eaten while leaf is expanding.

Herbivory rate (%) =100×leaf loss area/(actual leaf area + leaf loss area); Herbivory frequency (%) =100×number of damaged leaf/sample size.

Date analysis

One-way ANOVA for independent variables was employed to test the different in leaf traits and herbivory between young leaves in spring. We applied linear regression analysis to determine the relationship between herbivory and leaf traits of young leaves. Because leaf was not produced synchronously in a cohort, we selected leaves that leafed out earlier from each cohort to determine the curve of leaf area with leaf expansion. The average multiple curve was applied to present the dynamics of the species leaf area during leaf expansion. All data were analyzed with software of ORIGIN 6.0.

Results

Leaf production and development

In study site, *S. superba* produced leaves out of synchrony from early April to early May (Fig. 2). Leaf expansion rate was 14.43%. It took 27days for leaves from bud break to full size (Fig. 3, Table 1).

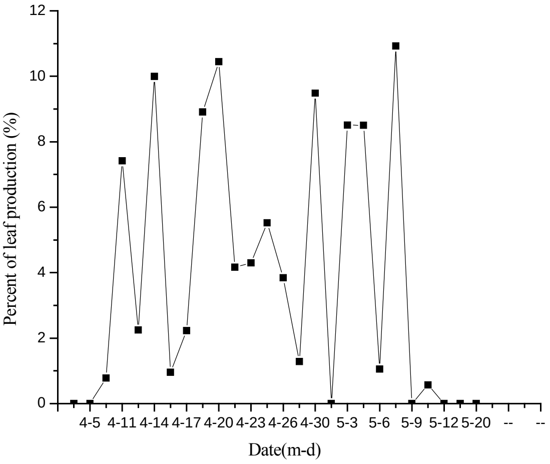

Fig. 2 Pattern of leaf production in spring. Leaf production is the percentage of new leaf production of total leaf production of 26 individuals.

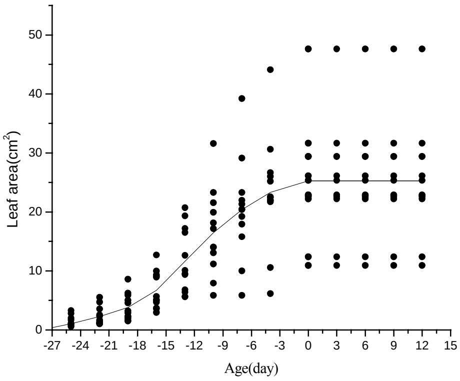

Fig. 3 Dynamic of leaf growth during leaf expansion. The curve is average multiple curve from average growth of leaves.

Table 1 Leaf expansion rate and herbeivory during leaf expansion.

	Mean (%)	SD	CV
Leaf expansion rate (%)	14.4	2.7	18.5
Herbivory rate (%)	7.9	7.6	96.0
Herbivory frequency (%)	50.8	32.9	64.9

Chlorophyll content, leaf toughness and water content all increased gradually while

LMA reduced slowly at the beginning of expansion. Water content reached peak with 78.3% and LMA reached the lowest value with 0.0036g.cm^{-2} when leaf reached full size. Chlorophyll content, toughness and LMA all increased rapidly while water content dropped dramatically over a few days after leaf reached full size (Fig. 4). Leaf toughness was significantly positively correlated with LMA (R=0.893, N=12, p<0.0001), indicating that the high the LMA, the high the leaf toughness was during leaf expansion. And toughness was also correlated significantly with chlorophyll content (R=0.627, N=12, p=0.029).

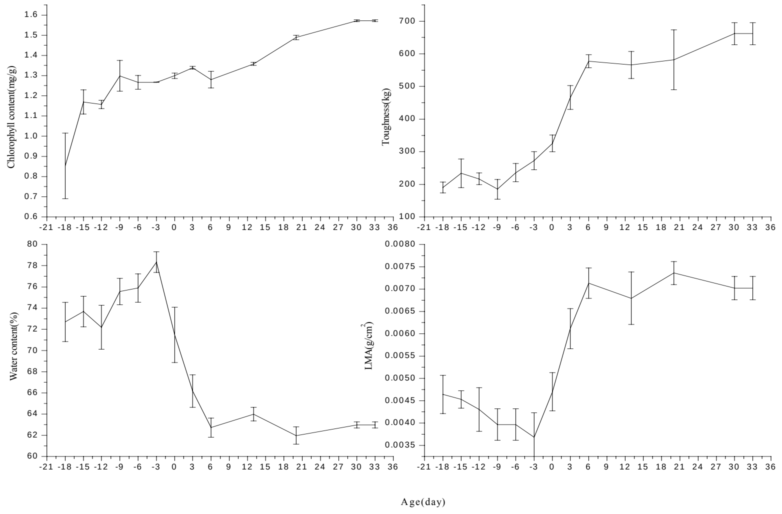

Fig.4 Dynamics of leaf traits during leaf expansion. Leaf traits here include chlorophyll content, leaf toughness, water content and special leaf weight (LMA).

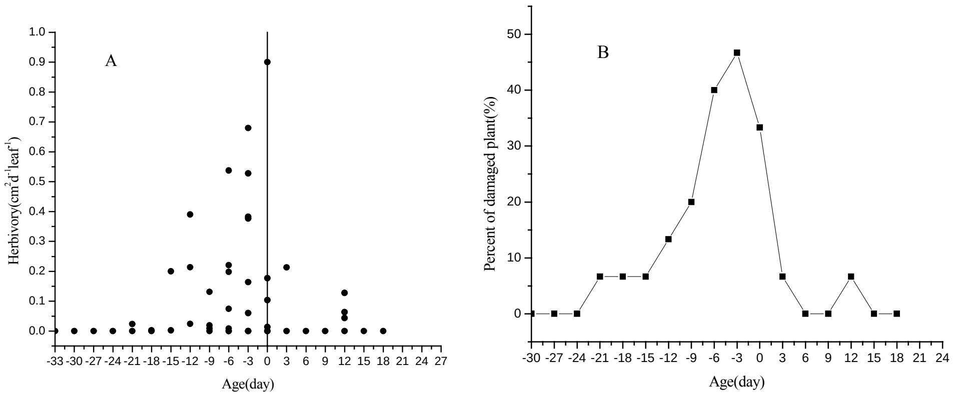

Fig.5 Dynamics of herbivory on leaves (A) and plants (B) during leaf expansion. Percent of damaged plants=100*damaged plants/ all plants sampled.

Herbivory on leaves and plants

Herbivory rate and herbivory frequency were 7.9% and 50.8% respectively when leaf is developing (Table 1).Changes of herbivory (cm^2d^{-1}) were dynamic with development of leaves. Herbivory was very low at the beginning of expansion and increased gradually with leaf expansion then reached peak with 0.9 cm^2d^{-1} when leaf reached full size. However, herbivory dropped dramatically over a few days after leaf reached full size (Fig. 5A). Furthermore, dynamic change of percent of damaged plants was similar to herbivory when leaf is developing (Fig. 5B). Thus, leaf tissue loss to herbivores was concentrated during a short window of leaf expansion.

Relationship between leaf traits and herbivory

Herbivory was positively correlated with water content (Fig. 6, y=66.6+5.86x, r=0.65, *p*=0.016). However, herbivory has negatively correlations both with LMA (y=0.006-0.001x, r=-0.62, *p*=0.023) and toughness (y=535.5-175.9x, r=0.51, *p*=0.03). No relationship was found between herbivory and chlorophyll content (r=-0.03, *p*=0.91). Thus, herbivory was strong correlated with water content, LMA and leaf toughness during leaf expansion.

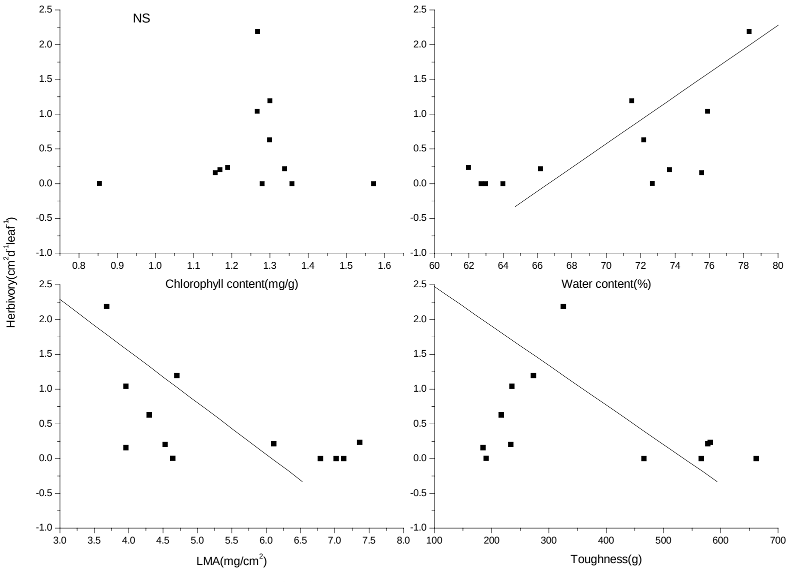

Fig. 6 Relationship between herbivory (cm^2d^{-1}) and leaf traits while leaf are young. Herbivory is positively correlated with water content (y=66.6+5.86x, r=0.65, p=0.016). And hebrivory are negatively correlated with LMA (y=0.006-0.001x, r=-0.62, p=0.023) and leaf toughness (y=535.5-175.9x, r=0.51, p=0.03). There is no correlation between hebrivory and chlorophyll content (r= -0.03, p=0.91). NS indicates no significant correlation.

Discussion

Leaf production may also be an adaptation to avoid herbivory (Coley and Barone 1996). Tree species that were more synchronous were less likely to suffer insect damage to young leaves (Lieberman and Lieberman 1984; Aide 1993), suggesting that leafing synchronously is advantage to reduce herbivory. In this study, *S. superba* produced leaves out of synchrony (Fig. 2) indicates that the species did not use synchrony leaf production as a defense to against herbivores. Leaves of *S. superba* need 27 days to reach full size from bud break, indicating leaf expansion rate of the species is low. Although low leaf expansion rate should increase the period of exposure to herbivores of young leaves, the study suggested that the species were not suffered more insect damage in the forest than plants in tropical (11.5%; Coley and Barone 1996) and Australian subtropical rain forest (11.3%; Lowman 1983).Furthermore, lower leaf expansion rate may result from the low temperature and absence of solar radiation in the forest due to long time spring raining in the site. Likewise, the development of herbivores might be restricted under the conditions. Leaves that are low expanded also indicate plants invest less nutrition to leaf growth. Reducing nutrition investment may decrease the negative impacts of a given amount of herbivory, an idea analogous to delayed greening as a way to decreasing energy losses (Kursar and Coley 1991, 1992).

Many forests have been recorded to be seriously attacked by herbivores during leaf expansion (Pimentel 1988, Coley and Barone 1996). And rate of herbivory is variable in different species. Rate of herbivory on young leaves of *S. superba* is 7.9% that was higher than mean herbivory rates of trees in temperate forest (1.9%), but lower than that in the tropics (11.5%) and Australian subtropical forest (11.3%). Rates of herbivory expressed by cm^2d^{-1} were similar with percent of damaged plant in dynamics of herbivory during leaf expansion. They both reached peak values when leaf is fully expanded (Fig. 5). It means plants and leaves were both most attractive to herbivores when leaf is young. Young leaves have significantly higher water content and lower leaf toughness due to the low cell wall in growing cells and lower leaf toughness. Those leaf traits enhance the attractiveness of young leaves to herbivores.

Toughness is a particularly effective defense that reduces nutritional value of the leaf and presents mechanical problems for chewing insect (Lowman and Box 1983; Coley 1983; Juniper and Southwood 1986). However, young leaves cannot toughen until leaves have reached full size and cells are no longer expanding. The higher the water content, the higher rates of herbivory (cm^2d^{-1}) were. Rates of damage dropped dramatically when water content depressed rapidly after leaf expanded fully. Regression analysis showed that herbivory on young leaves was significantly positively correlated with water content but negatively correlated with LMA and leaf toughness in spring, consistent with our suggestions mentioned above. It means that leaf traits are key factors to influence herbiovry patters during leaf expansion.

The changes in herbivory of poorly defended shade-species are usually very dramatic due to the toughness of mature leaves when leaf reached full size (Kursar and Coley 2003). Thus, the dramatic changes in herbivory on young leaves of S. su*perba* might result from poorly defended young leaves of the species during leaf expansion (Fig. 5). On the other hand, insect herbivores can alter their time according to leaf development in order to improve survivorship (Aide and Londoňo 1989). Herbivory is low at the beginning of expansion due to base instars of larvae. Young leaves were devoured by rapid growing larvae may result in high leaf area losses when leaf reached full size. And larvae that would be advanced reduced herbivory on leaves within a few days as soon as leaf was fully expanded. Thus, dynamic change of herbivory during leaf expansion may result in part from the effect of leaf traits. Undeniably, development of larva should responsible partly to the pattern of herbivory.

In general, the changes in herbivory were significantly correlated with dynamic changes of toughness, water content and LMA during leaf expansion. *S. superba* may be a poorly defended species during leaf expansion in the forest. It is not known whether secondary metabolites are used by juveniles of *S. superba* to defense herbivores in the site. Clearly this issue needs a great deal more attention.

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后记

本文是在蔡永立教授的精心指导下完成的。从研究立项，实验设计与实施、野外踏察选点、一直到论文的完成都凝结着导师的心血。

时光荏苒，转眼间三年过去，想起刚入学时对生态学肤浅的认识倍觉汗颜，面对知识海洋的浩瀚和学科日新月异的发展，感觉自己是那样的渺小和孤单。幸运的是，三年来导师始终以满腔的热情给予了我巨大的关怀和指点，将我引入生态学的广阔空间，不仅教我生态学的思维方法也教我做人的道理，学生将永记铭心。每当困惑之际，是导师指点迷津，每在艰难时刻，是导师深情的鼓励我向前。导师踏实的工作作风、严谨的治学态度、正直的性格、事必躬亲的敬业精神以及平和的心态将使耳濡目染的我终生受益。此刻，我把心中的敬意献给我尊敬的导师！导师对我的情谊将伴我永远......

人无法两次踏入同一条河流，林中也没有两片完全相同的树叶。时光一去不复返，三年的学习丰富了我的人生，沐浴在华师浓厚的学术氛围里，欣喜的享受在野外与蚊虫鸟兽、花草树木为伴的生活，也惊悚与竹叶青四目以对的邂逅，更对与雷电的亲密接触而后怕，但我无怨无悔。这里要特别感谢师弟田玉鹏，无论狂风暴雨还是严寒酷暑，都是师弟与我共同承受，是师弟的陪伴和帮助使我顺利的走到今天。

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感谢所有关心、支持我的老师、朋友和同学，衷心祝愿大家永远幸福安康!!

王宏伟

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