Stand-Level Defoliation Ratio by Herbivorous Insects along Altitudes, between Geological Features, and between Topography on Mt. Kinabalu, Borneo

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Abstract - Stand-level defoliation ratio by herbivorous insects (the ratio of consumed leaf mass to available leaf mass as food for herbivorous insects) was investigated by using litter leaves collected in litter traps to evaluate the variation of herbivory according to environmental conditions. Twelve plots have been set up at four elevations, on three geological substrates, and in two topographical units in Mt. Kinabalu, Borneo. The stand-level defoliation ratio 1) decreased with increasing altitude, 2) was lower at ultrabasic than Tertiary sedimentary sites at each altitude, and 3) was lower at ridge than lower slope sites at each geological substrate. These results indicate that the stand-level defoliation ratio increases with increasing forest productivity.

I. Introduction

Many workers have investigated percentage consumption by herbivorous insects. Defoliation ratio by herbivorous insects (the ratio of consumed leaf mass to available leaf mass as food for herbivores) ranged from 5-15% and 3-20% in tropical forests, respectively [1, 2]. These observations were limited to particular life stages such as seedlings and saplings, selected species, and specific habitats such as understory and gaps [3, 4, 5, 6, 7]. This may be because tropical forests have high species diversity and large tree height and it was very difficult to evaluate herbivory at the forest stand level.

Leaf characteristics are expected to affect the degree of herbivory. They represent the concentration of nutrients and defensive substances. Leaf N concentration generally has positive influences on the growth, fecundity, and survivorship of herbivores [8, 9]; on the other hand, defensive substances negatively influence them [10]. Concentrations of leaf N and defensive substances are associated with environmental conditions of the plant's habitat. For example, leaf N concentration rose with nutrient availability in soil [19]. Carbon-based defensive substances such as total phenolics and condensed tannin in leaves increased under poor soil nutrient conditions [12, 13] and under water deficits [12]. Herbivorous insect's activity itself as well as leaf characteristics as a food resource are important factors that influence the degree of herbivory and the activity depends on environmental conditions, especially air temperature [14]. Thus we expect that the degree of herbivory changes according to the environmental conditions of the habitat.

On Mt. Kinabalu 12 plots have been set up by using gradients of altitude, geological substrate and topography [11, 15, 16]. By using these plots, the herbivory in tropical rain forests can be evaluated systematically according to environmental conditions of the habitat. The objectives of this study are 1) to quantify the stand-level defoliation ratio by herbivorous insects and 2) to describe the pattern of the herbivory in relation to altitude, geological substrate, and topography.

II. Methods

A. Study site

Mt. Kinabalu is located at N6º latitude on Borneo Island, Malaysia and the elevation of the summit is 4095 m above sea level (a.s.l.). Primary forests are preserved very well in the Kinabalu Park. There are 12 plots in the Park according to three gradients [11, 15, 16].

As regards altitude, there are four elevations: 700, 1700, 2700, and 3100 m a.s.l. Average air temperature decreased with increasing altitude at a rate of 0.55˚C per 100 m [17]. Air temperature varied 13.3˚C between the sites with the highest and the lowest altitude (Table I). As regards geological substrate, there are three parent rocks: ultrabasic rock, Tertiary sedimentary rock, and Quaternary sediment. Soils on ultrabasic rock have relatively lower N and P contents and those on Quaternary sediment have relatively higher N and P contents than those on Tertiary sedimentary rock [11, 15]. Ultrabasic and Tertiary sedimentary rocks occur on each of the four elevations (Table I).

Ridge and lower slope topographical units were selected on each of the three geological substrates at the approximately 1700 m a.s.l. elevation [16, Table I]. Soil nutrient content was higher at the lower slope than the ridge site.

TABLE I
Environment and vegetation of the 12 sites on Mount Kinabalu.

Site	Exact altitude (m)	Mean annual temperature (degree C)[a]	Vegetation zone
07T	650	23.9	lowland
07U	700	23.7	lowland
17Q	1860	17.3	lower montane
17T	1560	18.9	lower montane
17U	1860	17.3	lower montane
17Q-R	1860	17.3	lower montane
17T-R	1560	18.9	lower montane
17U-R	1860	17.3	lower montane
27T	2590	13.3	upper montane
27U	2700	12.7	upper montane
31T	3080	10.6	subalpine
31U	3050	10.7	subalpine

These plots and data correspond to [15] and [16].
Q: Quaternary sedimentary rock, T: Tertiary sedimentary rock, U: ultrabasic rock, -R: ridge
[a]: Mean annual temperature estimated from mean lapse rate obtained by [17].

B. *Estimation of herbivory*

Plot size ranged from 0.05 to 1.00 ha according to altitude and topography. There were 10 or 20 litter traps in each plot and they were placed at regular intervals at a height of 1 m above the ground (Table II). The size of the litter trap opening was 0.5 m^2. Trapped litter was collected every two weeks, dried at 70°C for 3 days, and sorted into leaves, reproductive organs, twigs, epiphytes, palms and bamboos, frass from herbivorous insects, and dust. Stand-level defoliation ratio by herbivorous insects was measured by using a subsample of bulk litter (ranging from 20-62%) collected for one year from 15 June 1998 to 31 May 1999 (Table II). All physically broken leaves were excluded from the investigation.

Each litter leaf was weighed using an electronic balance, then it was soaked in water, flattened and digitized using a scanner (CanoScan N1220U, Canon, Tokyo). The shape and area of the damaged and original-form were measured by computer (NIH Image ver. 1.58 software) as follows. Most broad leaves were eaten on the inside and the edge. If the

TABLE II
Description of data used to investigate herbivory. Leaf litter mass was measured from June 1998 to May 1999 at the 12 sites. Symbols for the site names are described in Table I.

Site	Area (ha)	Number of litter traps	Sub-sampled fraction[a]
07T	1.00	20	0.20
07U	1.00	20	0.23
17Q	1.00	20	0.20
17T	0.50	20	0.21
17U	0.20	10	0.44
17Q-R	0.05	10	0.62
17T-R	0.05	10	0.61
17U-R	0.05	10	0.60
27T	0.25	10	0.22
27U	0.20	10	0.21
31T	0.20	10	0.22
31U	0.06	10	0.41

[a]: The ratio of used litter leaf mass for investigation to collected litter leaf mass within a plot.

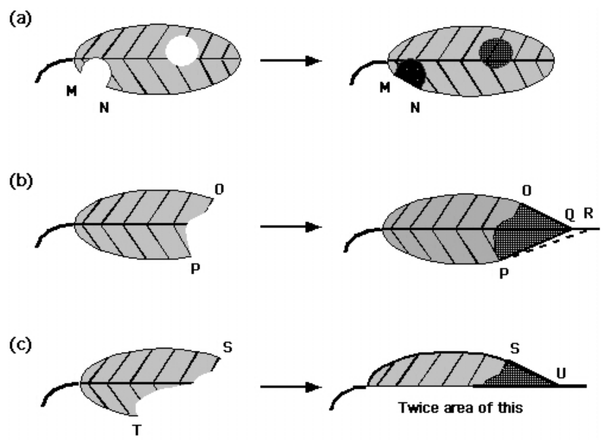

Fig. I Illustration of recovering the original-form for broad leaves.

middle edge of a leaf blade was eaten (Fig. I-a), the original area was estimated by connecting the two outer edges of the missing portion with a straight line. If the tip of a leaf blade was missing (Fig. I-b), a center line was projected from the midrib and two tangential lines were projected to intercept the center line. When the two tangential lines did not meet at the same point, the point closest to the leaf blade was selected to represent the tip of the original leaf. In the rare case where one of the two tangential lines at the point T did not intersect the center line (Fig. I-c), only one side of the leaf blade was used and the original area was estimated by doubling, with the assumption that the leaf was symmetric. For conifer shoots, we measured shoot length, the length of the eaten parts, the weight of the shoot, and the ratio of the eaten parts on the cross-section. We then calculated the weights of the missing parts consumed by herbivorous insects and the original-form for each individual leaf and shoot based on the weight of the remaining portion.

The stand-level defoliation ratio by herbivorous insects for a year (D) was calculated as follows,

$$D = \frac{M}{O} \times 100 \quad (\%)$$

where M and O are the summed weight of the missing parts and the estimated intact areas at each plot, respectively.

III. Results and Discussion

The stand-level defoliation ratio by herbivorous insects in tropical rain forests ranged from 1.6-8.4% on Mt. Kinabalu for the one-year period from 1998 to 1999. These values were lower and narrower in range than those of two reviews for tropical forests (5-15%: [1], 3-20%: [2]). This is because the previous studies were conducted in low-altitude forests and focused on the particular life stages, species, and habitats of plants with high defoliation ratios. Our study showed very low values for high-altitude forests that were not included in the previous studies.

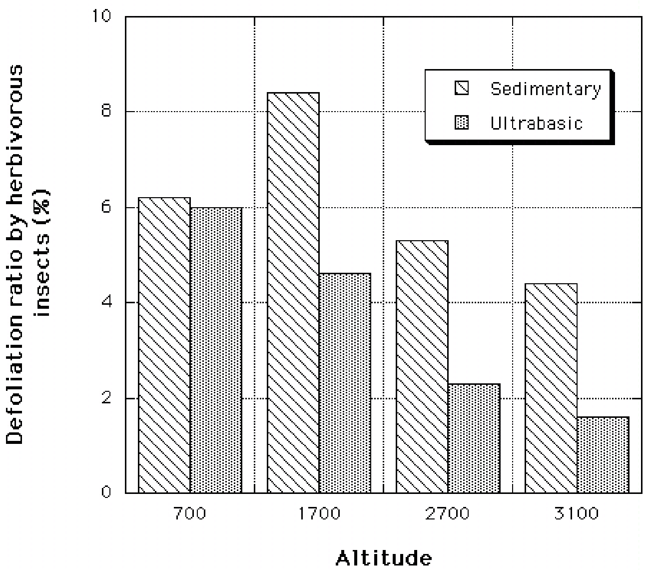

Fig. II Stand-level defoliation ratio by herbivorous insects for different altitudes and geological substrates.

The stand-level defoliation ratio decreased with increasing altitude (i.e. decreasing air temperature) except for the Tertiary sedimentary site at 700 m a.s.l. (Fig. II). Herbivore activity per se and leaf quality determine the defoliation ratio. Leaf mass per area (LMA) can be regarded as a good index for the latter (leaf quality as mechanical protection) because LMA is related to leaf toughness [18]. On Mt. Kinabalu, LMA increased with altitude (i.e. mechanical protection against insects increased [11]). Therefore, altitude has two parallel influences in reducing the activity of insects and increasing the mechanical protection.

Concentrations of leaf N and defensive substances were suitable indicators of the quality as food for herbivores [10, 20]. These leaf characteristics changed according to soil nutrient conditions. The concentration of nitrogen in live leaves generally increased with soil nutrient availability [19]. In the case of our study site, mean leaf N concentration was higher and LMA was lower at the Tertiary sedimentary than the ultrabasic site at each of the four elevations on Mt. Kinabalu [11]. On the other hand, the concentration of carbon-based defensive substances such as condensed tannins and polyphenols increased as soil nutrient contents decreased [20]. Such substances appear to exist in many tree species and are prevalent among woody plants in rain forests [21]. Taking these reports into account, leaf herbivory on trees was expected to be positively correlated with levels of soil nutrients . In this study, the stand-level defoliation ratio was lower at ultrabasic than Tertiary sedimentary sites at all altitudes. At the same altitude, the activity of herbivorous insects may be regarded as similar because of the likeness in air temperature. The positive but modest relationship between soil P content and the stand-level defoliation ratio was detected by using geology-topography sites. These results suggest that soil nutrient conditions exert influences on the stand-level defoliation ratio through the quality of foliage as food for herbivorous insects.

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