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What Causes Spatio-Temporal Variations in Leaf Herbivory Levels within a Canopy of *Fagus crenata*?

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Abstract - This paper investigates spatio-temporal variations in leaf herbivory levels within a single tree canopy. I observed leaf clusters of *Fagus crenata* under various light conditions without tearing leaves off, and monitored changes in leaf area consumed by insect herbivores. Although there was no clear relationship between relative photosynthetic photon flux density (rPPFD) and consumed leaf area (CLA) in May, immediately after leaf flush, a significant decrease in CLA with increasing rPPFD was observed after June, one or more months after leaf flush. Changes in such leaf characteristics as leaf mass per area (LMA), carbon concentration, nitrogen concentration, C/N ratio, concentration of total phenolics, and condensed tannin concentration, were observed within one month after leaf flush. Although values of these characteristics were generally not influenced by rPPFD for the first month after leaf flush, they subsequently showed a clear increase or decrease in values as rPPFD increased. In late season, significant positive or negative correlations were found between measured leaf characteristics and CLA.

I. Introduction

Spatial variations in leaf traits exist even in a single tree canopy. Leaves on a tall tree composing part of a forest canopy are exposed to various environments, and so leaves in different canopy layers vary in their characteristics. Such spatial changes in leaf traits lead to preferential feeding by herbivores such as aphids [1], ants [2] and larvae of moths [3]. By rearing insects on leaves sampled from the lower and upper regions of trees, Fortin and Mauffette found significantly higher insect performance, i.e. larger pupal masses and a greater number of eggs produced, among larvae fed with leaves from the upper part of the crown [4].

Traits of tree leaves, such as toughness or chemical composition, change during their lifetimes. Such temporal variation in leaf characteristics produces complex interactions between plants and herbivores. Young leaves, especially immediately after their emergence, are soft, and are vulnerable to insect herbivores. However, they become tougher with time, and accordingly their palatability for herbivores decreases [5]. Because of this temporal change, the suitability of leaves as food for insect herbivores varies with leaf age [6-9]. Several studies thus suggest that herbivores cannot develop successfully outside a well-defined phenological window of opportunity for using valuable leaves [10, 11].

The studies cited above investigated either spatial

variations or temporal variations. However, this kind of research does not make it clear whether and how patterns of spatial variations in leaf characteristics change temporally. Spatial differences are expected to change with time, and such spatio-temporal differences must have certain effects on the behavior of herbivores. For example, in the case of white spruce, there were within-tree variations in the budburst timing among buds in different positions, and this produced a temporal change in the within-tree distribution of buds that are suitable for spruce bud moth larvae [12, 13]. To clarify this kind of spatio-temporal variations in plants and their effects on herbivores, these studies adopted a non-destructive sampling method. This method made it possible to keep records of the same leaves in different positions of trees throughout the season.

In this research on spatio-temporal variations in leaf traits, I paid attention to the intensity of light to which leaves were exposed. Among extrinsic factors that change spatially [14], light availability is the most noticeably different within an individual tree. Because light is one of the major factors that regulates photosynthesis, variation in light causes variation in leaf characteristics such as the carbon concentration and the carbon/nitrogen ratio. According to the C/N balance hypothesis [15, 16], changes in the carbon/nutrient (such as nitrogen) ratio correlate with levels of plant defensive chemicals, such as phenolic metabolites. Some studies verified this hypothesis by documenting the indirect relationship between light and herbivores through the intermediary of phenolic plant chemicals [17-21].

Therefore, the objectives of this study were: (1) to clarify the pattern of spatio-temporal variations in leaf herbivory within a single tree canopy by a non-destructive sampling method; and (2) to speculate on the relationship between observed variations in leaf herbivory and their possible causes, such as light intensity and leaf characteristics.

II. Materials and Methods

A. Research site

This study was conducted in 2001-2002 at the Ashiu Forest Research Station, Field Science Education and Research Center, Kyoto University. This research station was located in the northeastern part of Kyoto Prefecture, Japan (35°18'N, 135°43'E). The mean annual temperature

in 2001 was 12.3 °C, and the mean monthly temperature ranged from -0.7 °C in January to 25.5 °C in August. The annual precipitation in 2001 was 2548 mm, and the monthly rainfall ranged from 56 mm in April to 380 mm in August. The forest was composed of *Cryptomeria japonica* D. Don var. *radicans* Nakai, *Fagus crenata* Blume, *Quercus crispula* Blume, *Betula grossa* Sieb. et Zucc. and of other deciduous species.

B. Seasonal changes in consumed leaf area

The research material was a *F. crenata* tree, which measured 17.2 m in height by 60 cm in diameter at breast height. A tree tower was built around the tree crown with steel pipes and steps. Taking advantage of this tower, I selected 24 leaf clusters from various layers of the tree crown so as to cover the wide range of light intensity. A leaf cluster was defined as a group of leaves attached to a branch about one meter long. Five twigs were chosen from each branch for observation. Each twig had from three to 49 current-year shoots and from 11 to 152 leaves.

First, I identified all 6,040 leaves attached to the five twigs in each of the 24 clusters by drawing a sketch of them. Then, observations of the leaves were carried out once a week from early May to late November in 2001, that is, from after the leaves flushed until they fell. At every observation, I checked the leaves for a mark of leaf herbivory. I used a digital camera to take pictures of the leaves that had been eaten by herbivores. Then, the area of each leaf was measured, and its original area, before consumption by herbivores, was estimated with the public domain NIH Image program (developed at the U.S. National Institutes of Health). These results were used to calculate the ratio of the eaten leaf area to the original leaf area for each leaf. Assuming that all leaves on each twig, whether eaten or not, originally had the same area, I computed the ratio of the eaten leaf area to the total area for each twig.

C. Light intensity of each leaf cluster

On an overcast day in early September, 2001, I simultaneously measured the photosynthetic photon flux density at the top of each leaf cluster and that at the top of the canopy using light meters (LI-COR, LI-190SA). The relative photosynthetic photon flux density (rPPFD) of each leaf cluster was then calculated.

On an overcast day in early September, 2002, rPPFD of each leaf cluster was measured in the same way as described above.

D. Analysis of physical and chemical traits of leaves

Ten leaves were collected from each leaf cluster on June 13, August 16, and October 16, 2001, and on April 17, April 30, May 22, June 26, August 22, and October 24, 2002. Leaves of the upper layer had fallen off by October; hence the samples collected in October were limited to leaves from ten leaf clusters. The leaf area of each sample was

measured with a digital camera and the photo retouch software mentioned above. The samples were dried for two weeks at 40 °C, and the leaf mass per area (LMA) of each sample was calculated. Dried samples were ground with a mill, and their carbon, nitrogen, total phenolics and condensed tannin concentrations were measured. The carbon and nitrogen concentrations were measured with a CN corder (Yanaco, MT-600). The sample leaf powders were extracted with 50% methanol for 24 hours, and their total phenolics concentrations were quantified with a spectrophotometer (Shimadzu, UV-1200), using tannic acid as a standard [22, 23]. Their condensed tannin concentrations were also quantified with a spectrophotometer [24], using cyanidin chloride as a standard.

Finally, correlation coefficients between consumed leaf area (CLA) after June and measured leaf traits, LMA, carbon concentration, nitrogen concentration, C/N ratio, total phenolics concentration, and condensed tannin concentration were calculated using SAS [25].

III. Results

A. Spatio-temporal variations in leaf herbivory level

Fig. 1 shows the seasonal changes in the percentage of consumed leaf area of leaf clusters at the top, middle and bottom of the *Fagus crenata* canopy in 2001. Leaves of *F. crenata* flushed at the end of April, and all of them fell by late November, 2001. The consumed leaf area (CLA) started increasing in May, i.e. immediately after bud burst, in all leaf clusters (Fig. 1). In the upper and middle layer of the canopy, no further consumption by insect herbivores was observed after June (Fig. 1). On the other hand, CLA of the lower layer clusters continued to increase after June (Fig. 1).

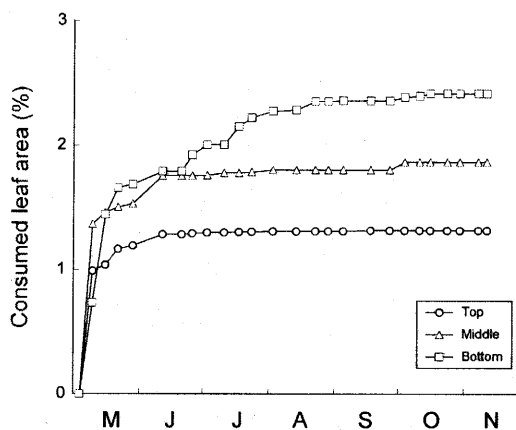


Fig. 1. Seasonal changes in percentage of consumed leaf area of leaf clusters at the top (rPPFD > 40%), middle (10% < rPPFD < 40%) and bottom of the canopy (rPPFD < 10%). Data represent the mean values of seven clusters at the top (open circles), seven clusters in the middle (open triangles) and ten clusters at the bottom of the canopy (open squares).

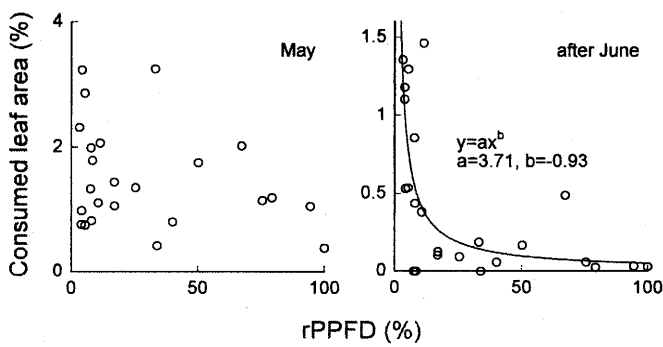


Fig. 2. The relationship between rPPFD and the percentage of the leaf area consumed in May (left), and after June (right). The mean value of each cluster is shown.

Fig. 2 indicates the relationships between rPPFD and CLA of all leaf clusters. Although no clear relationship was observed between rPPFD and CLA in May, there was a significant exponential decrease in CLA with increasing rPPFD after June ($R^2=0.53, P<0.01$) (Fig. 2).

B. Physical traits of leaves

LMA of each leaf cluster is shown in relation to its rPPFD in Fig. 3. In 2002, LMA values were almost the same among 24 leaf clusters in early season, i.e. within one month after leaf flush, and they increased with time. In late season of year 2001 and 2002, i.e. one or more months after leaf flush, LMA increased with an increase in rPPFD. In late season, there was no variation in LMA among the leaf-sampling times of June, August, and October.

C. Chemical traits of leaves

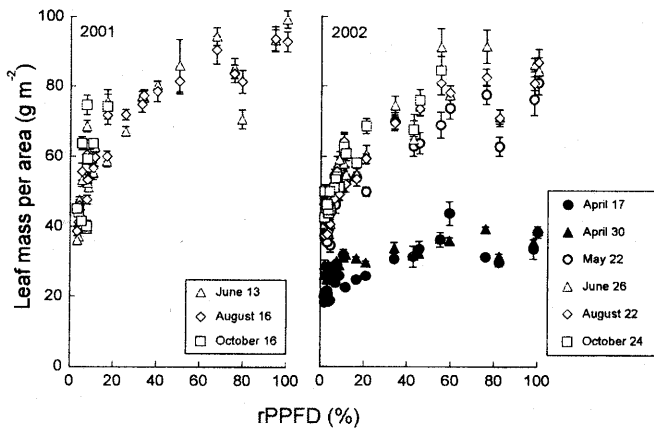


Fig. 3. The relationship between rPPFD and the mean value of leaf mass per area in each leaf cluster in early season (solid symbols) and in late season (open symbols) in 2001 (left) and in 2002 (right). Vertical bars show standard errors (n=10).

Fig. 4 shows the relationships between rPPFD and carbon concentration. Although the carbon concentration of leaves was about 50 % in all leaf clusters, it increased slightly as rPPFD increased. Values were generally lower in early than late season, 2002.

Fig. 5 illustrates the relationships between rPPFD and nitrogen concentration. The values of nitrogen concentration were rather high in early season, 2002, and they decreased with time. One month after leaf flush, the values of all clusters became stable. Throughout the season, the nitrogen concentration decreased as light intensity increased.

Fig. 6 shows the relationships between rPPFD and C/N ratio. The values of C/N ratio were rather low in early season, 2002, and they increased with time. One month after leaf flush, the values of all clusters became stable. The C/N ratio increased with increasing rPPFD, especially in 2001.

Fig. 7 indicates the relationships between rPPFD and total phenolic concentrations of leaves. Throughout the season, the total phenolic concentrations were higher in leaves under high rPPFD, than those of leaves under low rPPFD.

Fig. 8 shows the relationships between rPPFD and condensed tannin concentrations of leaves. In early season, 2002, the values of condensed tannin were rather low in all leaf clusters. They increased with time, and became stable one month after leaf flush. In late season, condensed tannin concentration increased with an increase in rPPFD, and the values at the top of the canopy were about three times as large as those at the bottom.

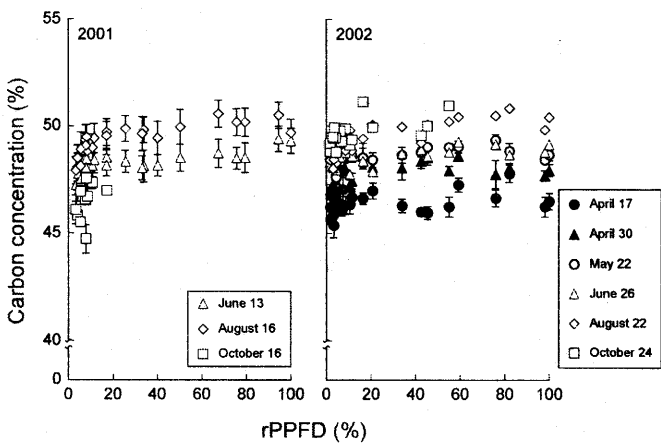


Fig. 4. The relationship between rPPFD and the mean value of the carbon concentration of leaves in each leaf cluster in early season (solid symbols) and in late season (open symbols) in 2001 (left) and in 2002 (right). Vertical bars show standard errors (n=10).

D. Correlations between CLA and measured leaf traits

Table 1 shows the correlation coefficients among the values of CLA, rPPFD, LMA, carbon concentration, nitrogen concentration, C/N ratio, total phenolics and condensed tannin. There were strong positive or negative correlations between the CLA and the measured leaf traits, except for the total phenolic concentrations.

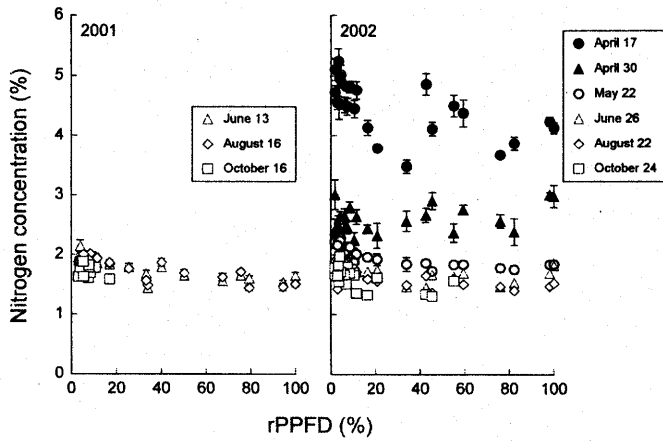


Fig. 5. The relationship between rPPFD and the mean nitrogen concentration of leaves in each leaf cluster in early season (solid symbols) and in late season (open symbols) in 2001 (left) and in 2002 (right). Vertical bars show standard errors (n =10).

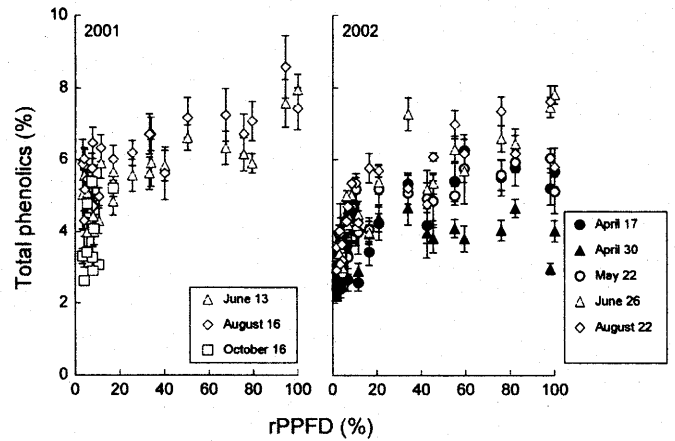


Fig. 7. The relationship between rPPFD and the mean total phenolics concentration of leaves in each leaf cluster in early season (solid symbols) and in late season (open symbols) in 2001 (left) and in 2002 (right). Vertical bars show standard errors (n =10).

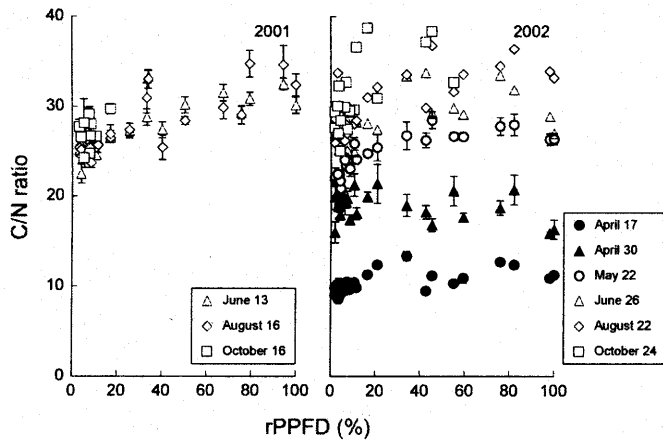


Fig. 6. The relationship between rPPFD and the mean C/N ratio of leaves in each leaf cluster in early season (solid symbols) and in late season (open symbols) in 2001 (left) and in 2002 (right). Vertical bars show standard errors (n =10).

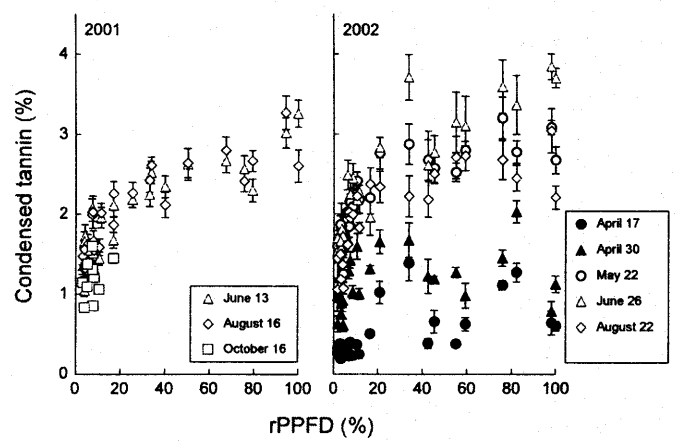


Fig. 8. The relationship between rPPFD and the mean condensed tannin concentration of leaves in each leaf cluster in early season (solid symbols) and in late season (open symbols) in 2001 (left) and in 2002 (right). Vertical bars show standard errors (n =10).

Table 1. Correlations between leaf characteristics measured in June and measurements of consumed leaf area and rPPFD taken after June. Arcsin transformed values were used for consumed leaf area and rPPFD.

	CLA (%)	rPPFD (%)	LMA (g m ⁻²)	C (%)	N (%)	C/N ratio	Phenolics (%)	Tannin (%)
CLA (%)	1.00							
rPPFD (%)	-0.54 **	1.00						
LMA (g m ⁻²)	-0.61 **	0.86 **	1.00					
C (%)	-0.54 **	0.79 **	0.83 **	1.00				
N (%)	0.54 **	-0.78 **	-0.81 **	-0.67 **	1.00			
C/N ratio	-0.56 **	0.81 **	0.84 **	0.70 **	-0.99 **	1.00		
Phenolics (%)	-0.33	0.80 **	0.80 **	0.79 **	-0.79 **	0.79 **	1.00	
Tannin (%)	-0.58 **	0.90 **	0.96 **	0.85 **	-0.87 **	0.89 **	0.92 **	1.00

** = P < 0.01

IV. Discussion

Spatio-temporal variations in leaf herbivory level within a canopy of *Fagus crenata* were studied in this research by repeated observations of leaves in various positions of the canopy. Herbivores started eating *F. crenata* leaves immediately after leaf flush in all leaf clusters within the canopy (Fig. 1). In early season, within one month after leaf flush, there were no clear variations in consumed leaf area (CLA) among leaf clusters under various light conditions (Fig. 2). CLA continued to increase after June mainly at the bottom of the canopy, where light availability was lower (Fig. 1). Because of this tendency, there was a clear decline in CLA with increasing light intensity in late season, one or more months after leaf flush (Fig. 2).

The analysis of physical and chemical characteristics revealed that spatio-temporal variations also exist in these characteristics. I found that the nitrogen concentration was rather high in early season, just after leaf flush (Fig. 5), while the LMA, carbon concentration, C/N ratio and condensed tannin were rather low in early season (Fig. 3, 4, 6, 8). These values changed with time and became stable one month after leaf flush. In late season, there is a clear gradient of some leaf characteristics as light intensity increased. That is, the LMA and C/N ratio, as well as the concentrations of total phenolics and condensed tannins, increased as light intensity increased (Fig. 3, 6, 7, 8).

I found that the values of the measured leaf characteristics did not change in a large way one or more months after leaf flush (Fig. 3, 4, 5, 6, 7, 8). It can be supposed from this that leaf maturation was finished within one month after leaf flush. Therefore, we can redefine early season as the period before leaf maturation and late season as the period after leaf maturation. Interactions between leaf characteristics and leaf herbivory may differ during these two periods.

In early season, the values of LMA were lower in all clusters than those in late season (Fig. 3). Young leaves in the early season are soft and therefore are supposed to be equally easy to consume for insect herbivores, regardless of their positions in the canopy. In late season, LMA increased with an increase in rPPFD (Fig. 3). Table 1 shows that there was a strong positive correlation between the values of LMA in June and rPPFD. Furthermore, there was a strong negative correlation between CLA and LMA (Table 3). Thus spatio-temporal variations in CLA found in late season can partially be explained by variations in LMA, which were probably caused by the heterogeneity of light [26-28]. These observations give support to the general recognition that leaves are defended against herbivores by toughness [29-31].

In late season, a significant negative correlation was found between rPPFD and nitrogen concentration, while there was a significant positive correlation between nitrogen concentration and CLA (Table 1). It follows from these results that light indirectly influences food availability for herbivores by varying the quantity of nitrogen. The positive correlation between nitrogen and CLA lends support

to Mattson's argument that the lower concentration of nitrogen in leaves means low food value for herbivores [32]. Thus the observed within-tree decrease in leaf nitrogen concentration may partly account for reduced consumption in leaves at the top of the canopy (Fig. 1). In addition, the rather high concentration of nitrogen in leaves in every position of the canopy in early season may partly account for the lack of variation in CLA in this season (Fig. 1).

The condensed tannin content of leaves was lower in all clusters in early than late season (Fig. 8). In late season, the condensed tannin of leaves was negatively correlated with CLA (Table 1). Tannin is considered to work as an inhibitor of digestion for herbivores [33, 34], causing slow growth and high mortality [35-37]. Therefore, the availability of leaves with low tannin concentrations in early season may be equally high for herbivores irrespective of their positions in the canopy. Ayres *et al.* [36] reported that the growth rate of leaf beetles was 30% lower when fed on leaves painted with condensed tannin solution, which is equivalent to 3% tannin in dry mass, than when fed on leaves without it. At the top of the canopy of *F. crenata*, the level of condensed tannin in leaves after June was about 3% of dry mass (Fig. 8). If the level of condensed tannin at the top of the canopy was too high for herbivores to consume in the late season, reduced levels of CLA at the top of the canopy in late season may be primarily attributable to this leaf characteristic (Fig. 2).

V. Conclusions

Spatio-temporal variations were observed in leaf herbivory level within a canopy of *Fagus crenata*. There was no clear variation in CLA among leaf clusters in different positions in early season, immediately after leaf flush, but a negative correlation was observed between rPPFD and CLA in the late season. Since the LMA and condensed tannin concentrations were relatively low, and the nitrogen concentrations were relatively high in early season throughout the canopy, leaves were equally available for insect herbivores irrespective of their positions in the canopy. In contrast, in the late season large spatial variations in leaf characteristics, which were likely caused by the heterogeneity of light, were highly correlated to the spatial variations in CLA.

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