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Herbivory in canopy gaps created by a typhoon varies by understory plant leaf phenology

Running title: Herbivory varies by plant leaf phenology

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Abstract

1. Availabilities of light and soil nitrogen for understory plants vary by extent of canopy gap formation through typhoon disturbance. We predicted that variation in resource availability and herbivore abundance in canopy gaps would affect herbivory through variation in leaf traits among plant species. We studied six understory species that expand their leaves before or after canopy closure in deciduous forests. We measured the availabilities of light, soil nitrogen, soil water content, and herbivore abundance in 20 canopy gaps (28.3–607.6 m^2) formed by a typhoon and in four undisturbed stands. We also measured leaf traits and herbivory on understory plants.

2. The availabilities of light and soil nitrogen increased with increasing gap size. However, soil water content did not. The abundance of herbivorous insects (such as Lepidoptera and Orthoptera) increased with increasing gap size.

3. Concentrations of condensed tannins, total phenolics, and nitrogen in leaves and the leaf mass per area increased in late leaf expansion species with increasing gap size, while none of the leaf traits varied by gap size in early leaf expansion species.

4. Herbivory increased on early leaf expansion species with increasing gap size, but decreased on late leaf expansion species. In these late leaf expansion species, total phenolics and C:N ratio had negative relationships with herbivory.

5. These results suggested that following typhoon disturbance, increased herbivory on early leaf expansion species can be explained by increased herbivore abundance, while decreased herbivory on late leaf expansion species can be explained by variation in leaf traits.

Key-words: deciduous forest, gap size, insect–plant interactions, resource availability, timing of leaf expansion

Introduction

Forest canopy gaps formed by natural disturbances produce variability in resource availabilities for the understory plant community. For example, light availability increases in canopy gaps (Carlton & Bazzaz, 1998; Denslow et al., 1990; Oguchi et al., 2006). This is also the case for soil nitrogen availability (Denslow et al., 1998; Oguchi et al., 2006; Prescott, 2002) because high soil water content and temperatures in canopy gaps accelerate decomposition of organic matter (Bormann et al., 1974). Natural disturbances play major roles in biological interactions by increasing variability in resource availabilities (Connell, 1978; Hiura, 1995; Menge & Sutherland, 1987; Pickett & White, 1985; Sousa, 1984). Variations in resource availability following natural disturbance alter insect–plant interactions in understory vegetation because herbivory in canopy gaps may increase (Chacon & Armesto, 2006; Dudt & Shure, 1994; Hunter & Forkner, 1999), decrease (Schowalter & Ganio, 1999; Shure & Wilson, 1993), and/or may not vary (Shure & Wilson, 1993). Responses of herbivory to canopy gaps remain largely underdetermined.

Leaf traits, such as concentrations of secondary metabolites, toughness, and leaf nitrogen content, alter feeding behaviors of herbivorous insects (e.g., Bryant et al., 1987; Coley, 1983; Coley & Barone, 1996; Feeny, 1970) and may be influenced by

variation in resource availability (Bryant et al., 1983, 1987; Close et al., 2003; Close & McArthur, 2002; Nakamura et al., 2008; Yamasaki & Kikuzawa, 2003). Secondary metabolites (e.g., condensed tannins and total phenolics) in plants often act as herbivore deterrents (Bryant et al., 1987; Coley & Barone, 1996; Feeny, 1970), and their concentrations in plant tissues increase when light availability is elevated (Bryant et al., 1983, 1987; Close et al., 2003; Close & McArthur, 2002). This increase in secondary metabolite concentrations is explained by two non-mutually exclusive hypotheses. First, the carbon-nutrient balance (CNB) hypothesis explains increasing secondary metabolite concentrations as a function of the balance between carbon and nitrogen (C:N ratio) within a plant (Bryant et al., 1983, 1987), although the generality of this hypothesis is debated (Hamilton et al., 2001; Koricheva, 2002; Nakamura et al., 2008). Second, taking no account of the C:N ratio, the photoinhibition hypothesis explains increasing secondary metabolite concentrations in terms of photodamage risk reduction (Close et al., 2003; Close & McArthur, 2002). Secondary metabolites often function as chemical deterrents of grazers, while the leaf mass per area (LMA) is closely correlated with toughness and physical defense against herbivores (Choong, 1996; Coley, 1983). In contrast, elevated leaf nitrogen content is an attractant for herbivores (Coley, 1983). All of these leaf traits increase under high light and/or high soil nitrogen availability (Mattson, 1980; Nakamura et al., 2008; Nordin et al., 1998; Oguchi et al., 2006;

Yamasaki & Kikuzawa, 2003). Thus, canopy gaps may affect herbivory by causing variation in leaf traits.

Physiological responses (e.g., photosynthetic adaptation, nitrogen-use efficiency) to seasonal resource variation vary among understory plant species with differing leaf expansion phenologies (Kudo et al., 2008; Rothstein & Zak, 2001a,b; Skillman et al., 1996). In deciduous forests, understory plants have two distinct strategies of leaf expansion timing for avoiding or tolerating shade from canopy trees in summer (Neufeld & Young, 2003; Uemura, 1994). Early leaf expansion species open their leaves before canopy trees, and thus avoid shading early in the season. This phenology allows expanded leaves to capture a large proportion of current-year photosynthate before canopy closure (Ida & Kudo, 2008). In contrast, late leaf expansion species have shade-tolerating strategies because the leaves open after canopy closure (Neufeld & Young, 2003). If leaf trait responses to canopy gaps differ between early and late leaf expansion species, responses of herbivory to canopy gaps likely depend on leaf phenology.

Herbivorous insects on understory plants are more abundant in canopy gaps than under closed canopy (Basset et al., 2001; Jokimaki et al., 1998; Louda & Rodman, 1996; Richards & Coley, 2007; Sipura & Tahvanainen, 2000). Elevated light availability and temperature in the gaps promote faster insect development and immigration of

grazers from forest shade (Cappuccino & Root, 1992; Courtney & Courtney, 1982; Sipura & Tahvanainen, 2000; Weiss et al., 1988). Increased herbivore abundance in canopy gaps probably increases feeding pressure on understory plants. Thus, both leaf traits and herbivore abundances should be considered as important determinants of herbivory in canopy gaps (Louda & Rodman, 1996).

In this study, we focused on the ways in which canopy gaps formed by a typhoon affect herbivory on understory plants through disturbance-induced variations in leaf traits and herbivore abundances. We studied leaf traits and herbivory in six perennial understory species (differing in leaf expansion timing) among various canopy gap sizes (28.3–607.6 m^2) created by a typhoon in a deciduous forest. In particular, we addressed the following questions: Do leaf trait responses (C:N ratio, LMA and concentrations of condensed tannins, total phenolics and nitrogen) to canopy gaps differ between early and late leaf expansion species? Do herbivore abundances respond to canopy gaps? Does herbivory in canopy gaps differ between early and late leaf expansion species?

Methods

STUDY SITE

This study was conducted in Tomakomai Experimental Forest (TOEF), Hokkaido University (42°41′ N, 141°36′ E; area: 2,715 ha), Hokkaido, Japan. A large part of TOEF is located on flat land, with a gradient of <5°. Mean monthly temperatures range from –3.2 to 19.1°C, and annual precipitation is 1450 mm. Snow cover reaches a depth of 50 cm from December to March. Minimum of 350 vascular plant species have been recorded in TOEF (Kudo & Yoshimi, 1916). The dominant canopy trees in natural stands are *Quercus crispula* (Fagaceae), *Acer mono* (Aceraceae), *Sorbus alnifolia* (Rosaceae), and *Tilia japonica* (Tiliaceae) (Hiura, 2001). The forest formed on 2-m-deep porous volcanic ash, which accumulated after the eruptions of Mt. Tarumae between 1669 and 1739 (Shibata et al., 1998).

Two typhoons in 1954 and 2004 were major natural disturbances from 1904 to 2004 in TOEF (Hiura et al., 2004; Takafumi & Hiura, 2009). The typhoon in 2004 disturbed about 32% of the forest area in TOEF (Hiura et al., 2004). To determine the effects of canopy gaps created by the typhoon on resource availabilities for understory plants, herbivore abundances, leaf traits, and herbivory on understory plants, we set up

20 study plots within varying gap sizes (28.3–607.6 m^2), and four undisturbed study plots under full canopy (total: 24 plots) in July 2005. The study plots had not been disturbed by harvesting over the previous 50 years (Takafumi & Hiura, 2009). We measured the lengths and widths of gaps with a steel tape and calculated areas of gaps assuming they were elliptical.

RESOURCE AVAILABILITY

To evaluate the availability of light in canopy gaps, we captured a hemispherical photographic image to measure canopy openness above each study plot. The hemispherical photographs were taken with a digital camera (Coolpix 990; Nikon, Tokyo, Japan) equipped with a fish-eye lens (FC-E8; Nikon). The top element of the lens was positioned 0.5 m above the ground. The hemispherical images were analyzed with CanopOn2 (free software programmed by A. Takenaka available at http://www.takenaka-akio.cool.ne.jp/etc/canopon2/) software based on a standard overcast sky condition.

To evaluate the availabilities of soil nitrogen in canopy gaps, N mineralization (NH_4^+) and nitrification (NO_3^-) in intact soil cores were determined in each study plot following the methods of Oguchi *et al*. (2006). Sampling points in each study plot under

a canopy gap were set at the center of the gap and at four midpoints between the center and the gap edges, avoiding pits and mounds (total: five sampling points per plot), when measurements were started in July 2005. In undisturbed study plots (no canopy gaps), sampling points were set at the center and four corners of a 5 × 5-m quadrat located at the center of each plot. Three cores (5.0 cm diameter × 5.0 cm long) were extracted from each sampling point (total: 15 cores per plot). One core from each sampling point was used for the analysis of initial soil nitrogen availability. The other two cores were reinserted into their holes in the plot and incubated in the field using the resin technique (Distefano & Gholz, 1986). The resin (active anion exchange resin, Amberlite IRA-400 and active cation exchange resin, Amberlite IR-120B; Rohm and Haas, Philadelphia, PA, USA) wrapped in fine mesh nylon was connected to the base of each soil core sample in polyvinyl chloride tubes. The resin packs collected ions leaching through soil core samples. At the end of measurement periods (September 2005, September 2006), cores were collected. Afterward, a solution of NO_3^- and NH_4^+ was extracted and analyzed with an autoanalyzer (AACS-4; BL-TEC Inc., Osaka, Japan). The availabilities of NO_3^- and NH_4^+ were calculated from the differences between start and endpoints of the measurement periods.

To evaluate soil water content (percentage by volume) in canopy gaps, we used time domain reflectometry (Trime-FM2/P2; IMKO, Ettlingen, Germany) (Topp & Davis,

1985; Topp et al., 1980) in August and November 2005, and in August 2006. We measured the soil water contents after 5 -6 days after a rainfall event. A pair of 5-cm-long reflectometry rods was installed in the soil near each resin bag.

UNDERSTORY PLANT SPECIES WITH DIFFERENT TIMINGS OF LEAF EXPANSION

To determine the effects of canopy gaps on understory plant species with different timings of leaf expansion, we observed four dominant herb species (*Trillium tschonoskii* Maxim., *Smilacina japonica* A. Gray, *Polygonatum odoratum* var. *maximowiczii* Koidz, *Desmodium podocarpum* DC.) and two canopy tree species (*Acer mono* Maxim., *Quercus crispula* Blume) in the understory. In late April, *T. tschonoskii* and *S. japonica* expand their leaves as soon as snow melts and before canopy closure. In early May, the other herb species, *P. odoratum* var. *maximowiczii* and *D. podocarpum*, expand leaves immediately following the start of canopy tree leaf expansion. In late May, seedlings (<130 cm tall) of two canopy tree species (*A. mono, Q. crispula*) expand leaves following canopy closure.

LEAF TRAITS OF UNDERSTORY PLANTS

To evaluate the leaf traits of understory plants in canopy gaps, we randomly sampled one leaf having the least herbivory (<10% leaf loss) from each of six individuals of each plant species in early August 2006. When less than six individuals of a plant species occurred in a plot, we randomly sampled one leaf from each of the individuals present (>2 individuals in all cases). Afterward, we punched five leaf disks (6 mm in diameter) out of each leaf, and the sampled disks were oven-dried for 72 h at 40°C. The LMA was calculated for each leaf. Using these punched disks, we measured concentrations of carbon and nitrogen using a CN analyzer (NC-900; Sumitomo, Osaka, Japan), and the C:N ratios were calculated. Condensed tannins and total phenolics in leaves were measured following Julkunen-Tiitto (1985). Since herbivory was evaluated by assessing the percentage of leaf area consumed, we also calculated condensed tannins, total phenolics, and nitrogen on unit-area bases.

HERBIVORE ABUNDANCE

To evaluate herbivore abundance in canopy gaps, herbivorous chewing insects were collected by hand from understory plants over 30-min periods in single 5 × 5-m quadrats in each plot in late July 2006. We sorted insects into orders (Lepidoptera,

Orthoptera, Coleoptera) and measured the dry mass of each order in each plot after oven-drying for 48 h at 60°C.

HERBIVORY ON UNDERSTORY PLANTS

To evaluate herbivory in canopy gaps, 100 leaves were randomly selected from each plant species in each plot. We assessed percentages of consumed leaf areas by chewing herbivore insects in late July 2006. We transformed these percentages into seven classes of herbivory as follows: 1: 0%, 2: 1–5%, 3: 6–10%, 4:11–25%, 5: 26–50%, 6: 51–75%, 7: 76–100%. When we had less than 100 leaves of a plant species in a plot, we assessed herbivory on all leaves present (>30 leaves in all cases). Leaves grazed by mammals and snails were omitted because we hardly observed leaves grazed by these herbivores.

DATA ANALYSIS

The availabilities of light and soil nitrogen, soil water content, herbivore abundance, and leaf traits of understory plants were analyzed using generalized linear models with gap size as the explanatory variable. We analyzed herbivory by gap size using ordinal logistic models (= proportional odds models) (McCullagh, 1980) as each class of

consumed leaf area was an ordinal category. The relationships between herbivory and leaf traits were also analyzed with ordinal logistic models. We selected best-fit models from linear and log-linear models using Akaike's information criterion (AIC). We used the likelihood ratio test to determine whether the data supported selected models over a null model. All statistical analyses were conducted with R Version 2.4.1. software (R development Core Team, 2006).

Results

RESOURCE AVAILABILITY

Canopy openness increased significantly from 7.8% to 38.3% with increasing gap size (gap size: 0–607.6 m^2) (Table 1). Nitrate in soil between July 2005 and October 2006 increased significantly with increasing gap size. Only NH_4^+ mineralized in soil between July and October in 2005 (i.e., not at other times) increased significantly with increasing gap size. However, soil water content did not vary by gap size during the measurement period ($P > 0.05$).

LEAF TRAITS OF UNDERSTORY PLANTS

The responses of leaf traits of understory plants to canopy gaps differed between early and late leaf expansion species. Most leaf traits varied in late leaf expansion species by gap size, but no significant variation in leaf traits of early leaf expansion species was observed as gap size increased (Table 2). In all late leaf expansion species, condensed tannin and total phenolic concentrations in leaves, and LMA increased with increasing gap size. With increasing gap size, the C:N ratio increased in *D. podocarpum*, did not vary in *A. mono*, and decreased in *Q. crispula*. Leaf nitrogen content did not vary in *D. podocarpum*, but increased in *A. mono* and *Q. crispula* with increasing gap size.

HERBIVORY ON UNDERSTORY PLANTS

Herbivory responses to canopy gaps differed between early and late leaf expansion species. Herbivory increased on early leaf expansion species (*T. tschonoskii* and *S. japonica*) with increasing gap size, but decreased on late leaf expansion species (*D. podocarpum* and *Q. crispula*) (Table 3). In addition, the total dry mass of herbivorous insects increased with increasing gap size (Fig. 1), particularly in the orders Lepidoptera and Orthoptera.

RELATIONSHIP BETWEEN HERBIVORY AND LEAF TRAITS

Among leaf traits of late leaf expansion species that varied by canopy gap size, the C:N ratio in *D. podocarpum* and total phenolics in *Q. crispula* had negative relationships with herbivory (Table 4).

Discussion

This study clearly showed that with increasing gap size, concomitant increases occurred in the availabilities of plant resources (light and soil nitrogen) and herbivore abundance. Furthermore, most leaf traits varied by gap size in late leaf expansion species but not in early leaf expansion species. Herbivory increased on early leaf expansion species with increasing gap size but decreased in late leaf expansion species.

CHANGE IN RESOURCE AVAILABILITY IN CANOPY GAPS

The availability of soil nitrogen increases in canopy gaps (Denslow et al., 1998; Oguchi et al., 2006; Prescott, 2002) through accelerated decomposition of organic matter

resulting from elevated soil water contents and temperatures (Bormann et al., 1974). We found that availabilities of NO_3^- and NH_4^+ increased with increasing gap size, but soil water content did not, probably because this forest is well drained (being formed on 2-m-deep porous volcanic ash with a very shallow soil layer) (Shibata et al., 1998). In general, the soil temperature increases in canopy gaps (Gray et al., 2002; Naidu & DeLucia, 1997, 1998; Phillips & Shure, 1990; Ritter, 2005; Wright et al., 1998). For example, Phillips & Shure (1990) reported that soil temperature increased with increasing gap size (160–20000 m^2) in a southern Appalachian deciduous forest (USA). Although our study did not measure soil temperature, the high soil nitrogen availability might have been caused by increased soil temperatures in canopy gaps.

DIFFERENT LEAF TRAIT RESPONSES AMONG PLANTS DIFFERING IN TIMING OF LEAF EXPANSION

Understory plants with different leaf expansion phenologies have different physiological responses to changing light availability (Kudo et al., 2008; Rothstein & Zak, 2001a; Skillman et al., 1996). We found that concentrations of total phenolics, condensed tannins, and nitrogen in leaves, and the LMA increased in late leaf expansion species with increasing gap size, but none of these traits varied by gap size in early leaf

expansion species. Late leaf expansion species usually grow under limited light conditions after canopy closure, but canopy gaps provided illumination for these species, which may have led to variation in the leaf traits. Two non-mutually exclusive hypotheses propose different mechanisms by which higher light availability may lead to increased secondary metabolite concentrations. First, the CNB hypothesis explains that the balance of carbon and nitrogen within a plant (C:N ratio) regulates the allocation of resources to primary and secondary metabolites (Bryant et al., 1983, 1987). Under high light conditions, excess C is used preferentially to synthesize C-based secondary metabolites (Bryant et al., 1983; Coley et al., 1985). We found that in *D. podocarpum*, both the C:N ratio and secondary metabolites (condensed tannins and total phenolics) increased with increasing gap size, but N content did not; thus responses of this species alone support the CNB hypothesis. The photoinhibition hypothesis explains that plants are induced to produce secondary metabolites (regardless of C:N ratio) as a way of reducing the risk of photodamage by oxidants to photosynthesis (Close et al., 2003; Close & McArthur, 2002). Plant usually increase carotenoids under high light condition to protect the photosystems (Demmig-Adams et al., 1996; Havaux, 1998). Previous studies have shown that total phenolics and condensed tannins also had similar function (Hagerman et al., 1998; Kuhlmann & Muller, 2009; Mole et al., 1988; Treutter, 2006). We found that secondary metabolite (total phenolics and condensed tannins)

concentrations increased in all late leaf expansion species with increasing gap size. Thus, the photoinhibition hypothesis may agree with all our results for later leaf expansion species. Similar to secondary metabolite concentrations, the LMA and leaf nitrogen increased in late leaf expansion species with increasing gap size. Studies have reported that higher light availability increases the LMA and leaf nitrogen under canopy gaps due to an elevation of photosynthetic production (Oguchi et al., 2006; Poorter et al., 2009). We found that soil nitrogen increased with increasing gap size, which may have led to increases in leaf nitrogen in late leaf expansion species.

In contrast to late leaf expansion species, no leaf trait variation with increasing gap size was observed in early leaf expansion species. Since these species produce the largest proportion of current-year photosynthate before canopy closure (Ida & Kudo, 2008), higher light availability in canopy gaps would not affect concentrations of secondary metabolites and nitrogen in leaves, or the LMA.

Alternatively, the first four species to expand their leaves are herbs, while the two late leaf expansion species are canopy tree species. Canopy gaps are essential for growth and recruitment of most of canopy trees species (Denslow, 1987; Pickett & White, 1985). Thus, not only different leaf expansion phenologies but also different life forms may explain the different responses of leaf traits to canopy gaps.

INCREASED HERBIVORE ABUNDANCE IN CANOPY GAPS

Herbivorous insects on understory plants are more abundant in canopy gaps than under closed canopy because the high light availability and warmer condition lead to faster insect development and immigration (Basset et al., 2001; Jokimaki et al., 1998; Louda & Rodman, 1996; Richards & Coley, 2007; Sipura & Tahvanainen, 2000). We found that the abundance of herbivorous insects, such as Lepidoptera and Orthoptera, increased with increasing gap size. This is probably because lepidopteran larvae prefer the edges of canopy gaps (Cappuccino & Martin, 1997; Cappuccino & Root, 1992; Courtney & Courtney, 1982), and they migrate from the canopy to the understory as canopy leaf quality degrades (leaf toughness and tannin increased, while the nitrogen and water contents decreased) in late season (Murakami & Wada, 1997). These lepidopteran larvae feed canopy trees and understory plants (Murakami & Wada, 1997), thus, most of these Lepidoptera larvae may be generalists. Furthermore, the majority of orthopterans are open landscape species, and their abundances are also elevated in canopy gaps compared to closed canopy (Bouget & Duelli, 2004; Richards & Coley, 2007; Shure & Phillips, 1991).

DIFFERING HERBIVORY RESPONSES BETWEEN PLANTS WITH DIFFERENT

TIMINGS OF LEAF EXPANSION

Herbivory rates may be determined by a combination of variation in leaf traits and herbivore abundances (Louda & Rodman, 1996). We showed that herbivory increased on early leaf expansion species (*T. tschonoskii* and *S. japonica*) with increasing gap size, but decreased on late leaf expansion species (*D. podocarpum* and *Q. crispula*). None of the leaf traits varied in early leaf expansion species in canopy gaps, although herbivore abundance increased. Thus, increased herbivory on early leaf expansion species in canopy gaps may be explained by increased herbivore abundance. In contrast, most leaf traits in late leaf expansion species varied by gap size. Among these traits, the C:N ratio in *D. podocarpum* and total phenolics in *Q. crispula* had negative relationships with herbivory. However, measured secondary metabolite (condensed tannins and total phenolics) concentrations in *D. podocarpum* were not negatively related to herbivory. Thus, other (as yet unmeasured) secondary metabolites may be responsible for decreased herbivory in canopy gaps. Decreased herbivory on late leaf expansion species can be explained by increased secondary metabolite concentrations in canopy gaps. These results suggest that important determinants of herbivory in canopy gaps differed between early and late leaf expansion species.

In conclusion, we clearly showed that following typhoon disturbance, increased

herbivory on early leaf expansion species can be explained by increased herbivore abundance; decreased herbivory on late leaf expansion species in canopy gaps can be explained by variation in leaf traits. Several studies have reported that understory plants with different timings of leaf expansion have different physiological characteristics (Kudo et al., 2008; Rothstein & Zak, 2001a,b; Skillman et al., 1996). Our findings emphasize that initial responses of herbivory to canopy gaps formed by the typhoon also varied between plants with different timings of leaf expansion. To consider both leaf traits and herbivore abundance as important determinant of herbivory, we can understand how herbivory responds to canopy gaps.

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Figure legend

Fig. 1. Relationships between dry mass (g) of herbivorous insects and gap size (m^2). Symbols represent collected data, and lines indicate the best-fit and significant models ($P < 0.05$). The best-fit models were selected from among linear and log-linear models using the AIC. All selected models were linear and significant. Significance of differences was determined by the likelihood ratio test ($P < 0.05$). Proportions of total herbivorous insect dry mass were Lepidoptera (81.8%), Orthoptera (15.0%), and Coleoptera (3.2%).

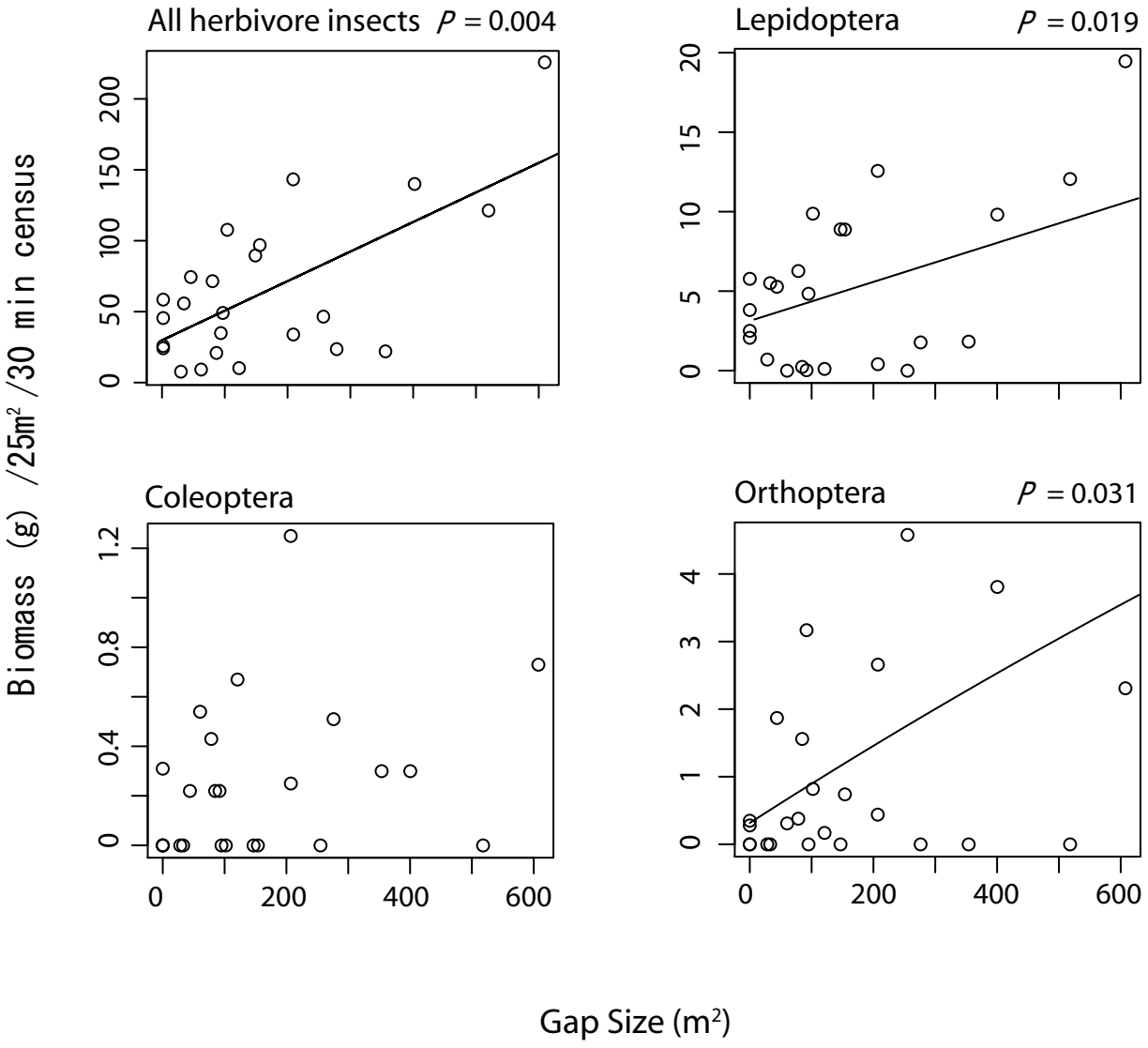

All herbivore insects P = 0.004
Lepidoptera P = 0.019
Coleoptera
Orthoptera P = 0.031
Biomass (g) /25m² /30 min census
Gap Size (m²)
0
50
100
150
200
5
10
15
20
0.4
0.8
1.2
1
2
3
4
200
400
600

Table 1. Relationships between gap size (m^2) and canopy openness, soil nitrogen, and soil water content.
Values are means ± SE (n = 24) of plots. Coefficients, P-values for best-fit significant models are shown.
The best-fit models were selected among linear and log-linear models using the AIC.

Environment factors	Measurement	Average	Coefficients	P	Selected model
Canopy openness (%)	Aug. 2005	19.71 ± 1.51	2.97	****	Log-linear
$NO3^-$-N (mg/cm^3)	Jul. 2005 (content of initial)	0.09 ± 0.01	0.01	***	Log-linear
	Jul. 2005-Oct. 2005	83.22 ± 7.15	9.60	****	Log-linear
	Oct. 2005-Oct. 2006	165.37 ± 19.39	22.56	***	Log-linear
$NH4^+$-N (mg/cm^3)	Jul. 2005 (content of initial)	0.41 ± 0.02	-	-	Null
	Jul. 2005-Oct. 2005	1.53 ± 0.23	0.32	****	Log-linear
	Oct. 2005-Oct. 2006	4.86 ± 0.65	-	-	Null
Soil water content (%)	Aug. 2005	19.68 ± 0.89	-	-	Null
	Nov. 2005	26.78 ± 0.51	-	-	Null
	Aug. 2006	25.88 ± 0.52	-	-	Null

P: The likelihood ratio test was used to test the difference in deviance between the selected model and the null model.
***: $p<0.01$, ****: $p< 0.001$.

Table2. Relationships between gap size (m^2) and concentrations of condensed tannins and total phenolics, LMA, C:N ratio, and nitrogen content.Values are means ± SE (n = 24) of plots. Coefficients, *P*-values and best fit significant models are shown. The best fit models were selected from linear and log-linear models using the AIC.

Species name	Leaf expansion	Leaf traits	Average	Coefficients	*P*	Selected model
Trillium tschonoskii	1st	Condensed tannins (mg/mm^2)	0.022 ±0.001	0.001	n.s.	Log-linear
		Total phenolics (mg/mm^2)	6.560 ±0.327	0.003	n.s.	Linear
		LMA (mg/mm^2)	221.033 ±4.497	3.687	n.s.	Log-linear
		CN ratio	13.476 ±0.176	0.180	n.s.	Log-linear
		N (mg/mm^2)	7.000 ±0.134	-	-	Null
Smilacina japonica	2nd	Condensed tannins (mg/mm^2)	0.103 ±0.007	-	-	Null
		Total phenolics (mg/mm^2)	5.950 ±0.310	-	-	Null
		LMA (mg/mm^2)	218.366 ±7.447	6.192	n.s.	Log-linear
		CN ratio	15.796 ±0.415	-	-	Null
		N (mg/mm^2)	5.800 ±0.237	0.197	n.s.	Log-linear
Polygonatum odoratum var. *maximowiczii*	3rd	Condensed tannins (mg/mm^2)	0.903 ±0.088	-	-	Null
		Total phenolics (mg/mm^2)	13.350 ±1.504	-	-	Null
		LMA (mg/mm^2)	160.032 ±7.388	3.525	n.s.	Log-linear
		CN ratio	12.384 ±0.381	-	-	Null
		N (mg/mm^2)	5.800 ±0.347	0.002	n.s.	Linear
Desmodium podocarpum	4th	Condensed tannins (mg/mm^2)	0.078 ±0.008	0.002	****	Linear
		Total phenolics (mg/mm^2)	3.760 ±0.180	0.039	****	Linear
		LMA (mg/mm^2)	209.746 ±4.804	0.141	***	Linear
		CN ratio	12.384 ±0.381	0.414	*	Log-linear
		N (mg/mm^2)	7.100 ±0.191	0.003	n.s.	Linear
Acer mono	5th	Condensed tannins (mg/mm^2)	0.905 ±0.115	0.094	*	Log-linear
		Total phenolics (mg/mm^2)	22.130 ±1.077	1.402	***	Log-linear
		LMA (mg/mm^2)	301.445 ±9.978	15.787	****	Log-linear
		CN ratio	12.412 ±0.135	-	-	Null
		N (mg/mm^2)	6.900 ±0.237	0.345	****	Log-linear
Quercus crispula	6th	Condensed tannins (mg/mm^2)	0.517 ±0.076	0.002	***	Linear
		Total phenolics (mg/mm^2)	33.270 ±1.721	1.882	**	Log-linear
		LMA (mg/mm^2)	338.024 ±10.854	0.208	****	Linear
		CN ratio	19.709 ±0.242	-0.003	*	Log-linear
		N (mg/mm^2)	8.500 ±0.340	0.007	****	Linear

P : The likelihood ratio test was used to test the difference in deviance between the selected model and the null model.

*: $P < 0.1$, **: $P < 0.05$, ***: $P < 0.01$, ****: $P < 0.001$.

P-values were corrected for multiple pairwise testing with the sequential Bonferroni technique.

Intercepts and coefficients of tannins and total phenolics content, LMA, and nitrogen content are 10^4 times.

Table 3. Relationships between herbivory and gap size (m^2).
Values shown are coefficients and *P*-values for best-fit and significant models.
The best-fit models were selected among linear model and log-linear models using the AIC.

Species name	Leaf expansion	Coefficients	*P*	Selected model
Trillium tschonoskii	1st	0.072	***	Log-linear
Smilacina japonica	2nd	0.137	****	Log-linear
Polygonatum odoratum var. *maximowiczii*	3rd	-	-	Null
Desmodium podocarpum	4th	-0.001	***	Linear
Acer mono	5th	-	-	Null
Quercus crispula	6th	-0.056	***	Linear

P: The likelihood ratio test was used to test the difference in deviance between the selected model and the null model.
***: $p<0.01$, ****:$p< 0.001$.

Table 4. Relationships between herbivory and concentrations of condensed tannins and total phenolics, LMA, C:N ratio, and nitrogen content. Values shown are coefficients and *P*-values for best-fit and significant models. The best-fit models were selected from among linear model and log-linear models using the AIC.

Species name	Leaf expansion	Leaf traits	Coefficients	*P*	Selected model
Trillium tschonoskii	1st	Condensed tannins (mg/mm^2)	-	-	Null
		Total phenolics (mg/mm^2)	927.7	n.s.	Log-linear
		LMA (mg/mm^2)	-	-	Null
		CN ratio	0.1	n.s.	Linear
		N (mg/mm^2)	-	-	Null
Smilacina japonica	2nd	Condensed tannins (mg/mm^2)	-	-	Null
		Total phenolics (mg/mm^2)	-	-	Null
		LMA (mg/mm^2)	-	-	Null
		CN ratio	-	-	Null
		N (mg/mm^2)	-	-	Null
Polygonatum odoratum var. *maximowiczii*	3rd	Condensed tannins (mg/mm^2)	-	-	Null
		Total phenolics (mg/mm^2)	-	-	Null
		LMA (mg/mm^2)	-165.9	****	Linear
		CN ratio	-0.3	*	Linear
		N (mg/mm^2)	-	-	Null
Desmodium podocarpum	4th	Condensed tannins (mg/mm^2)	-2884.1	n.s.	Log-linear
		Total phenolics (mg/mm^2)	-181.6	n.s.	Log-linear
		LMA (mg/mm^2)	-	-	Null
		CN ratio	-0.3	****	Linear
		N (mg/mm^2)	585.3	*	Log-linear
Acer mono	5th	Condensed tannins (mg/mm^2)	-	-	Null
		Total phenolics (mg/mm^2)	-	-	Null
		LMA (mg/mm^2)	-	-	Null
		CN ratio	-1.5	***	Log-linear
		N (mg/mm^2)	-	-	Null
Quercus crispula	6th	Condensed tannins (mg/mm^2)	-	-	Null
		Total phenolics (mg/mm^2)	-159.0	**	Log-linear
		LMA (mg/mm^2)	-	-	Null
		CN ratio	-3.7	****	Log-linear
		N (mg/mm^2)	1055.8	n.s.	Log-linear

P: The likelihood ratio test was used to test the difference in deviance between the selected model and the null model.
*: $p<0.1$, **: $p< 0.05$, ***: $p<0.01$, ****: $p< 0.001$.
P-values were corrected for multiple pairwise testing with the sequential Bonferroni technique.