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Larval Morphology and Feeding Behavior in Notodontidae (Lepidoptera) in Relation to Leaf Toughness of Host Plants

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Abstract

The relationship between larval body size traits of herbivores and the leaf toughness of their host plant species was evaluated by examining the data from 30 notodontid (Notodontidae) species and 10 host plant species. For last instar larvae, higher allocations to the head parts and the mandibles relative to their body sizes were observed, when the larvae feed on tougher host plants leaves. On the other hand, none of relationships of relative allocation to body parts in relation to the leaf toughness of their hosts was observed for first instar larvae. These results showed that the last instar larvae feeding on tougher leaves tend to have the larger-size body, in particular, head and mandible parts. Furthermore, substantial changes in mandibular morphology from first to last instar larvae were detected on *Rabta cristata*, which might be a response to seasonal increase in leaf toughness of the host plant. These results show that the quality of host plant species had major roles to determine the morphological changes attributing allometric relations between body size traits for herbivorous insects.

Key words: allometry, body size, head, mandible, plant-insect interaction

Introduction

Body size is one of the most important ecological and physiological traits for herbivorous insects to cope with variety of biological and environmental hurdles such as competition, predation, parasitism, and metabolic constraints (Barbault 1988; Roff 1992). The clarification of the factors determining the body size is the central topics in the studies on the life history of herbivorous insects (Barbault 1988; LaBarbera 1989; Klingenberg and Spence 1997). It has been suggested that the body size of herbivorous insects varies in response to the leaf quality of host plants to successfully feed on their specific hosts (Scriber and Slansky 1981; Brunt *et al.* 2006; Coley *et al.* 2006). Some studies have suggested that the leaf toughness affects the body size, and hence population dynamics and community structure of herbivorous insects (Summerville and Crist 2003; Lewinsohn *et al.* 2005; Woodward *et al.* 2005; Filin and Ovadia 2007).

In temperate deciduous forests, leaf qualities show dynamic seasonal changes with leaf ageing (Feeny 1970; Riipi *et al.* 2002; Murakami *et al.* 2005); young leaves in early spring are high in nutrients (high nitrogen and water contents), less in defensive compounds such as condensed tannin and soft with less fiber and lignin, while mature leaves in summer are low in nutrients, high in defensive compounds, and tough. Therefore, the mature leaves in summer have generally been regarded as poor food resources being hard to be utilized by herbivorous insects (Feeny 1970). However, many lepidopteran larvae can overcome to feed on tough leaves even during summer (Yoshida 1985; Schroeder 1986; Le Corff and Marquis 1999; Forkner *et al.* 2008).

Several examples showed the morphological

difference within an herbivorous insect species to cope with tough leaves. For instance, Bernays (1986) showed a significant relationship between body size of grass-feeding caterpillar, *Pseudaletia unipuncta* Haworth, and leaf toughness of its host plants. He documented the significant effect of leaf toughness on the morphogenesis of head; the larvae having been fed on hard grass developed the head with twice as large in width and weight as those on soft artificial diets. Other previous examples on moth, *Nemoria arizonaria* (Grote) (Greene 1989) and Pierid butterfly, *Pieris napi* (Ohata *et al.* 2010, 2011a, b), grasshopper, *Melanoplus femurrubrum* (De Greer) (Thompson 1999) and beetle, *Galerucella nymphaeae* Linnaeus (Pappers *et al.* 2001), have also reported that such morphological changes in body sizes were attributed to the changes in allocation to foraging effort by bearing stronger muscles to produce more powerful bite force and enable to process the tougher leaves.

In the present study, the allocation between couples of body size traits and the morphs of mandible parts are compared among notodontid species in relation to the leaf toughness of their host plants. Although many lepidopteran families with large body sizes, e.g., Notodontidae, Sphingidae and Saturniidae, are typically summer-feeding species, several spring-feeding species are also included in notodontid species (Mattson 1980; Yoshida 1985), which can be the advantage to study the relationship between seasonal variation in leaf toughness and the larval body size. The other advantage of notodontid moth is that they are mostly monophagous on their host plant, thus the effect of leaf toughness on the body size can be simply analyzed by species-specific manner.

Materials and Methods

Thirty species of Notodontidae were selected for the present study (Appendix 1). They have narrow ranges of host plants, being monophagous to a particular plant species or family. They include two larval phenological types: summer-feeding species overwinter as pupae and their larvae emerge during summer, while spring-feeding species overwinter as egg and the larvae emerge during spring. Both types are univoltine in this study forest.

Rearing and measurements

Eggs were taken from wild-caught females collected in Tomakomai Experimental Forest (TOEF) of Hokkaido University in Hokkaido, northern Japan during five summer seasons from 1990 to 1994. The newly eclosed larvae were reared individually in plastic cup (10 cm in diameter x 4.5 cm in depth). Fresh leaves of their host plants were supplied every two days until the ecdysis to the last instar larvae. The larvae were used to measure the following traits representative of body sizes at respective developmental stages, egg width (EW mm, $n = 10$ for each species), head width of first instar larvae (1stHW mm, $n = 10$); head width (HW mm, $n = 5$), mandible width (MW mm, $n = 5$), mandible mass (MM mg, $n = 5$) and body mass (BM mg, $n = 5$) of last instar larvae of 30 notodontid species. Larvae were measured at 2 days after hatching in first instar, and at 3 days after molting in last instar larvae. The widths of egg, head and mandible were measured by a binocular microscope fitted with an eye-piece micrometer (0.05 mm in accuracy). Larvae were dried to constant mass at 60°C for 24 hrs, and weighed on an electrobalance nearest to 0.001 mg. The last instar larvae were dissected to invest the food contents from their gut lumen before drying to improve the accuracy of body mass measurement.

Leaf toughness ($n = 10$) of each host plant species was measured weekly throughout the growing season of moth larvae from mid-May to late August at TOEF, using a Penetrometer with punch of 3 mm in diameter (Feeny 1970). Ten leaves were measured with avoiding the main vine of leaf for each tree species, respectively.

To understand the biomechanical function of larval mandibles, the ultrastructure of mandibular morphology was examined by a scanning electron microscope (SEM; KEYENCE, VE 8800). To examine the ontogenetic changes in the morphology and function, the mandibular morphology was compared between the first and last instar larvae in a typical summer-feeding species, *Rabta cristata* (Butler), of which larvae occurred in July to August feeding on genus *Quercus crispula* Blume in study area.

Statistical analysis

The relationships between leaf toughness and body size traits were analyzed by generalize linear models, GLMs with Gaussian error structure in which 6 body size traits were the response variables and leaf toughness was the explanatory variable. The relationship between leaf toughness and the allometry between the couples of body size traits was analyzed on

a logarithmic scale using glm using gamma distribution with log links including an offset term. Because the body size traits are correlated each other, the traits as the references were inserted to the model as the offset term; a quantitative variance whose regression coefficient is set to be 1.0 and not estimated in the model (McCullagh and Nelder 1989). In this study, egg width for head width of first instar larvae, body mass for head width, mandible mass, and mandible width of last instar larvae were examined as offset. The data of leaf toughness applied to first instar larvae were taken on 29th May for spring-feeding species, and on 5th July for summer-feeding species. For the last instar larvae, the leaf toughness data were taken on 25th June for spring-feeding species and on 5th August for summer-feeding species. For all models, chi-square tests were performed with null models of no effect of leaf toughness. All the analyses were performed using R (R Development Core Team 2005).

Results

Leaf toughness and larval growing season

Most of the tree species displayed young leaves from the budbreak in mid-May until the end of leaf development in mid- to late June (Fig. 1). In July and August, the leaves became toughest.

Leaf toughness and body size

Significant correlations between leaf toughness and body size traits for last instar larvae were observed, whereas none of relationships were detected for the traits in egg and first instar larvae (Fig. 2). There was none of significant effect of leaf toughness on egg width ($df = 1, 24, P = 0.995$ by chi-square test). In the first instar larvae, the head width was not affected by the leaf toughness ($df = 1, 24, P = 0.494$). On the other hand, for the body size traits for last instar larvae, all the traits measured showed significant correlation with the leaf toughness (HW; $df = 1, 28, P = 0.022$, MW; $df = 1, 28, P = 0.009$, MM; $df = 1, 28, P = 0.016$, BM; $df = 1, 28, P = 0.011$).

With regard to the allocation between several body size traits, the effect of leaf toughness was not significant on the relationship between 1stHW and EW ($df = 1, 24, P = 0.18$). On the other hand, the allocations between body size traits of last instar larvae were significantly affected by the leaf toughness (HW: $df = 1, 28, P = 0.024$; MM: $df = 1, 28, P = 0.011$, MW; $df = 1, 28, P = 0.013$).

Morphology of larval mandible

Larval mandibular morphology showed the striking change from 1st to last instar larvae in *R. cristata* (Fig. 3a, b). In 1st instar larvae, the mandible has the 'toothed shape' with five distinct sharp teeth on the distal edge and shallow grooves between the teeth on the inner surface. In last instar larvae, on the other hand, the mandible bears no teeth but a semi-circular blade and becomes more robust. In addition, there are numerous microsculptures on the surface of mandibles in the last instar larvae (Fig. 3c, d).

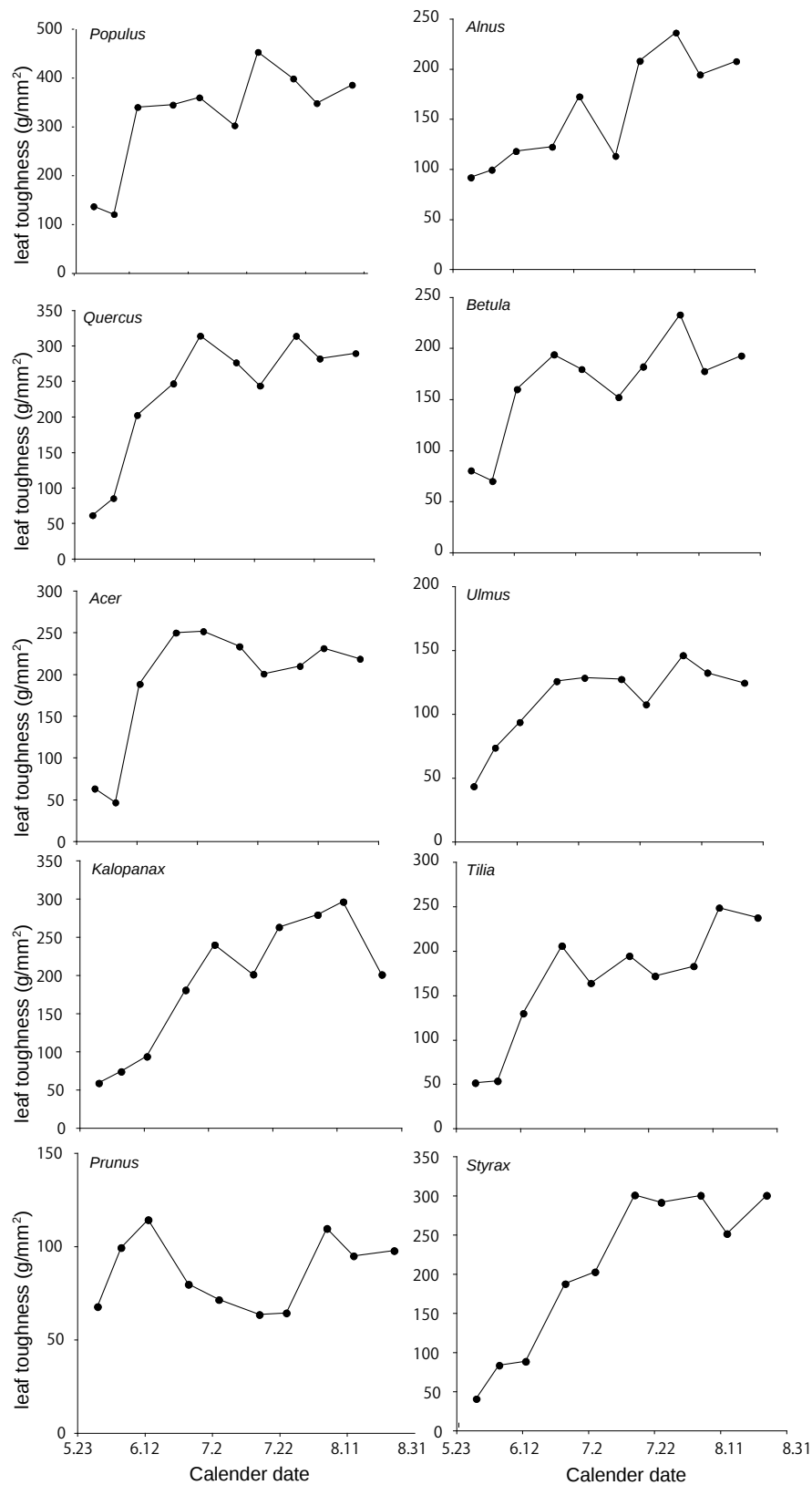


Fig. 1. Seasonal changes in leaf toughness of 10 host plants for the studied notodontid species during larval growing season from May to August, 1995. Mean values of 10 leaf measurements were shown for each tree species (see text).

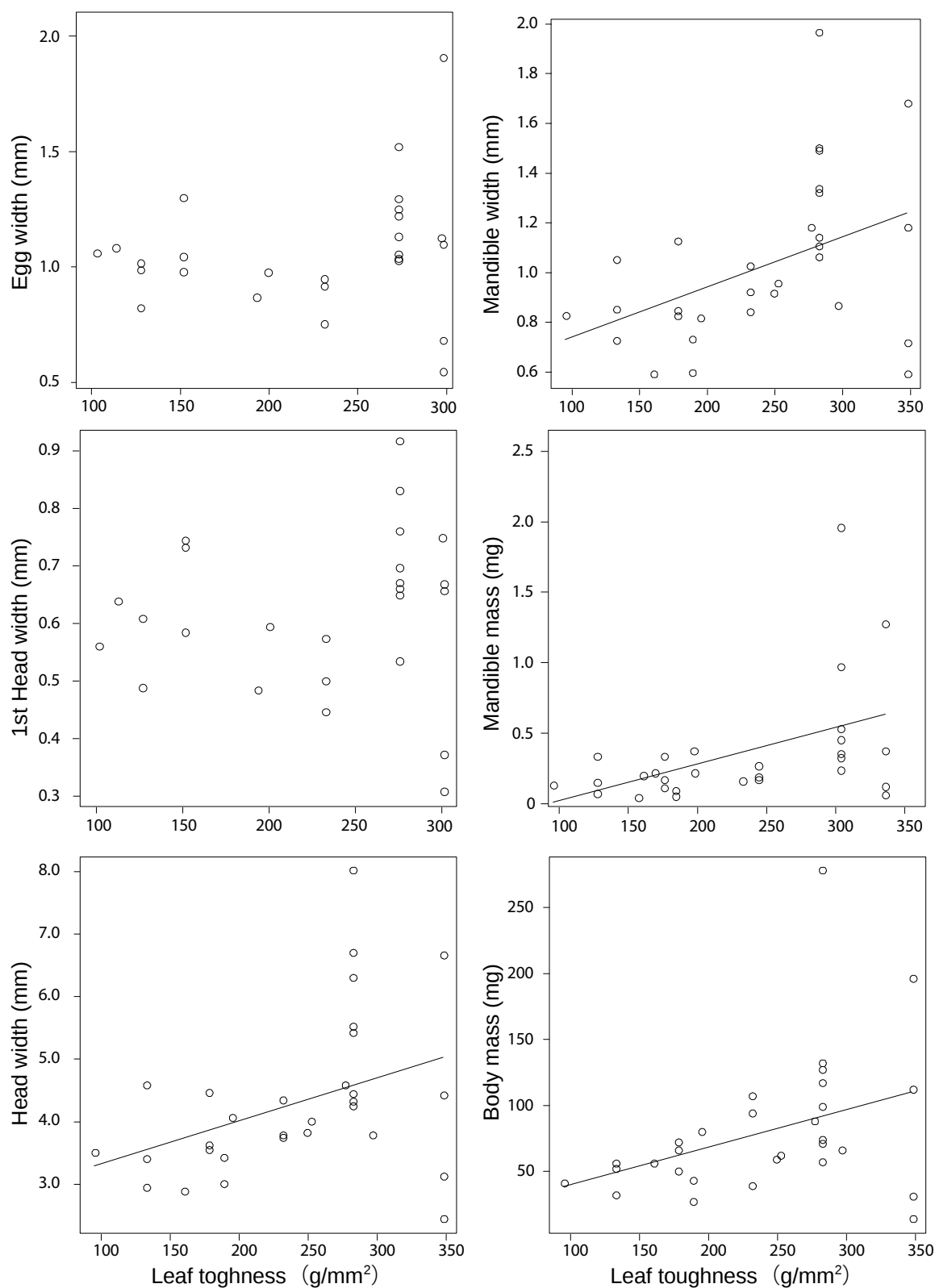


Fig. 2. Correlations between larval morphological traits in 30 notodontid species. The effects of leaf toughness of host plant were shown by the arrows in the top panel. Each point indicates mean values for head width of first instar larvae (1stHW mm, $n = 10$), and head width (HW mm, $n = 5$), mandible width (MW mm, $n = 5$), mandible mass (MM mg, $n = 5$) and body mass (BM mg, $n = 5$) of last instar larvae.

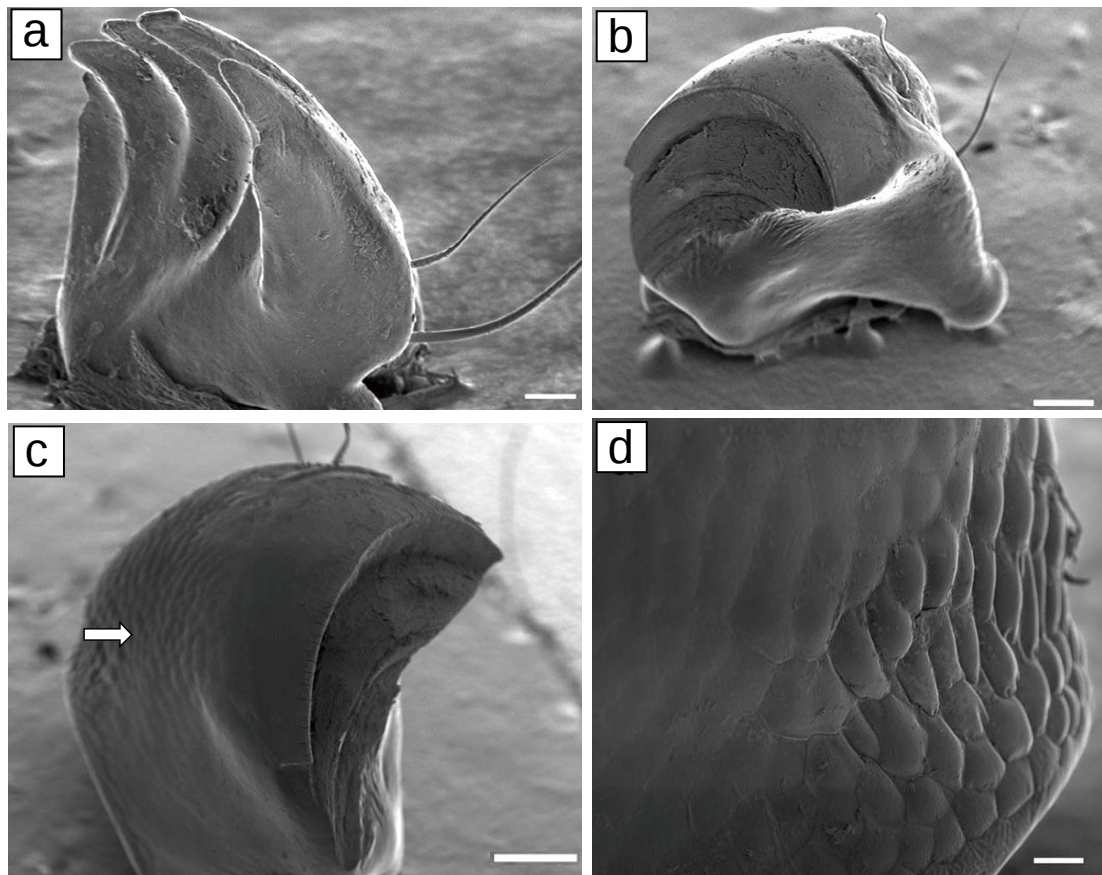


Fig. 3. Mandibular morphology and ultrastructure of first and last instar larvae of *R. cristata*. a: 'toothed type' mandible of first instar larva (scale line = 20 µm). b: 'blade-bearing type' mandible of last instar larvae (scale line = 333 µm). c: microsculpture (allow) on the surface of mandible of last instar larvae (scale line = 333 µm). d: ditto in detail (scale line = 66.6 µm).

Discussion

For the larvae of spring feeders, young leaves (high-nitrogen and soft) are available until mid-June, during which they can complete their larval development. On the other hand, the summer feeders lay their eggs in late June to early July and their early instar larvae emerge in mid- and late July. Therefore, their larvae should face mature leaves and are forced to feed on the low-nitrogen and tough leaves. The analysis of the relationships between body sizes and leaf toughness showed significant correlations at stage of last instar, but not at the stages of egg and first instar larvae. Body mass, head width, and width and mass of mandible of last instar larvae were significantly larger in the species feeding on plant species with tougher leaves. Larger body size being accompanied by larger head and mandible should be adaptive to cope with tough leaves (Mattson 1980; Bernays 1986, 1991).

Kause *et al.* (1999, 2001) showed that the constraint factors of host leaves for determining body size of

herbivorous insects under seasonally varying leaf quality should be divided into two traits, leaf toughness and inadequate nitrogen. If the herbivores are predominantly affected by the leaf toughness, the larvae will be forced to increase to their maximum final body sizes for favorably utilizing the deteriorated leaves of host plants. On the other hand, if the inadequate nitrogen acts as major constraint on larval growth, smaller body sizes will be promoted by the shortage of nutrition. Our results suggested that the constraint factor induced by leaf toughness play predominant role for determining the body size in last instar of notodontid larvae.

The results of allometric analysis can further strongly support this conclusion. The allometry of head and mandibles to the whole body size significantly increased in larvae depending on host plants with tougher leaves. The allometric change in head size implies the increase in mandibular adductor muscles (Eaton 1988; Bernays 1991). Therefore, the larvae of

bigger head with stout and bigger mandibles are advantageous for processing tougher leaves. Bernays and Hamai (1987) reported that the grass feeder species of Acridoidea grasshoppers clearly exhibited larger heads and mandibles than forb feeders, attributing to tougher leaves of grasses than forbs.

However, why did the degree of allocation to the head parts clearly responded to leaf toughness of host plants only in last instar larvae, but not 1st instar larvae? We observed the striking change in mandibular morphology from the 'toothed shape' in the first instar larvae to the 'blade-bearing shape' in the last instar larvae (Fig. 3a, b) of summer-feeder species, *R. cristata*, as like several previous studies (Godfrey et al. 1989; Godfrey 1993; Dockter 1993) and also our observations on the other notodontid species (K. Yoshida, pers. obs.). This morphological change appears to closely associate with the changes in feeding behavior between the first and last instar larvae. By using the sharply toothed mandible (Fig. 3a), newly hatched first instar larvae gouge into relatively soft adaxial surface tissue, not into harder abaxial surface tissue covered with cuticle (Casher 1996; K. Yoshida, pers. obs.). This manner is effective for first instar larvae to selectively feed on the relatively soft mesophyll tissue between the veins, avoiding strongly fibrous and sclerophyllous tissues and leaf veins. On the other hand, the feeding manner of last instar larvae is 'snipping type', feed on most parts of a tougher leaf by cutting even the toughest main veins with the mandibles that can create very strong bite force. The feeding manner of 'snipping type' should require a biomechanically considerable strength of bite force to deal with tough leaves. The strength of bite force, which attributes to the mandibular adductor muscle, may be an important factor for the larvae to successfully acquire their food. The last instar larvae of Notodontidae allocated more growth substances and energy to the head part to increase their bite forces. Herbivorous insects are considered to be in a dilemma between taking more food and minimizing the feeding time to avoid predators (Bernays 1991, 1998; Steiner and Pfeiffer 2007). Under the late summer condition where only tough, less nutritious leaves are available, the 'snipping type' should be the adaptive feeding strategy for the larvae to compromise the two demands by ingesting more diets in a short time period.

We conclude that leaf toughness of food plants affected the life history strategy in Notodontidae, resulting in the larger body size and also the increased allocation to the head and mandibles in last instar larvae. Such functional approach shown in this study can help in our understandings of life history strategies with intricate mechanism that involves ecological, morphological and behavioral traits induced as the adaptive response to food availability in temporal environmental condition in temperate forest.

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Appendix 1. List of 30 notodontid species and their 10 host plants studied. The moths are classified into two types of larval feeding phenology: spring (sp)- and summer (su)- feeders.

Moth species	Feeding phenology	Host plant species
<i>Cerura menciata</i> (Moore)	su	<i>Populus maximowiczii</i> Henry
<i>Quadricalcarifera cyanea</i> (Leech)	su	<i>Styrax obassia</i> Sieb. Et Zucc.
<i>Harpyia umbrosa</i> (Staudinger)	su	<i>Quercus crispula</i> Blume
<i>Fentonia ocypete</i> (Bremer)	su	<i>Q. crispula</i>
<i>Urodonta arcuata</i> Alphéraky	su	<i>Ulmus davidiana</i> var. <i>japonica</i> Nakai
<i>U. branickii</i> (Oberthür)	su	<i>Q. crispula</i>
<i>U. viridimixta</i> (Bremer)	su	<i>Tilia japonica</i> Simonkai
<i>Nerice bipartita</i> Butler	su	<i>Prunus maximowiczii</i> Rupr.
<i>Rabta cristata</i> (Butler)	su	<i>Q. crispula</i>
<i>R. splendida</i> (Oberthür)	su	<i>Q. crispula</i>
<i>Shaka atrovittatus</i> (Bremer)	su	<i>Acer mono</i> Maxim.
<i>Lophocosma atriplaga</i> (Staudinger)	su	<i>Betula platyphylla</i> var. <i>japonica</i> Hara
<i>Notodonta dembowskii</i> Oberthür	su	<i>B. platyphylla</i> var. <i>japonica</i>
<i>N. torva</i> (Hübner)	su	<i>P. maximowiczii</i>
<i>Peridea lativitta</i> (Wileman)	su	<i>Q. crispula</i>
<i>P. oberthueri</i> (Stauginger)	su	<i>Alnus hirsuta</i> Turcz.
<i>Suzukiana cinerea</i> (Butler)	su	<i>Q. crispula</i>
<i>Semidonta biloba</i> (Oberthür)	su	<i>A. mono</i>
<i>Epodonta lineata</i> (Oberthür)	su	<i>Kalopanax pictus</i> Nakai
<i>Phalerodonta manleyi</i> (Leech)	su	<i>Q. crispula</i>
<i>Hexafrenum leucodera</i> (Staudinger)	su	<i>B. platyphylla</i> var. <i>japonica</i>
<i>Ptilodon jezoensis</i> (Matsumura)	su	<i>Q. crispula</i>
<i>P. okanoi</i> (Inoue)	su	<i>A. mono</i>
<i>Odontosia sieversii</i> (Ménétriés)	sp	<i>B. platyphylla</i> var. <i>japonica</i>
<i>Lophontosia cuculus</i> (Staudinger)	su	<i>U. davidiana</i> var. <i>japonica</i>
<i>Himeropteryx miraculosa</i> Staudinger	sp	<i>A. mono</i>
<i>Ptilophora nohirae</i> (Matsumura)	sp	<i>A. mono</i>
<i>Spatialia dives</i> Oberthür	su	<i>U. davidiana</i> var. <i>japonica</i>
<i>Micromelalopha troglodyta</i> (Graeser)	su	<i>P. maximowiczii</i>
<i>Gonoclostera timoniorum</i> (Bremer)	su	<i>P. maximowiczii</i>