

Kazumi Miura · Naota Ohsaki

Relationship between physical leaf characteristics and growth and survival of polyphagous grasshopper nymphs, *Parapodisma subastris* (Orthoptera: Catantopidae)

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Abstract Common types of plant defense mechanisms are thought to affect the host ranges of polyphagous herbivorous insects, yet few studies have examined the relationship between host plant suitability for polyphagous insects and defense against them. We investigated the suitability of the 19 plant species growing in the habitat of the polyphagous grasshopper, *Parapodisma subastris*, to determine the relationship between the physical characteristics of leaves and the growth and survival of grasshopper nymphs. We examined leaf toughness, trichome density, and length. Nymph survival was greater on plants with characteristics ranging from soft leaves and dense trichomes to tough leaves and few trichomes than on plants with soft leaves and few trichomes. The exception was *Rorippa indica*, a plant with soft leaves and few trichomes that uses biotic defense, on which nymph survival was maximal. Higher-quality plants that share common physical characteristics over families may favor polyphagy by grasshoppers that possess ability to overcome the physical defense easily with their robust mandibles.

Keywords Diet · Food selection · Generalist herbivore · Host range · Plant defense strategy

Introduction

In general, herbivorous insects are divided into two feeding categories, oligophagous and polyphagous, although such strategies are actually on a continuum (Bernays and Chapman 1994). Oligophagous insects feed on plants of a single family, whereas polyphagous

insects feed on plants belonging to many families (Bernays and Chapman 1994). Since most herbivorous insects are oligophagous (Bernays and Chapman 1994) and some species and populations of polyphagous herbivorous insects are often observed to be oligophagous at the individual level (Fox and Morrow 1981), host-plant specialization is thought to have selective advantages over polyphagy, although the evidence is still speculative (Dethier 1954; Feeny 1975; Barbosa 1988). A main reason for host specialization is thought to be that polyphagous insects might incur greater costs than do oligophagous insects, which they must defeat various types of plant defense (Ehrlich and Murphy 1988; Joshi and Thompson 1995; Fry 1996).

Some taxonomic groups, such as grasshoppers, are typically polyphagous, even at the individual level (Bernays and Chapman 1994). Polyphagous grasshoppers do not necessarily prefer all plants equally (Chapman 1990). Some researchers have suggested that not only host plant abundance but also host plant intrinsic characteristics affect the preference and distribution of polyphagous grasshoppers (Joern 1979; Chapman and Sword 1994; Sword and Chapman 1994). Therefore, some defense traits may decrease the performance of a polyphagous grasshopper less than other defenses. If a polyphagous insect has the potential to defeat a certain type of defense possessed by various plant families, feeding on many unrelated plants with common defensive characteristics may not be costly. This factor may favor polyphagy in grasshoppers. However, few studies have examined which defensive characteristics are common across plant families (Feeny 1975; Otte 1975; Bernays and Graham 1988).

Plants exhibit several types of defense (Strong et al. 1984; Marquis 1992). In particular, secondary chemicals, frequently family specific, can affect insect performance (Bernays and Chapman 1994; Schoonhoven et al. 1998). Physical defenses, such as leaf toughness and pubescence are common in plants belonging to many families (Feeny 1970; Coley et al. 1985; Levin 1973). Biotic defenses, including the attraction of natural enemies, are also

K. Miura (✉) · N. Ohsaki
Laboratory of Insect Ecology,
Graduate School of Agriculture,
Kyoto University, Kyoto 606-8502, Japan
E-mail: miura@kais.kyoto-u.ac.jp
Tel.: +81-75-7536147
Fax: +81-75-7536474

important (Strong et al. 1984; Bernays 1988; Marquis 1992). No plant can develop every defense because of limited nutrients (Coley et al. 1985), life history (Feeny 1976), or the trade-offs between defensive traits (Mauricio 1998). Therefore, plants develop a few prominent defense mechanisms, and one particular type of defense can predominate in many unrelated plant species.

Parapodisma subaistris Huang (Orthoptera: Catantopidae) is a polyphagous grasshopper that feeds throughout its life cycle on a wide range of dicotyledonous plant families (Miyatake and Kanô 1992). No study has examined the relationships among defense traits of dicotyledonous plants in this grasshopper's habitat, plant quality, and the use of each plant by grasshoppers. Therefore, this study addressed two questions. (1) What kind of defense traits do the plant species frequently used by the grasshoppers have, regardless of plant family? (2) What kind of relationships are there between the defense traits of plants and their quality for this grasshopper? We focused on two physical defense characteristics of leaves, toughness and pubescence, to identify the common defense characteristics over families (Feeny 1970; Coley et al. 1985; Levin 1973), and studied dicotyledonous plant species growing in the habitat of *P. subaistris*. To examine this, we observed plant use by grasshopper nymphs in the field. We also assessed the relationship between the defensive traits and the growth and survival of *P. subaistris* nymphs in the laboratory.

Materials and methods

Study site and organism

The study site (approximately 300×90 m) was located along Otowa-gawa Brook on the south slope of Mt. Hiei in Kyoto City, Japan (35°03'N, 135°48'E; 160 m above

sea level). The brachypterous grasshopper *P. subaistris* occurs only in the Tohkai and Kinki districts of Japan (Miyatake and Kanô 1992). This grasshopper is univoltine and polyphagous, feeding on a wide range of dicotyledonous plants (Miyatake and Kanô 1992). At the study site, nymphs hatch from eggs between mid April and late May, and the adults appear between late July and November (K. Miura, personal observation). Although four *Parapodisma* species occur in Kyoto Prefecture (Miyatake and Kanô 1992), only *P. subaistris* was found at the study site.

Plant use by nymphs in the field

To document the flora at the study site, we sampled 55 quadrats measuring 1.0×0.8 m along the road. The area covered by each plant species was recorded and its biomass estimated on 19 June 1997. Some plant species that were not found in the quadrats but in neighbor plots along the road were also recorded.

To assess how nymphs utilized the plants at the study site, we recorded the time they stayed on, and fed on different plants in the quadrats between June and July 1997. The total observation time was 200 h for 50 individuals.

Growth and survival of nymphs in the laboratory

To assess the growth and survival of nymphs reared on dicotyledonous plant, we collected 19 plant species belonging to 14 families from the study site (see Table 1). In the laboratory, we reared first-stadium nymphs collected on study-site plants between May and July in 1996, 1998, and 1999. We measured survival to adult emergence, development time from second stadium to adult emergence, and body mass of adults immediately after emergence.

Table 1 Plant species used in the nymph-rearing experiments and the plant use by nymphs at the study site

Plant species	Symbol	Family	Cover (%)	Staying time (%) (feeding time (%))
<i>Amorpha fruticosa</i>	Af	Leguminosae	0.2	0.3 (1.1)
<i>Achyranthes japonica</i>	Aj	Amaranthaceae	14.0	0.5 (5.0)
<i>Artemisia princeps</i>	Ap	Compositae	26.4	69.5 (56.0)
<i>Boehmeria nivea</i>	Bn	Urticaceae	2.7	2.4 (2.1)
<i>Boehmeria spicata</i>	Bs	Urticaceae	^a	–
<i>Cayratia japonica</i>	Cj	Vitaceae	<0.1	1.1 (0.0)
<i>Humulus scandens</i>	Hs	Moraceae	0.6	0.03 (0.0)
<i>Malachium aquaticum</i>	Ma	Caryophyllaceae	0.6	–
<i>Plantago asiatica</i>	Pa	Plantaginaceae	^a	–
<i>Polygonum cuspidatum</i>	Pc	Polygonaceae	1.2	11.7 (5.1)
<i>Pueraria lobata</i>	Pl	Leguminosae	2.5	1.5 (3.7)
<i>Paederia scandens</i>	Ps	Rubiaceae	<0.1	1.2 (1.1)
<i>Rorippa indica</i>	Ri	Cruciferae	^a	–
<i>Rosa multiflora</i>	Rm	Rosaceae	0.3	0.014 (11.6)
<i>Rubus palmatus</i>	Rp	Rosaceae	^a	–
<i>Solidago altissima</i>	Sa	Compositae	2.9	1.9 (3.4)
<i>Solanum lyratum</i>	Sl	Solanaceae	0.3	–
<i>Vitis ficifolia</i>	Vf	Vitaceae	^a	–
<i>Weigela hortensis</i>	Wh	Caprifoliaceae	19.9	11.0 (9.8)

^aPlant species growing near the study site, but not in the quadrats studied

Each nymph was placed in a 430-ml plastic cup, along with a fresh leaf with the petiole inserted into a water-filled 1.6-ml glass vial. The cup was covered with nylon mesh for adequate ventilation. The nymphs were reared at 25 °C under a 16 h:8 h light–dark cycle. Every 1 or 2 days, we refilled the glass vials with water as needed and replaced the leaves with fresh leaves that had been collected at the study site the previous one day, packed in plastic bags, and stored at 15°C.

Initially, we prepared 20 nymphs per plant species, but five nymphs escaped during the course of the experiment while leaves were being replaced. All of the nymphs were checked daily for survival and developmental stage. Newly emerged adults were weighed on an electric balance to the nearest 0.1 mg immediately after emergence.

Leaf characteristics and nymph survival

We measured the toughness and pubescence of the leaves of the 19 species of dicotyledonous plants found at the study site (Table 1). For each species, we collected 22 leaves from the middle stems of seven to eight individual plants during June and July 1999. Of these, 12 leaves were used to measure toughness and 10 to measure pubescence.

Leaf toughness was measured using a penetrometer with a 2-mm pin diameter (Aikoh Engineering, Tokyo, Japan). After we measured the penetration load for six points on each leaf, we calculated the average value. Pubescence was measured as the density and length of trichomes per mm² at ten points on both the upper and lower surfaces of each leaf. To measure length accurately, trichomes were pressed straight using a glass slide. For plants with very long and dense trichomes on the lower leaf surface, three pieces were cut with tweezers from the leaf as fine as possible and each piece area was measured under microscope. The trichomes were pulled apart with tweezers before investigating the trichomes.

Leaf pubescence involves four traits: the density and length of trichomes on the upper and lower leaf surfaces. We determined which of the five physical characteristics tested (the four pubescence traits plus toughness) significantly affected the nymph survival rate using stepwise regression analysis. Then, we used a scatterplot to examine the relationships between the nymph survival rate and the leaf characteristics.

Statistical analysis

Since we did not distinguish between female and male first-stadium nymphs, the combined survival of male and female nymphs was compared among plant species, with respect to diet, using a χ^2 -test. We analyzed the correlations between survival rates and adult mass or development time using the Kendall rank correlation coefficient. We also determined whether adult mass and

development time were correlated between sexes using the Kendall rank correlation coefficient.

All physical defense characteristics were analyzed for difference among host plants using analysis of variance (ANOVA) after log-transforming the data. We determined which physical characteristics significantly affected the nymph survival rates using a stepwise multiple regression analysis with 0.2 as the *P*-to-enter and *P*-to-remove values after the nymph survival rates had been arcsine-square root transformed. We used JMP version 4.0 for ANOVA and multiple regression.

Results

Plant use by nymphs in the field

We found 19 plant species at the study site, of which 14 species grew in the sample quadrats. During observations of the nymphs, we confirmed that the nymphs fed on ten of the 12 plant species on which nymphs were observed in the sample quadrats (Table 1). The staying and feeding time of the nymphs on different plant species were correlated with the abundance of different plant species (Kendall rank correlation coefficient: $\tau=0.53$, $P=0.02$, for total time of staying; $\tau=0.49$, $P=0.03$, for total time of feeding; $n=12$).

Growth and survival of nymphs in the laboratory

The survival of nymphs varied significantly among all 19 plant species ($\chi^2=182$, $P<0.001$) (Table 2). Since sex could not be determined for nymphs, the nymph survival rate was assumed to be the same for males and females. As expected, the survival rate was correlated negatively with development time and positively with adult mass (Table 3). Males and females showed similar variation in adult mass (Kendall rank correlation coefficient: $\tau=0.74$, $P<0.001$, $n=13$) and development time (Kendall rank correlation coefficient: $\tau=0.86$, $P<0.001$, $n=13$). These facts suggest that the survival rate is an appropriate index of plant quality.

Relationship between nymph survival and leaf characteristics

The five leaf physical traits measured, leaf toughness, trichome density on the upper and lower surface, and trichome length on the upper and lower surface, varied significantly among all 19 plant species (Table 4). All four leaf pubescence traits were positively correlated among plant species, some significantly so: trichome density on the upper and lower surfaces, trichome length on the upper and lower surfaces, and trichome density and length on the lower surface (Table 5). The four pubescence traits were not significantly correlated with leaf toughness (Table 5).

Table 2 Performance of *P. subastrictis* nymphs on the 19 plant species in order of increasing survival to emergence

Plant species	No. of nymphs examined	Survival to adult ^a	Male			Female		
			No. of adults	Development time (day) ^b	Adult mass (mg) ^b	No. of adults	Development time (day) ^b	Adult mass (mg) ^b
<i>Malachium aquaticum</i>	19	0.00	0	–	–	0	–	–
<i>Boehmeria nivea</i>	20	0.00	0	–	–	0	–	–
<i>Rubus palmatus</i>	20	0.00	0	–	–	0	–	–
<i>Solidago altissima</i>	20	0.00	0	–	–	0	–	–
<i>Vitis ficifolia</i>	20	0.05	0	–	–	1	47	336.7
<i>Achyranthes japonica</i>	20	0.10	2	37 (2.5)	294.0 (21.3)	0	–	–
<i>Solanum lyratum</i>	20	0.10	1	53	220.4	1	57	367.2
<i>Polygonum cuspidatum</i>	19	0.26	2	45 (1.0)	348.5 (28.0)	3	58 (6.8)	424.5 (63.6)
<i>Rosa multiflora</i>	20	0.35	4	67 (2.3)	217.9 (20.4)	3	84 (3.3)	259.3 (64.0)
<i>Weigela hortensis</i>	20	0.35	2	78 (12.5)	202.9 (15.9)	5	74 (4.5)	309.4 (22.4)
<i>Cayratia japonica</i>	20	0.40	4	40 (3.2)	268.9 (31.6)	4	42 (3.1)	467.9 (53.3)
<i>Boehmeria spicata</i>	20	0.55	8	31 (1.2)	316.5 (15.2)	3	32 (0.9)	483.1 (20.1)
<i>Paederia scandens</i>	20	0.65	5	36 (1.8)	314.9 (32.1)	8	42 (1.4)	389.9 (41.9)
<i>Amorpha fruticosa</i>	20	0.75	9	46 (1.5)	321.1 (12.4)	6	54 (2.6)	515.3 (23.6)
<i>Artemisia princeps</i>	19	0.79	10	31 (0.5)	378.2 (8.5)	5	36 (0.7)	590.0 (35.5)
<i>Pueraria lobata</i>	20	0.80	7	30 (0.4)	396.3 (14.4)	9	31 (0.3)	551.9 (14.0)
<i>Rorippa indica</i>	20	0.80	10	28 (0.4)	393.2 (14.1)	6	32 (1.1)	584.6 (28.5)
<i>Humulus scandens</i>	18	0.89	8	31 (0.6)	397.4 (17.0)	8	34 (0.5)	557.5 (10.2)
<i>Plantago asiatica</i>	20	1.00	11	27 (0.3)	425.1 (17.0)	9	30 (0.4)	636.9 (25.9)

^aMales and females were combined^bMean (SE)**Table 3** Kendall's rank correlation coefficients between nymph survival and development time or the adult mass. Only the plant species ($n=14$) from which adults emerged were examined. The nymph survival rate was assumed to be the same between the sexes

	Development time	Adult mass
Male	-0.60 ($P=0.003$)	0.72 ($P<0.001$)
Female	-0.57 ($P=0.004$)	0.70 ($P<0.001$)

Based on the results of the stepwise multiple regression analysis, toughness ($F=5.54$, $P=0.032$) and trichome density on the upper leaf surface ($F=4.90$, $P=0.042$) were selected as representative measures of leaf defenses. This multiple regression ($F=3.81$, $P=0.04$, coefficient of determination: $R^2=0.32$) revealed that the survival rate increased with increasing toughness (partial regression coefficient: $b=34.0$) and increasing trichomes density ($b=1.19$).

Table 4 Physical resistance traits of the 19 plant species studied. All data are given as the mean (SE). The plants are listed in alphabetical order

Plant species ^a	Leaf toughness (Newton)	Leaf pubescence			
		Upper surface		Lower surface	
		Density (per mm ²)	Length (mm)	Density (per mm ²)	Length (mm)
<i>Amorpha fruticosa</i>	0.19 (0.01)	36.7 (5.4)	0.13 (0.01)	31.5 (4.43)	0.18 (0.01)
<i>Achyranthes japonica</i>	0.19 (0.01)	0.76 (0.1)	0.57 (0.03)	0.32 (0.04)	0.47 (0.03)
<i>Artemisia princeps</i>	0.28 (0.04)	17.0 (2.0)	0.51 (0.03)	512 (75.0)	0.80 (0.06)
<i>Boehmeria nivea</i>	0.27 (0.01)	1.2 (0.2)	0.54 (0.06)	344 (56.2)	0.93 (0.05)
<i>Boehmeria spicata</i>	0.86 (0.07)	1.9 (0.3)	0.48 (0.04)	0.92 (0.08)	0.33 (0.02)
<i>Cayratia japonica</i>	0.62 (0.04)	3.6 (0.3)	0.12 (0.01)	0.40 (0.10)	0.23 (0.02)
<i>Humulus scandens</i>	0.18 (0.02)	14.6 (5.5)	0.66 (0.03)	1.71 (0.5)	0.66 (0.03)
<i>Malachium aquaticum</i> ^a	0.20 (0.02)	0	–	0	–
<i>Plantago asiatica</i>	1.16 (0.09)	0.79 (0.31)	0.30 (0.08)	1.69 (0.8)	0.23 (0.04)
<i>Polygonum cuspidatum</i> ^a	1.23 (0.09)	0	–	0	–
<i>Pueraria lobata</i>	0.93 (0.05)	14.0 (1.8)	0.43 (0.03)	22.4 (2.34)	0.43 (0.02)
<i>Paederia scandens</i>	0.81 (0.08)	0.79 (0.13)	0.71 (0.08)	5.43 (0.65)	0.72 (0.12)
<i>Rorippa indica</i> ^a	0.26 (0.02)	0	–	0	–
<i>Rosa multiflora</i>	0.19 (0.03)	18.2 (4.5)	0.31 (0.02)	44.0 (3.01)	0.66 (0.01)
<i>Rubus palmatus</i>	0.51 (0.06)	1.3 (0.42)	0.27 (0.02)	6.18 (1.60)	0.44 (0.08)
<i>Solidago altissima</i>	0.32 (0.03)	12.3 (1.0)	0.12 (0.00)	24.6 (1.94)	0.28 (0.02)
<i>Solanum lyratum</i>	0.12 (0.01)	6.8 (0.50)	0.76 (0.07)	8.19 (0.51)	0.69 (0.04)
<i>Vitis ficifolia</i>	0.49 (0.03)	6.2 (0.9)	0.46 (0.05)	170 (41.5)	2.71 (0.19)
<i>Weigela hortensis</i>	0.73 (0.05)	1.6 (0.3)	0.21 (0.03)	42.6 (4.54)	0.49 (0.02)
Plant difference	$F=50.3$ $P<0.0001$	$F=42.1$ $P<0.0001$	$F=25.9$ $P<0.0001$	$F=182.7$ $P<0.0001$	$F=66.8$ $P<0.0001$

^aTrichomes absent

Table 5 Matrix of Kendall's rank correlation coefficients among the leaf physical traits of the 19 plant species. *UD* trichome density on the upper surface, *UL* trichome length on the upper surface, *LD* trichome density on the lower surface, *LL* trichome length on the lower surface

	LL	LD	UL	UD
Toughness	-0.19	-0.14	-0.23	-0.24
UD	0.26	0.52*	0.16	
UL	0.62*	0.30		
LD	0.54*			

* $P < 0.003$ (by Bonferroni multiple comparison)

We used a scatterplot to examine the relationships between nymph survival and leaf toughness and trichome density on the upper surface. All lower-quality plants had relatively soft leaves and few trichomes (shown within the gray box in Fig. 1). *Rorippa indica* was the only plant with these characteristics but with high-quality (Fig. 1). The higher-quality plants (except *R. indica*) (survival rates ≥ 0.25) had a range of characteristics, from relatively soft leaves with dense trichomes to those with relatively tough leaves with few trichomes (Fig. 1).

Discussion

The 19 plant species growing within the range of the polyphagous grasshopper *P. subastricta* exhibited great variation in their leaf characteristics (Table 4). Although the variation in the leaf characteristics among plant species was continuous (Fig. 1), some plants tended to exhibit one predominant trait (such as leaf toughness or leaf trichomes), as compared to the others (Fig. 1).

Plant quality was related to the leaf characteristics. The higher-quality plants, in terms of nymph survival (except *R. indica*), tended to have either soft leaves with dense trichomes or tough leaves with few trichomes. These physical defense traits might be effective against very small, immature insects with fragile mandibles, but

P. subastricta can feed on these plants easily using its tough mandibles. Therefore, the grasshoppers are not affected by the physical defense trait and benefitted, in terms of nymphal growth and survival, by using plants that employ physical defenses. Since plants that employ physical defenses are better food for polyphagous grasshoppers, such plants may be their main food plants (Table 1). In fact, nymphs fed on the high-quality plant, such as *Artemisia princeps*, for 70% of the total feeding time (Table 1).

All the lower-quality plants had soft leaves with few trichomes (except *R. indica*) (Fig. 1). These plants probably had more non-physical defenses, such as chemical defenses, than the higher quality plants. The grasshopper nymphs had the lowest survival rates on such plants, presumably because of secondary metabolites or low levels of essential nutrients (Marquis 1992) that lower the performance of herbivores (Augner 1995). A trade off between physical and chemical defenses has been reported (Hanley and Lamont 2002). Consequently, plants tended to exhibit one defense trait predominantly. In the field, the nymphs fed on both higher and lower quality ones (Table 1). When they feed on low-quality plants, they may defeat chemical defenses by mixing their diets (Miura and Ohsaki 2004). Survival is frequently increased when polyphagous grasshoppers feed on a mixture of low-quality plants (MacFarlane and Thorsteinson 1980; Bernays and Bright 1993; Bernays et al. 1994; Miura and Ohsaki 2004). Such improved performance is known as the effect of diet mixture (Bernays and Bright 1993). This effect is considered to be one of the main factors maintaining polyphagy in grasshoppers. When they feed on small amounts of each plant species, they might obtain complementary nutrients (Pulliam 1975; Westoby 1978) or dilute the toxin each plant possesses (Freeland and Janzen 1974).

Rorippa indica was classified as a high-quality plant, although it had few trichomes and soft leaves. *R. indica* produces nectar continuously, which attracts ants that guard the plant from herbivorous insects (Yano 1994). Therefore, a biotic defense mechanism might be the main type of defense in this species. Our results suggest that this plant has reduced physical and chemical defenses. Since none of the other plants studied in this habitat used biotic defenses, we have not confirmed any effects of this type of defense on the grasshopper nymphs.

Various factors determine the costs and benefits of the dietary range of an herbivorous insect (Bernays and Graham 1988). Some classic theories of plant-herbivore coevolution assume that chemical defense and counter-defense evolve between plants and herbivores (Ehrlich and Raven 1964; Thompson 1994). Therefore, the host ranges of oligophagous insects may be closely related to specialization on family-specific chemical defenses (Ehrlich and Raven 1964). Conversely, our results suggest that nymphs of the polyphagous grasshopper *P. subastricta* can defeat plant physical defenses and thereby utilize plants from a wide range of families.

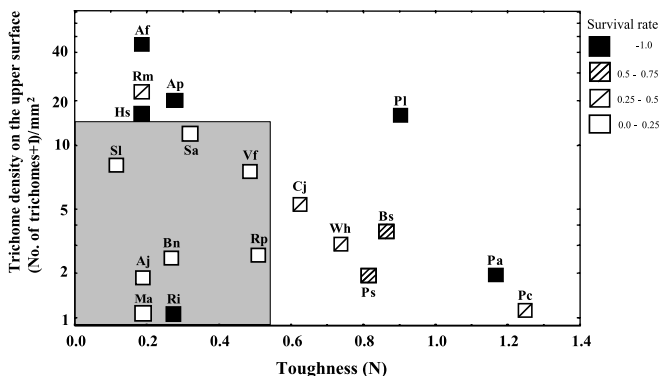


Fig. 1 Relationship between the physical characteristics of leaves (leaf toughness and trichome density on the upper surface) and nymph survival. *Open squares* nymph survival ≤ 0.25 , *squares with diagonal line* nymphal survival 0.25–0.5, *cross-hatched squares* nymph survival 0.5–0.75, *solid squares* nymph survival ≥ 0.75

Plant defenses might evolve through interactions with multiple herbivore species, since pairwise coevolution between a plant and an herbivore is rare (Fox 1988). To better understand defense characteristics of a plant, polyphagous and oligophagous herbivores on the plant should be examined comprehensively.

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