Insect Science

Insect Science (2025) 0, 1–13, DOI 10.1111/1744-7917.70142

ORIGINAL ARTICLE

Offspring performance does not explain oviposition preference in the leafminer *Stigmella sorbi* (Lepidoptera: Nepticulidae): a tri-trophic perspective

Mikhail V. Kozlov and Vitali Zverev

Department of Biology, University of Turku, Turku, Finland

Abstract The non-random distribution of herbivorous insects on plants is often assumed adaptive. However, many studies fail to demonstrate this adaptiveness. To test the predictions of the preference–performance and optimal foraging hypotheses, while addressing adaptiveness of oviposition site selection for progenies (larvae) and females, respectively, we examined larval mine distributions (a proxy for egg distribution) of the pygmy moth *Stigmella sorbi* across shoots, compound leaves and leaflets of rowan (*Sorbus aucuparia*). The study was conducted near the subarctic town of Kirovsk, in northwestern Russia, from 1992 to 2007. Larvae survived best on long vegetative shoots, yet *S. sorbi* females showed no preference for shoot type, even though generative shoots are a potential carbohydrate source. They preferentially oviposited on basal leaflets, despite offspring mortality from both bottom-up and top-down factors being unaffected by leaflet position. This preference may benefit females rather than offspring by reducing sunlight and predator exposure. The presence of multiple *S. sorbi* mines on the same leaf did not affect parasitism rates or cocoon weight compared to solitary mines. However, clumping significantly increased the mortality of newly hatched larvae and explained the more even mine distribution among leaflets observed in high-density years. Our findings do not unequivocally support the preference–performance or apparency hypotheses. However, some patterns may appear adaptive when viewed through the lens of an optimal foraging strategy, proposing that *S. sorbi* maximizes overall fitness through oviposition behaviour that prioritizes female performance over offspring performance.

Key words apparency hypothesis; competition; insect–plant interactions; Kola Peninsula; optimal foraging hypothesis; parasitism; preference–performance hypothesis; *Sorbus aucuparia*; within-plant distribution

Introduction

Herbivores searching for feeding or oviposition sites encounter highly heterogeneous resource whose quality depends on multiple factors and varies across phylogenetic, spatial and temporal scales (Denno & McClure, 1983; Roslin *et al.*, 2006; Herrera, 2009). Their selection is influenced by chemically mediated resource suitability (including nutritional quality) and abundance, predation and parasitism risks, and competitive interactions (Bultman & Faeth, 1985, 1986; West, 1985; Boomsma *et al.*, 1987; Tack *et al.*, 2009; Jiao *et al.*, 2012). The adaptiveness of such selection is often evaluated within the framework of the preference–performance hypothesis, which posits that female insects preferentially oviposit on plants or plant parts where their offspring will perform best (Jaenike, 1978, 1990; Thompson, 1988; Gripenberg *et al.*, 2010).

Correspondence: Mikhail V. Kozlov, Department of Biology, University of Turku, 20014 Turku, Finland. Email: mikoz@utu.fi

The seeming non-adaptiveness of some herbivory distribution patterns (Mayhew, 1997; Gripenberg *et al.*, 2010)—observed, albeit at varying frequencies, in both specialist and generalist herbivores, and more commonly on native than non-native hosts (Jones *et al.*, 2019)—can be reconciled through the optimal foraging theory, which proposes that fitness is maximized by obtaining the maximum offspring for minimum cost for an ovipositing female (Pyke *et al.*, 1977). For low-mobility herbivores, such as leafmining insects, female feeding sites and related female performance may explain most of the variation in oviposition site selection (Scheirs *et al.*, 2000). Finally, the plant apparency hypothesis (Feeny, 1976) suggests that herbivores save energy and minimize predation risks by preferentially exploiting the most apparent resource rather than searching for the best plant or its highest-quality parts.

Simultaneous testing of the predictions derived by the preference–performance, optimal foraging and apparency hypotheses requires data on the availability and quality of resources not only for the offspring but also for the ovipositing females. These data are rarely reported in plant–herbivore studies, even though such data could reveal the adaptive value of herbivore oviposition strategies when the preference–performance hypothesis does not hold (examples listed by Faeth, 1991; Valladares & Lawton, 1991; Gripenberg *et al.*, 2007). Additionally, intraspecific competition, which reduces the size and survival of insect herbivores, particularly leafminers (Digweed, 2006; Sugiura *et al.*, 2007), can also lead to mismatches between oviposition preference and offspring performance, especially in high-density years.

Plant traits are generally assumed to vary more between than within species (Garnier *et al.*, 2001; McGill *et al.*, 2006; Shipley *et al.*, 2016). Accordingly, studies on insect–plant interactions usually focus on host use at the species level (Marques *et al.*, 2000; Gripenberg *et al.*, 2010; Novotny *et al.*, 2010) or, less frequently, on differences in palatability among individuals of the same plant species (Suomela & Ayres, 1994; Laitinen *et al.*, 2000; Roslin *et al.*, 2006). However, resource characteristics can also vary within individual plants, depending on the shoot type, leaf position within a shoot, leaf size and shape (including asymmetry), and even feeding site location within a leaf (Denno & McClure, 1983; Viswanathan & Thaler, 2004; Roslin *et al.*, 2006; Gripenberg *et al.*, 2007; Malishev & Sanson, 2015; Kozlov *et al.*, 2018). Despite its importance, this within-individual trait variation has largely been overlooked in plant ecology (but see Sánchez-Bermejo *et al.*, 2023; and references therein), even though it could account for more than 25% of total trait variation (Davrinche *et al.*, 2023) and may have evolutionary implications (Herrera, 2009). Consequently, the impact of within-individual plant heterogeneity on the distribution of herbivorous insects remains poorly understood.

Uncertainties surrounding the effects of within-individual variation in plant traits on insect herbivores are compounded by the dynamic nature of tri-trophic interactions. These interactions are shaped by feedback linking resource quality and quantity, herbivore abundance and fitness, and abiotic factors, such as weather. For example, insect herbivores often prefer specific shoot types or sizes (Fritz *et al.*, 1987; Santos *et al.*, 2008; Johns *et al.*, 2015). Consequently, year-to-year variations in shoot production (Luomajoki, 1999; Ishihara & Kikuzawa, 2009) can influence both the quantity and quality of preferred resources, with unknown effects on herbivore oviposition preferences and larval performance.

Finally, previous studies have considered plant quality as the key determinant of offspring performance (Yamaga & Ohgushi, 1999), despite repeated emphasis on the importance of top-down factors for shaping herbivore oviposition preferences (Björkman *et al.*, 1997; Garvey *et al.*, 2020). Consequently, meta-analysis that has evaluated the predictions of the preference–performance hypothesis (Gripenberg *et al.*, 2010) has been limited to bitrophic interactions, leaving top-down influences on population fitness outside its scope.

Our goal in the present study was to explore the adaptiveness of within-individual herbivore distribution patterns within the frameworks of three theoretical models: preference–performance, optimal foraging and plant apparency. To achieve this goal, we examined the mine distribution of the pygmy moth *Stigmella sorbi* (Stainton) across shoots, compound leaves and leaflets of rowan (*Sorbus aucuparia* Linnaeus), and we compared the identified patterns with the resource availability and quality for ovipositing females and their offspring. We tested the following predictions: (1) mine distribution within a host plant is clumped, with preferences for certain shoot types (generative vs. vegetative shoots, long vs. short vegetative shoots), for leaves within a shoot and for leaflets within a leaf (basal to apical, large to small); (2) oviposition preference patterns match the distribution of female carbohydrate resources (rowan corymbs); (3) larval performance (in terms of plant-driven larval survival, parasitism rate, and cocoon weight) is highest at sites preferred by ovipositing females; (4) co-occurrence of two or more larvae in the same leaflet or leaf decreases larval performance; and (5) the strength of oviposition site preferences within a rowan tree decreases as the leafminer intensity increases.

Materials and methods

Study site

The study was conducted on the southwestern outskirts of Kirovsk, Murmansk district, Russia (67°36′10″N, 33°40′16″E, 320 m above sea level), approximately 100 km north of the Arctic Circle. The region experiences a mean temperature of −14 °C in January and 13 °C in July, with annual precipitation averaging 740 mm. The frost-free period lasts between 50 and 100 d, and the cool summer season extends for about 2.5 months.

We explored rowan trees planted from native seedlings in the mid-1960s to protect the road leading to Kirovsk from snowdrifts. The first habitat, referred to as forest, contained approximately 400 trees growing on natural soils with dense field layer vegetation, spanning an area of 100 × 300 m. The second habitat, referred to as roadside, comprised about 100 trees planted in a 5 m wide belt along a 200 m stretch of constructed, sandy, trampled soil practically devoid of field layer vegetation. The central points of the two habitats were separated by about 200 m.

Insect and host plant

Stigmella sorbi (Stainton) (Lepidoptera: Nepticulidae) is a very small (wing span 5–7 mm), oligophagous, univoltine nepticulid moth, widely distributed across boreal Europe and Siberia. In the Murmansk region of Russia, leaf mines of *S. sorbi* have been observed on rowan (*Sorbus aucuparia* Linnaeus) and common cotoneaster (*Cotoneaster integerrimus* Medikus). In more southern areas, its mines were also found on other species of *Sorbus* and *Cotoneaster*, as well as on *Amellanchier* and *Malus* species (van Nieukerken, 1986).

In the study area, moths are on the wing from late June to early July. Nepticulids take sugar water, honey or water in captivity (van Nieukerken *et al.*, 1990). Females of *S. sorbi* lay eggs on the undersides of the host plant leaves. At the time of oviposition, rowan corymbs are the only source of carbohydrates available to the females. The mines of *S. sorbi* are distinctive, as young larvae produce a narrow gallery, whereas mature larvae form a characteristic blotch. Larvae feed within the mine for 2–3 weeks before dropping to the ground, where they spin cocoons, pupate and hibernate.

Rowan is a stress-tolerant competitor plant that grows in the study region as a multi-trunk shrub reaching heights of 5–8 m. This deciduous species has compound pinnate leaves (Fig. 1) ranging from 40 to 295 mm in length (median 147 mm) with 5–19 elongated-lanceolate, sharply serrated leaflets (median 14 leaflets). Foliage emerges in late May to mid-June and turns yellow to dark red by late August to early September. Rowan is monoecious and matures at around 10 years of age. It flowers from June to the beginning of July, producing yellowish-white corymbs containing 50–250 flowers. The fruits, round pomes 6–8 mm in diameter, ripen from August to September, turning orange to scarlet.

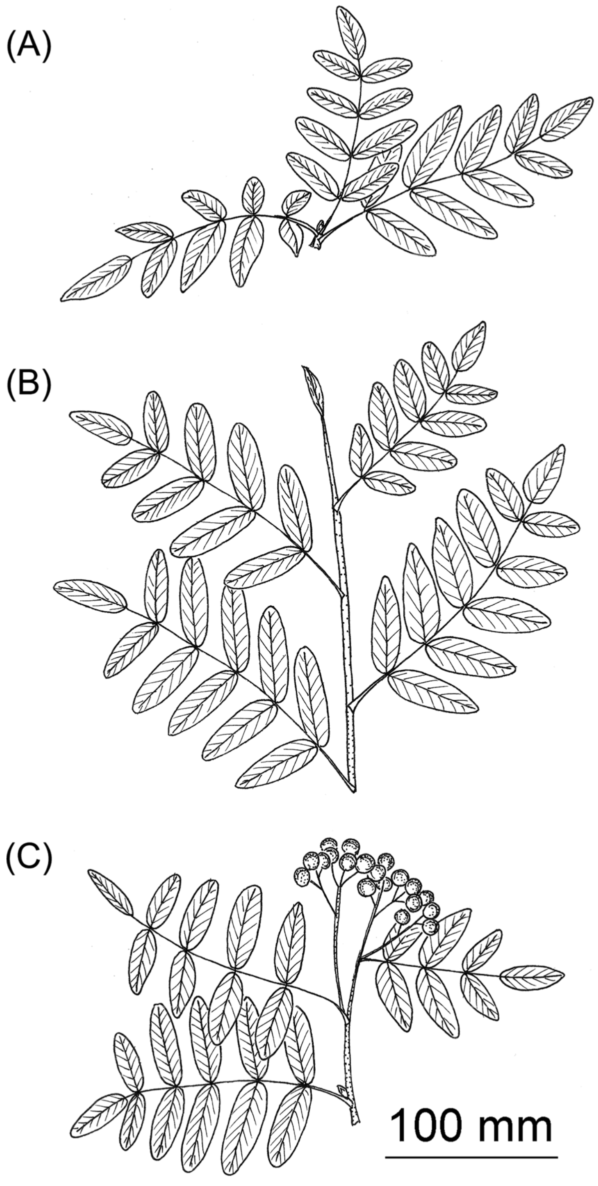

Fig. 1 Shoot types of rowan, *Sorbus aucuparia*: (A) short vegetative shoot; (B) long vegetative shoot; and (C) generative shoot.

Rowans produce three types of shoots. Vegetative short shoots (Fig. 1A) bear 1–9 leaves (usually 3) and grow

1–17 mm per year (median 5 mm); their main function is photosynthesis. Vegetative long shoots (Fig. 1B) bear 2–13 leaves (usually 6–7), and grow 18–360 mm (median 180 mm); their main function is canopy expansion. Generative long shoots (Fig. 1C) bear 1–9 leaves (usually 3–4) and a corymb, and grow 26–173 mm (median value 105 mm); their main function is reproduction.

Rowan traits

We tested whether mines were randomly distributed among shoot types, leaves and leaflets by assessing the occurrences of respective traits from 1996 to 2002 on each of 10 individually marked rowan trees in each of the two habitats (Data S1). The starting points for these censuses were selected haphazardly within each tree, and the observer recorded the type of the first 100 shoots and the number of leaves on these shoots while moving clockwise around the tree. The first shoot of each type was collected from each tree for measurements of leaf length and leaflet number (Data S2). Leaflet areas were measured from samples collected in 2007 (Data S3).

Insect herbivory

The intensity of *S. sorbi*, expressed as the number of mines per 100 leaves (Data S4), was recorded from 1992 to 2007 in the same individually marked rowan trees studied for trait variations. The census starting point was chosen haphazardly within each tree, and the observer counted the mines on the first 100 leaves while moving clockwise around the tree. From 1996 to 2001, we conducted 10 censuses per tree, while in the remaining years, we conducted one census per tree. The censuses were conducted in late summer (early- to mid-August in our study area), after the larvae had completed their development.

In 1997 and 1999, we also measured foliage losses of rowan to externally feeding defoliators (Data S5), using shoots collected for leaf trait measurements. In the laboratory, the leaves were categorized into the following damage classes based on a visual assessment of the percentage of the consumed leaf area: 0% (intact), 0.01%–1% and 1%–5%. No leaves exhibited damage exceeding 5%. Herbivory levels were calculated by multiplying the number of leaves in each damage class by its median percentage (0.5% for 0.01%–1% and 3% for 1%–5%). The resulting values were summed across all classes and divided by the total number of leaves in the sample (Alliende, 1989; Kozlov *et al.*, 2015).

Herbivory distribution within rowan trees

Mine distribution within trees—which served as a proxy for egg distribution—was examined from 1992 to 2005 using leaf samples collected from haphazardly selected trees in both habitats (Data S6). The number of mines collected each year varied with the *S. sorbi* population density, ranging from 118 in 2003 to 902 in 1992 (mean = 340 mines). We recorded the shoot type, the position of the mined leaf within the shoot and the number of leaves in the shoot, the position of the mined leaflet within the leaf and the number of leaflets in the leaf. We measured the leaf lamina length (to the nearest 1 mm) as the distance from the base of the first (proximal) leaflet to the apex of the last (distal) leaflet. The within-leaf distribution of damage imposed by externally feeding defoliators was explored only in 1997 and 1999.

Cocoon weight

In 1992, after recording mine positions, we placed all leaflets with mines containing live larvae into individual plastic vials and monitored larval development for about a week. Larvae that successfully formed cocoons were dried at 105 °C for 48 h, and both cocoons and mined leaflets were weighed to the nearest 0.01 mg (Data S7). The cocoon weight was used as a proxy for leaf quality.

Larval survival

Mines collected for distribution analysis (see above) were categorized as either completed or failed. Completed mines included mines vacated by larvae and those still containing live larvae at the time of collection. Failed mines were further divided into two classes (Data S6): early failures (small gallery mines) and late failures (medium-sized to large blotch mines). Parasite identity was determined based on adults that eclosed from failed mines after hibernation.

Data analysis

The distributions of rowan foliage and *S. sorbi* mines across shoot types, leaves and leaflets—as well as differences in these distributions between habitats and years—were explored using frequency analysis (SAS FREQ procedure; SAS Institute, 2009) and compared using a goodness-of-fit test (Sokal & Rohlf, 2000). Clumping of mines within leaves and leaflets was quantified by an aggregation index (the variance/mean ratio), which measures the deviation of the mine distribution from the random (Poisson) model (Taylor, 1984). A random mine distribution results in an aggregation index of one, while higher values indicate mine clumping.

For mine distribution among leaflets (the only nonrandom pattern found; see Results), we calculated the year-specific values of feeding niche breadth (FNB = $\Sigma_j \sqrt{p_j a_j}$), where p_j represents the proportion of *S. sorbi* mines found on leaflet j, and a_j represents the proportion of leaflet j's area relative to the total leaf area (Smith, 1982). The standard error of the FNB was calculated following Zhivotovsky (1982).

Leaf length and cocoon weight were analyzed using mixed-model ANOVA (SAS GLIMMIX procedure). The relationships between leaf area and leaf length were assessed via regression analysis (SAS REG procedure). The proportion of leafminers that died due to different causes was analyzed using a generalized linear mixed model with a binomial error distribution and a logit link function employing the event/trial syntax and residual pseudo-likelihood estimation method (SAS GLIMMIX procedure). Associations between variables were evaluated using Pearson linear or Spearman rank correlation coefficients, depending on the data properties (SAS CORR procedure).

Results

Rowan traits

The shoot population (n = 13 934, across two habitats and all study years; Data S1) was dominated by vegetative short shoots, followed by vegetative long shoots and generative shoots (Fig. 2A). The proportions of shoot types varied significantly across the study years ($\chi^2_{12} = 434.9$, $P < 0.0001$) and between habitats ($\chi^2_2 = 1050.2$, $P < 0.0001$).

The percentage of generative shoots ranged from 6.5% in 2002 to 13.4% in 1998 ($\chi^2_6 = 12.8$, $P = 0.046$). In the roadside habitat, the percentage of generative shoots was one-third of the percentage in the forest habitat (4.3% and 14.9%, respectively; $\chi^2_1 = 45.3$, $P < 0.0001$). Among vegetative shoots, the percentage of long shoots varied from 5.5% in 1998 to 25.8% in 2001 ($\chi^2_6 = 25.9$, $P = 0.0002$). In the roadside habitat, the percentage of long vegetative shoots was three times higher than in the forest habitat (24.1% and 8.1%, respectively; $\chi^2_1 = 54.6$, $P < 0.0001$). The annual variations in shoot type frequencies were inconsistent between habitats (generative shoots: $r_S = 0.14$, $n = 7$ years, $P = 0.76$; long vegetative shoots: $r_S = 0.21$, $n = 7$ years, $P = 0.64$).

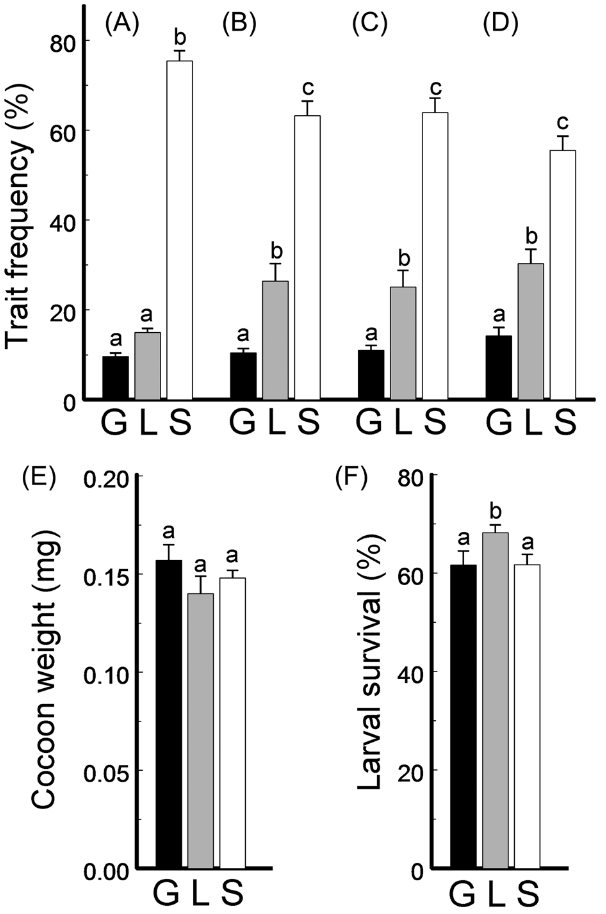

Fig. 2 Variation in rowan, *Sorbus aucuparia* and the leafminer, *Stigmella sorbi* among shoot types: (A) shoot number; (B) leaf number; (C) leaf area; (D) mine number; (E) cocoon weight; and (F) larval survival. Shoot types: G, generative; L, long vegetative; S, short vegetative. Bars marked with different letters differ significantly ($P < 0.05$) from each other.

The numbers of leaves per shoot differed significantly between habitats ($\chi^2_7 = 995.7$, $P < 0.0001$), study years ($\chi^2_{42} = 1177.6$, $P < 0.0001$) and shoot types ($\chi^2_{24} = 12200.4$, $P < 0.0001$), with an average of 2.98 leaves in short vegetative shoots, 6.36 in long vegetative shoots and 3.78 in generative shoots. Consequently, the distribution of leaves among shoot types (Fig. 2B) differed significantly ($\chi^2_2 = 10.7$, $P = 0.0047$) from that of the shoots (Fig. 2A). Shoots with 5–13 leaves comprised 10% of the shoot population (Fig. 4A).

Leaf length (Data S2) was significantly ($F_{1,\,3346} = 3.98$, $P = 0.0460$) greater in the forest habitat (mean ± SE: 143.8 ± 1.2 mm, $n = 1602$ shoots) than in the roadside habitat (139.1 ± 1.0 mm, $n = 1797$ shoots). It varied from 126.9 ± 2.76 mm in 2002 to 174.6 ± 2.6 mm in

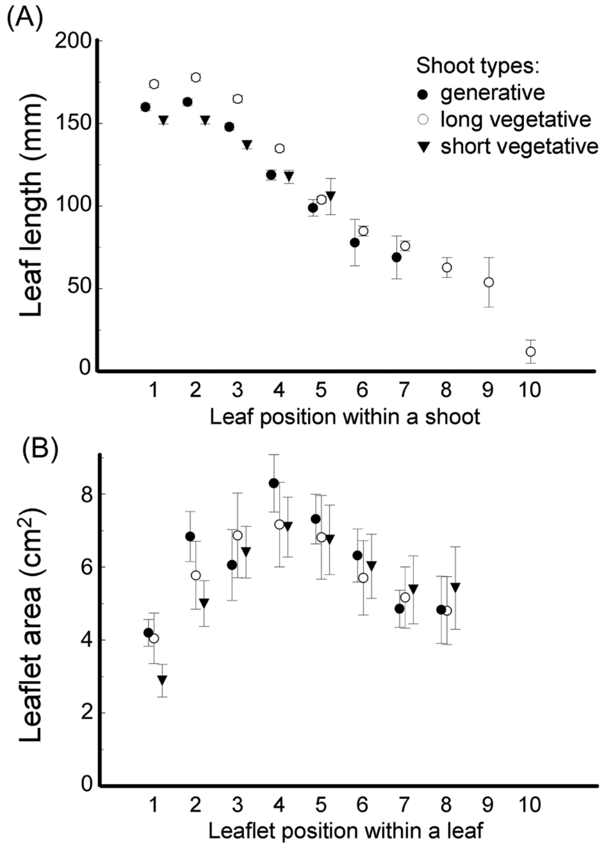

Fig. 3 Within-plant variation in rowan, *Sorbus aucuparia*: (A) leaf length within a shoot and (B) leaflet area within a leaf.

1999 ($F_{11,\,3346} = 36.7$, $P < 0.0001$), although this variation was not synchronized between habitats ($F_{11,\,3346} = 28.8$, $P < 0.0001$). The differences in leaf length between shoot types were highly significant ($F_{2,\,3346} = 13.2$, $P < 0.0001$), but relatively minor (Fig. 3A). Consequently, the distribution of leaf area among shoot types (Fig. 2C) did not differ significantly ($\chi^2{}_2 = 0.06$, $P = 0.97$) from the distribution of leaf numbers (Fig. 2B). Leaf length varied within a shoot ($F_{7,\,3346} = 149.9$, $P < 0.0001$), reaching a maximum at the second leaf and decreasing toward the shoot apex (Fig. 3A), with a similar pattern across all shoot types (interaction term: $F_{10,\,3368} = 1.51$, $P = 0.13$). Consequently, shoots with 5–13 leaves contributed less than 5% to the total leaf area (Fig. 4C).

Leaf area (LA, cm^2; Data S3) increased with leaf length (LL, mm) according to the equation: LA $= 0.00265 \times$ LL$^2 + 5.34$ ($R^2 = 0.77$; $F_{1,\,28} = 95.4$, $P < 0.0001$). The relationship between LL and LA did not differ between shoot types ($F_{2,\,24} = 0.75$, $P = 0.48$).

The number of leaflets per leaf (1 to 19; median = 14) increased significantly with leaf length ($r = 0.54$, n

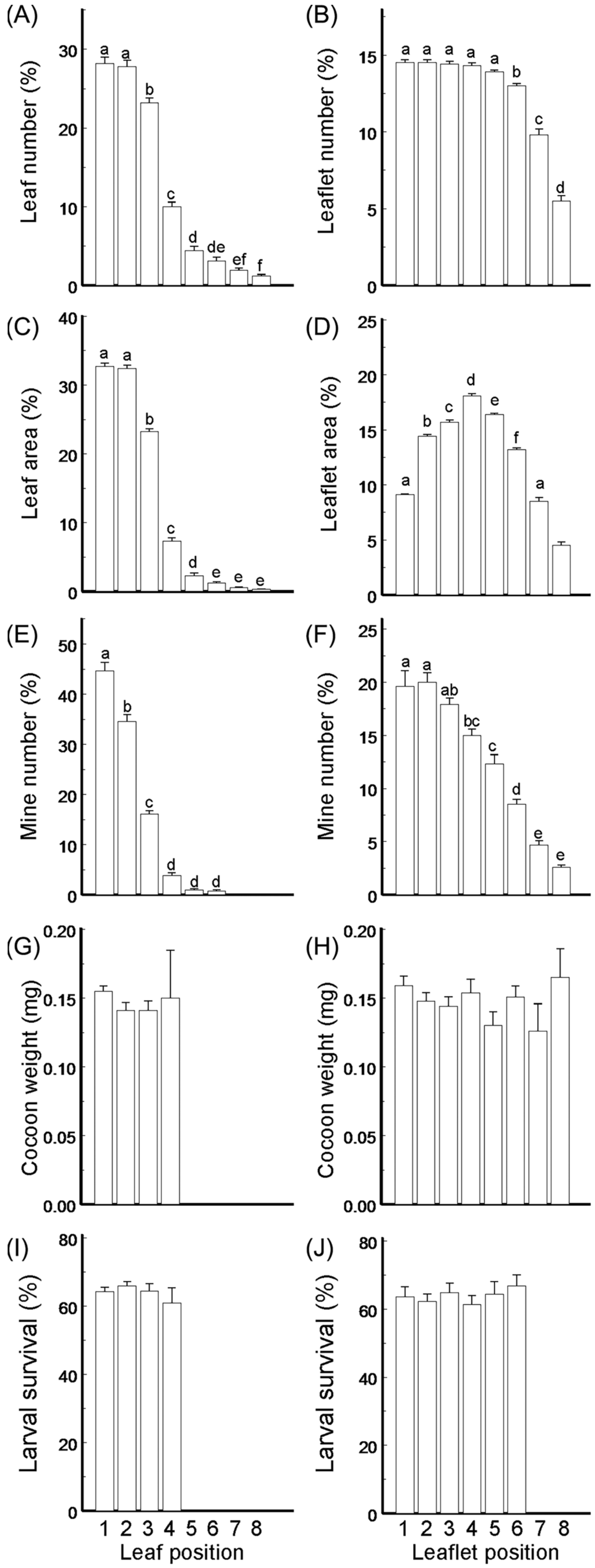

Fig. 4 Variation in rowan, *Sorbus aucuparia* and the leafminer, *Stigmella sorbi* among leaves within a shoot (A, C, E, G, I) and among leaflets within a leaf (B, D, F, H, K): (A) leaf number; (B) leaflet number; (C) leaf area; (D) leaflet area; (E, F) mine number; (G, H) cocoon weight; and (I, J) larval survival. Bars marked with different letters differ significantly ($P < 0.05$) from each other.

= 3390 leaves, $P < 0.0001$). The leaflet area (Fig. 3B) was independent of shoot type ($F_{2,\,195} = 0.62$, $P = 0.54$) but varied significantly with leaflet position within a leaf ($F_{8,\,195} = 8.41$, $P < 0.0001$), peaking at mid-leaf (Fig. 3B). The relationship between leaflet area and leaflet position did not differ between shoot types (interaction term: $F_{15,\,195} = 0.23$, $P = 0.99$). Superposition of the leaflet frequency (Fig. 4B) on the leaflet area (Fig. 3B) resulted in a dome-shaped distribution of leaflet area within the leaf population (Fig. 4D).

Insect herbivory

Leafminer intensity (Data S4) over the 13 study years varied 36 fold, from 0.36 mines per 100 leaves in 1998 to 12.95 mines per 100 leaves in 1994 ($\chi^2{}_{12} = 91.9$, $P < 0.0001$). In the roadside habitat, leafminer intensity was 3.4 times higher than in the forest habitat (4.09 and 1.20 mines per 100 leaves, respectively; $\chi^2{}_{1} = 64.3$, $P < 0.0001$), but the intensity fluctuations among years were synchronous between habitats ($r_S = 0.70$, $n = 13$ years, $P = 0.0075$). Within habitats, the intensity did not differ among individual trees (forest: $\chi^2{}_{9} = 2.89$, $P = 0.97$; roadside: $\chi^2{}_{9} = 5.87$, $P = 0.75$).

Since the area of a completed blotch mine accounts for 1%–2% of the rowan leaf area and since 16% of the mines failed to develop a blotch, the annual leaf area consumption by *S. sorbi* in our study habitats ranged from 0.005% to 0.163%. Losses of rowan to externally feeding defoliators (Data S5) were of a similar magnitude: 0.072% ± 0.023% in 1997 and 0.141% ± 0.041% in 1999.

Mine distribution within rowan trees

We examined positions of 4762 mines, with 2717 originating from vegetative short shoots, 1383 from vegetative long shoots and 662 from generative shoots (Data S6). Mine distribution among shoot types (Fig. 2D) differed significantly from the distribution of shoot numbers (Fig. 2A; $\chi^2{}_{2} = 24.3$, $P < 0.0001$) but matched the distribution of leaf numbers (Fig. 2B; $\chi^2{}_{2} = 2.90$, $P = 0.23$) and leaf areas (Fig. 2C; $\chi^2{}_{2} = 3.11$, $P = 0.21$).

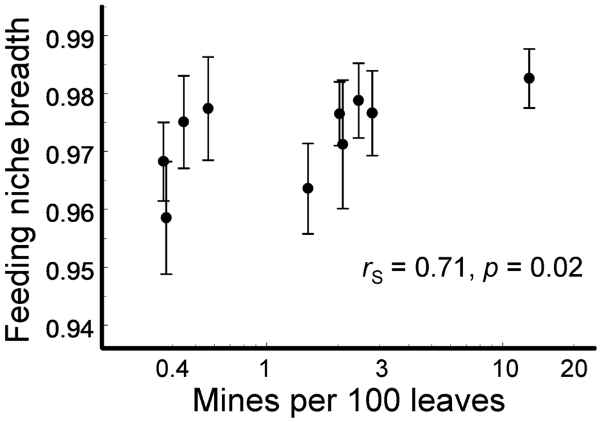

Fig. 5 Feeding niche breadth within a compound leaf of rowan, *Sorbus aucuparia* (mean ± SE) in relation to the intensity of the leafminer, *Stigmella sorbi*.

Within a shoot, the highest number of mines (2224) was found in the first leaf, with frequencies declining toward the shoot apex (Fig. 4E). The mine frequencies differed significantly from the leaf number distributions (Fig. 4A; $\chi^2{}_{5} = 24.7$, $P = 0.0002$) but aligned with the distribution of leaf areas within shoots (Fig. 4C; $\chi^2{}_{5} = 9.41$, $P = 0.09$). The number of mines within an infested leaf ranged from 1 to 7. The aggregation index, calculated using combined data from the study period, was 1.1, indicating slight clumping of mines at the leaf scale.

Within a leaf, the greatest number of mines (1015) occurred in the first leaflet, with frequencies decreasing toward the leaf apex (Fig. 4F). These frequencies corresponded to the distribution of leaflet numbers (Fig. 4B; $\chi^2{}_{7} = 10.7$, $P = 0.15$) but differed significantly from the distribution of leaflet areas within a leaf (Fig. 4D; $\chi^2{}_{7} = 18.6$, $P = 0.0097$). The number of mines within an infested leaflet ranged from 1 to 4. The aggregation index was 1.2 in 1992 and 1.3 in 1999, indicating slight mine clumping at the leaflet scale. The within-leaf distribution of the foliar damage caused by externally feeding defoliators did not differ from the distribution of *S. sorbi* mines (1997: $\chi^2{}_{7} = 6.64$, $P = 0.47$; 1999: $\chi^2{}_{7} = 10.7$, $P = 0.15$). The within-leaf FNB increased with leafminer intensity across study years (Fig. 5).

Cocoon weight

The cocoon weight (Data S7) did not vary between habitats (Table 1), shoot types (Fig. 2E), leaves within a shoot (Fig. 4G), leaflet sizes ($r = 0.03$, $n = 273$ leaflets, $P = 0.57$) or leaflet positions within a leaf (Fig. 4H). Larvae that shared a leaflet with 1–4 conspecifics produced

Table 1 Sources of variation in cocoon weight and larval mortality of *Stigmella sorbi* (SAS GLIMMIX procedure, type 3 sum of squares).

Source of variation	Cocoon weight			Larval mortality		
	F	df	*P*	*F*	df	*P*
Habitat	1.92	1, 228	0.17	2.14	1, 4719	0.14
Shoot type (ST)	0.24	2, 228	0.79	3.91	2, 4719	0.02
Leaf position (LF)	0.44	3, 228	0.73	0.55	3, 4719	0.65
Leaflet position (LT)	0.79	7, 228	0.60	0.45	5, 4719	0.82
ST × LF	1.31	4, 228	0.27	2.58	6, 4719	0.02
ST × LT	0.94	12, 228	0.51	1.72	10, 4719	0.07
LF × LT	0.86	13, 228	0.60	1.42	15, 4719	0.13

cocoons of similar weight to those that developed alone (0.158 ± 0.004 mg, $n = 19$ cocoons and 0.148 ± 0.003 mg, $n = 254$ cocoons, respectively; $F_{1,271} = 0.62$, $P = 0.43$).

Larval survival

Of the 4762 collected mines, 1746 (36.7%) contained dead larvae (Data S6). Leafminer mortality over the 14 study years varied 3.4 fold, from 17.6% in 1994 to 60.0% in 1996 ($\chi^2_{13} = 490.2$, $P < 0.0001$). In the roadside habitat, leafminer mortality was slightly but significantly lower than in the forest habitat (35.2% and 38.6%, respectively; $\chi^2_1 = 5.84$, $P = 0.0157$). Leaves with failed mines were slightly but significantly longer than leaves with completed mines (151.7 ± 12.9 mm and 147.0 ± 12.9 mm, respectively; $F_{1,3195} = 15.2$, $P = 0.0001$).

A total of 765 larvae (16.1%) died during the gallery mine stage, whereas 981 larvae (20.6%) perished after developing a blotch. No parasitoids were reared from the gallery mines, hinting that mine failure was caused by plant antibiosis. More than 90% of the larval deaths in blotch mines resulted from parasitism by wasps of the family Eulophidae, including *Chrysocharis pentheus* (Walker), *Pnigalio agraules* (Walker) and *Burkseus vittatus* (Walker). No predation of *S. sorbi* by ants or birds was observed.

Larval survival varied among shoot types (Table 1), being highest in long vegetative shoots (Fig. 2F), but it did not vary within shoots (Fig. 4I) or within leaves (Fig. 4J). However, early-stage mortality (in gallery mines) was significantly lower in long vegetative shoots (estimated marginal means ± SE: 11.8% ± 1.3%) than in short vegetative shoots (17.1% ± 1.8%). In generative shoots, early-stage mortality (14.6% ± 2.3%) did not differ significantly from that in vegetative shoots. Mortality at the blotch stage was significantly higher in the apical (4th–7th) leaves of long vegetative and generative shoots (26.3% ± 4.4% and 31.0% ± 4.9%, respectively) than in their basal (1st) leaves (15.5% ± 1.6% and 17.4% ± 2.3%, respectively).

Larvae that shared a leaf with 1–6 conspecifics experienced significantly higher mortality than those developed alone (48.3% and 38.2%, respectively; $\chi^2_1 = 27.0$, $P < 0.0001$). This pattern was driven by increased mortality among young larvae in groups compared to solitary mines (34.2% and 20.5%, respectively; $\chi^2_1 = 51.2$, $P < 0.0001$), which did not increase with leafminer intensity ($r_S = -0.42$, $n = 10$ years, $P = 0.23$). In contrast, mortality at the blotch stage was not affected by conspecific presence (26.6% and 29.4%, respectively; $\chi^2_1 = 1.97$, $P = 0.15$).

Discussion

The preference–performance hypothesis

The relationship between oviposition preference and offspring performance is fundamental to understanding plant–herbivore interactions, particularly the distribution of insects within host plants. Natural selection is expected to favor ovipositing females that select sites with high plant quality for their progeny (Jaenike, 1978, 1990; Thompson, 1988; Gripenberg *et al.*, 2010), given the environmental and phylogenetic constraints that influence female decision-making (Bergamini & Almeda-Neto, 2015).

The meta-analysis by Gripenberg *et al.* (2010) supported several predictions of the preference–performance hypothesis, particularly the influence of host quality on larval survival; however, empirical evidence remains limited. That meta-analysis was based on only 21–29 plant-type comparisons, depending on the response variable, with fewer than half addressing within-plant variation. Since then, only a handful of studies have explored this topic using a multiscale approach.

Leafmining insects, their host plants, and their natural enemies represent an ideal system for testing the preference–performance hypothesis, as the position of mines within a plant depends solely on the female oviposition preference. Furthermore, measurements of leaf and mine characteristics offer reliable insights into the behaviour of ovipositing females and the fate of individual larvae (Zvereva & Kozlov, 2006; Morton & Pereyra, 2011; Kozlov *et al.*, 2023). However, the inability to account for potential variation in egg mortality represents a notable limitation in studies using leafminers as model organisms. Nevertheless, given the persistent scarcity of empirical data, we revisited a dataset on *S. sorbi* leafminers collected over two decades ago (initially set aside due to a lack of strong patterns) to test hypotheses explaining within-plant herbivore distribution.

Rowan trees exhibited significant variations in shoot type and size, as well as in leaf and leaflet traits between habitats, among shoots and leaves, and across study years. Nevertheless, cocoon weight (a measure of larval performance) remained consistent across these scales, indicating stable plant quality. Similarly, *S. sorbi* females showed no preference for specific trees, shoot types or leaf positions; instead, they oviposited in proportion to the available leaf area. This lack of variation in both preference and performance limits the testing of the preference–performance hypothesis to scales where significant variation in either trait was detected.

We found that solitary *S. sorbi* larvae suffered significantly lower mortality at the gallery mine stage when compared with larvae sharing a leaf with conspecifics, suggesting that the mine clumping in this species is non-adaptive. However, the absence of a significant correlation between population intensity and early larval mortality across study years indicates that the observed increase in within-leaf FNB mitigates competition-related effects, thereby aligning with the preference–performance hypothesis, although not providing unequivocal support for it. The low infestation of rowan by *S. sorbi* (a median of two mines per 100 leaves) makes the detection and avoidance of previously oviposited plant parts (as reported for dipteran leafminers: Quiring & McNeil, 1987) an unlikely driver of an observed FNB increase. Instead, we propose that *S. sorbi* females adjust their oviposition behaviour by decreasing their preference for basal leaflets in response to the sex pheromones of conspecific females, as previously suggested for two leafroller species (Stelinski *et al.*, 2014).

Although larval survival was 10% higher on long vegetative shoots, *S. sorbi* females did not preferentially oviposit on these shoots. This mismatch with the preference–performance hypothesis suggests that the scarcity of long shoots on a plant (Fig. 2) makes locating them costly or risky for females, outweighing the minor advantage in larval survival.

The apparency hypothesis

The apparency hypothesis predicts that herbivores preferentially exploit highly apparent resources (Feeny, 1976). Under the random oviposition strategy observed in *S. sorbi*, larger or more exposed shoots and leaves receive more eggs simply because they are more noticeable or accessible (Gripenberg *et al.*, 2007; and this study). However, since leafminer intensity does not differ between the more and less abundant shoot types or leaf sizes, the observed pattern neither aligns nor contradicts the apparency hypothesis.

In contrast to the random distribution of oviposition sites at broader scales, *S. sorbi* females exhibited a strong preference for the basal leaflets of rowan, where mines were twice as frequent as expected from the leaflet area. This pattern clearly contradicts the predictions of the apparency hypothesis.

The optimal foraging hypothesis

The optimal foraging hypothesis views female performance as a key component of overall fitness (Scheirs & De Bruyn, 2002) that may shape the spatial distribution of oviposition sites, as demonstrated for the grass miner *Chromatomyia nigra* (Meigen) (Scheirs *et al.*, 2000). The lack of spatial association between *S. sorbi* mines and rowan corymbs suggests that *S. sorbi* females may not require carbohydrates during oviposition—glucose and fructose being components of rowan nectar—and instead rely on pure water. This finding invalidates our prediction based on the optimal foraging hypothesis. However, we identified another spatial pattern that likely aligns with this hypothesis. Because none of the studied measures of larval performance varied among leaflets, we suggest that the preference for basal leaflets benefits ovipositing *S. sorbi* females rather than their progeny.

The oviposition behaviour of *S. sorbi* remains unknown, but studies of related species offer insights.

Females of *Fomoria septembrella* (Stainton) have been observed running along the margins of the lowest leaves on a *Hypericum* shoot, seemingly measuring them before ovipositing or moving to a higher leaf (van Nieukerken *et al.*, 1990). Since these females run rather than fly between leaves, they first reach the leaf base. We suggest that a female's preference for leaf parts closest to the petiole likely minimizes energy expenditure and predation risk.

The avoidance of bright light, as observed in *S. malella* (Stainton) females (Chambon, 1968), could also explain the preference for basal leaf parts, as the basal leaflets provide a more shaded environment compared to apical leaf parts. The overlapping basal leaflets offer protection from direct sunlight and wind, reducing desiccation risk and increasing the persistence of water droplets (arising from fog and rain) that can be used by females. These factors could also explain the steeper decline in mine numbers from the shoot base to its apex (Fig. 2E) compared to the available leaf area (Fig. 2C).

Conclusions

Despite a multi-scale approach and long-term observations, we found only equivocal support for predictions based on the preference–performance hypothesis. This finding corroborates previous conclusions (Roslin & Salminen, 2009; Ruhnke *et al.*, 2009) that selection may not consistently favor a particular oviposition behaviour in herbivores that face substantial and unpredictable variations in host quality across space and time. However, certain patterns that are not explained by the preference–performance or apparency frameworks may be better understood as potentially adaptive when considering female fitness through the lens of the optimal foraging hypothesis. These results underscore the need to integrate existing plant–herbivore interaction models into a cohesive framework.

Acknowledgments

We thank E. Haukioja for methodological advice and support during the initial phase of the project; E. Melnikov, A. Vassiliev, E. L. Zvereva, A. Wolf, and S. Koutaniemi for their contributions to data collection; C. Hansson for identifying parasitic wasps; E. J. van Nieukerken for information on pygmy moth biology; and E. L. Zvereva for insightful discussions and valuable comments on an earlier draft of the manuscript. This study was supported by the Research Council of Finland (formerly the Academy of Finland; projects 122133, 214824 and 362371), the European Commission through the BASIS and BALANCE projects (contracts ENV4-CT97-0637 and EVK2-2002-00169), the Turku University Foundation, and the Maj and Tor Nessling Foundation.

Open access publishing facilitated by Turun Yliopisto, as part of the Wiley - FinELib agreement.

Disclosure

The authors declare no conflict of interests.

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Manuscript received March 29, 2025
Final version received July 1, 2025
Accepted July 7, 2025

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1 The occurrences of shoot types in each of 10 individually marked rowan trees in each of the two habitats from 1996 to 2002.

Data S2 Leaf length and leaflet number in the first shoot of each type collected from each of 10 individually marked rowan trees in each of the two habitats from 1994 to 2007.

Data S3 Leaflet areas in leaves collected in 2007.

Data S4 The number of *Stigmella sorbi* mines per 100 leaves in each of 10 individually marked rowan trees in each of the two habitats from 1992 to 2007.

Data S5 Foliage losses of rowan to externally feeding defoliators in 1997 and 1999.

Data S6 Fate and distribution of *Stigmella sorbi* mines within rowan trees from 1992 to 2005.

Data S7 Dry weight of *Stigmella sorbi* cocoons and mined leaflets collected in 1992 relative to mine position within rowan trees.