Is plant chemistry determining mortality and dispersal of young
Epirrita autumnata larvae?

SAMANTEKT

hør er ophøyiende at alværda þá þætti sem valda mismunandi lauf-
skada ef skilja á þróun varna gege júttaætum. Þú í náttunni er tveimt
sem orsaka þau Það einstök þa verða lýr menu laufskada en önnur tré
vöru dregur, mérilegum. Það getur staðið undir fleiri júttaætum, eða
hver einstök júttaætta getur 48 mill. meira magn laufa mæli í biliða.
Mis-
mun í atvelli við landbýr í ekki orsaka dauða lífvernar munn
þádæglega hala afrit það hafa lífiðstöðu vesta lengri og endanaegle staða
júttaætum, á meðan breskeiði í fjöldi júttaætta mun að lækkiðum
alværda mun í laufskála plána innan plöntunsumsins.

Val skórdyra á varýntað, og drifling og aflið á ungum lífum alværda
sniðilega fjöldi skórdyra sem næstest til tilvikinna plöntu. Það er vitl
lyr húnstöðvandi, Epirita autumnata, að meður eru ekki vendýskur
þær eru eru á 6 veppa. Hinnið er lítið vitlað um dreifingu og aflið
a ungum E. autumnale lífum. Hér sýnið er niðurstöður við tvíevum til-
lagnum þar sem sviðsdreifing á spjallvbúð, og aflið a ungum lífum
vors umhliðu á einstökum bóttni sem vitlað var að höfða mismun-
andi lífisfræðismiður. Niðurstöður við þessum lágnum benda a
óttu leggða húnna gett það afrit á aflið hafa ungum E. autumnale lífum,
af seru líkt til að hala afrit á dreifingu þeirra.

traits affecting oviposition selec-
tion, dispersal and mortality of
young larvae could be consid-
ered as the most efficient plant
defenses against herbivorous
insects since they will determine the
final number of consumers sustained and, thus, the defolia-
tion experienced by different
plants. Instead, plant characteris-
tics modifying feeding behavior
without affecting mortality of
individuals i.e., pre capita con-
sumption, will mostly determine
the affect the length of larval period
and the final size of individuals

that will not drastically change the defoliation of the plants in the
current season. Furthermore, both aspects may be determined,
caused by the same factors with additive or non-additive effects,
and they can also modulate the responses of the natural enemies of
the herbivores (Leather and
Walsh 1991; Thompson 1999a,
Hunter and Ellerton 2000).
Furthermore, distinguishing
these different steps in the inter-
action between plants and her-
 biforous insects can also be is
relevant to understand the evolu-
tion of their relationships since
mother selection and young lar-
vae selection both imply active
selection by the herbivores who
would in turn play the role of
selection pressure on plant char-
acteristics, whereas, survival of
young larvae implies differential
mortality and thus plants would
be in this case the selection
pressure on herbivores (Thomp-
son 1998b). Only detailed field
studies of herbivore densities
and defoliation can distinguish
these different sources of varia-
tion under natural conditions
(e.g., Hunter et al. 1997; Hunter
and Ellerton 2000). In addition,
indoor controlled experiments
may be useful, however, to eval-
uate the potential relevance of
these different stages and spe-
cially to discard those with
low possibilities to affect the in-
teraction between particular
species.
The interaction between the
autumn moth (Epirrita autumna-
lla) and one of its main host
plants the white birch (Betula
pendula), has been studied from
many different perspectives
(Kochmalski et al. 2001 and ref-
erences therein). Epirrita autumna
is a univoltine geometrid species.
Individuals overwinter as eggs,
and the new generation hatches
in spring, when synchrony with leaf
flush is important for larval de-
velopment (Hayes and McLean
1967). Duration of the larval stage
depends on temperature and
foliage quality. The pupal ni-
sted reached at the end of larval
development is a good estimate of
utilized adult fecundity (Tammaru
et al. 1996). The short-lived adults
active in autumn. Females do not
usually fly before oviposition and
they are not selective while ov-
position (Tammaru et al. 1999, 1996). Although E. aestivalis larvae are polyphagous leaf chewers, mountain birch (Betula pubescens subsp. compassus (Orfisia) Hämet-Ahti) due to its abundance is their main host plant in Northern Fennoscandia (Kallio and Lehikoinen 1973), where the species periodically cause severe defoliations. Mountain birch leaves contain relatively high levels of different phenolic compounds (Olovsson et al. 1997) whose quantities vary among individual trees and with leaf development (Siaunu et al. 1999, Nummi et al. 1996) and can affect E. aestivalis performance (e.g., Kause et al. 1999). Among these phenolic compounds high gallic acid concentrations are characteristic of young developing leaves (Olovsson et al. 1997, Kause et al. 1999) and thus, they are potentially suitable defensive compounds against the earliest season leaf fed larvae. The neonate larvae of E. aestivalis. However, little is known about the effects of birch chemistry on dispersal and mortality of young E. aestivalis larvae.

The dispersal of neonate larvae by ballooning has been described in some other Lepidopteran species such as Lynxiptera cupreata (Lynn) (Lymantridae) (Hunter and Eklinton 2000). Geometra stigma (Geometridae) (Tikkonen 2000), Oasiris vitula (Lynn) (Lym- mantridae) (Harrison 1995, and Tribe (1994). Psychidae) (Chent 1999), in relation to host plant species, budburst pherom- ological, natural enemies and abiotic conditions. None of these studies has tried, however, to test if larvae can use the same mech- anism to discriminate conspecific plants differing in leaf characteristics other than phenochemistry (see Harrison 1999). Here present results from two experi- ments where ballooning dispersal and mortality of young larvae were studied in individual mountain birch trees known to differ in their foliage chemistry.

Materials and methods
Balloon experiment
Ballooning studies were carried out on early June 1998 using the same 30 mountain birch trees whose leaves had been previously analyzed and tested for quality as food for E. australis larvae (Lemak et al. 2000). Two other substrates than mountain birch, a glass bar and a branch of pine, were also used to test the capa- bility of E. australis larvae to balloon under laboratory condi- tions. As a standard procedure a table home ventilator (Finnell) was used to produce a continuous air flow that allow larvae to ex- cepe from the host using silk fila- ments (ballooning). Both larvae found on the table and those observed while ballooning were recorded as "ballooning" individ- uals. All the experiments were done at room temperature (22-23°C). Larvae used in both experiments belonged to labora- tory reared strains maintained at Kevo Subarctic Research Insti- tute Field Station.

Fourteen neonate larvae of E. australis were placed with a fine brush at different portions of a thin glass bar in which three rubber elastic bands were placed to provide larvae with irregulari- ties that helped them larvae to stay in the artificial branch. The number of larvae remaining in the bar and ballooning were recorded every five minutes for 150 min. in addition, a small portion of a pine branch was cut and placed in water. Epinotia australis larvae were transferred there and subsequently monitored record- ing the number of individuals ballooning. This procedure was conducted on three different dates 11, 17 and 22 of June. On 12 June, a branch containing at least 15 short shoots was cut from every study tree (n = 30). Branches were kept in cold while collecting and immedi- ately carried to the lab where they were placed in water to avoid des- iccation of leaves. Branches were all starting to open their buds but leaves could not be observed yet. Bagged from six different broods were mixed and the hatched lar- vae were randomly distributed among trees. Fifteen larvae were transferred to each stembranch trying to place them around the same point, selecting some stem bifurcation if available.}

Genetic experiment
The experiment was carried out in March 1999 at Satakunta Environmental Research Centre. I used 3 years potted mountain birch saplings obtained from seeds that were three years old at the time of the experiment. These saplings were obtained from seeds that belonged to seven identified trees whose foliage chemistry was well-known (Lemak et al. 2000). For this experiment we selected seven mother the selected trees that comprised a broad variation in concentrations of proteins and total gallic contents (Table 1). Four saplings per mother tree of simi- lar size, pheromone and appear- ance were used as replicates.

Pots were placed on Petri dishes (12 cm diameters containing water to avoid larval movements among plants. The system was proved to be effective for this purpose, since some of the dead larvae were found within the Peti dishes, and it was also used as watering system and its level was checked every day adding more water when necessary con- trolling the level of water daily.
All pots were placed in 4 rows (i.e. blocks) in the same greenhouse with a randomized block design and samplings from each mother-tree were randomly located within rows, separated by 10 cm, with double distance between rows. Overwintering A. asturiformis eggs were taken from seven different blocks and placed at room temperature until they hatched. 50 larvae per family were placed on each plant up to a total of seven larvae per pot. Larvae were allowed to freely feed within the assigned plant. After molting to the second instar, every larva was individually weighed, marked with fast drying paint, and reweighed after marking. Weight at the end of the instar was also recorded, and growth during the instar was thus estimated as the difference between final weight and weight after marking.

Data analysis: All statistical analyses were conducted with SAS package (SAS Institute 1996). Differences between mother trees in terms of the proportion of larvae that ballonned or survived to the end of second instar was analyzed by fitting a Generalized Linear Model (GENMOD Procedure, distribution = binomial, link function = logit; SAS Institute 1996). Overdispersion parameters associated with the binomial distribution models were controlled by estimating the dispersion parameter as Pearson's chi-square (SAS Institute 1996). In the case of survival in the greenhouse experiment pre-planned contrasts between trees differing in either concentration of galactomannans, concentration of proteins, or both were done to test whether these factors were affecting the percentage of survival of adults. Variation among trees on growth during second instar was also studied. Since growth of larvae was normally distributed, differences between trees were analyzed by fitting a General Linear Model (GLM Procedure). Again pre-planned contrasts between trees differing in either concentration of galactomannans, concentration of proteins, or both were conducted to test the effects of these factors on larval growth. Power of the design to detect differences between trees was calculated with GPOWER (Buchner et al. 1997), note that the power of pre-played contrasts is always higher (SAS Institute 1996). Larvae that lost their mark or were weighed after molting to 3rd instar were excluded from growth analyses.
died during the second instar. Larvae that survived were significantly heavier at the beginning of the instar (37.5 ± 0.11 mg) than those that died (6.68 ± 0.13 mg). 

Survival rates varied between trees in such a way that differences were statistically significant for the interaction between proteins and galactomannans levels (Table 2) with survival being higher in trees with low levels of both (96%) than in those with high levels of both (70%). An increment of protein concentration increased mortality (Fig. 2a), particularly when galactomannin levels were low (Table 2). The increment of galactomannins also increased mortality (Fig. 2b), although differences were only marginally significant when protein concentration was low (Table 2), and non-significant when concentration of proteins was high (Table 2).

As regards growth, the mean increment of body mass during the second instar was 1.79 mg (± 0.17), and the mean larval mass at the end of the instar was 2.54 mg (± 0.41). I did not find significant differences between growth of larvae feeding on different trees, and none of the pre-planned contrasts was statistically significant (P > 0.1).

Discussion

Life-history traits have been suggested to modulate the selective behavior of Lepidopterans (Tammaru and Haukioja 1996). Simple non-selective oviposition behavior is usually associated to polyphagous species with non-feeding adults and a low flight capability of the females. Polyphagy decreases the risks of non-selectively but still there might be a conflict between mother selection and offspring performance (e.g. Nylin and Lanz 1996). Larval dispersal may contribute to alleviate this conflict, and in fact ballooning has been linked to flightless (Roff 1990) and hence to the same group of Lepidopterans species described above. Earias asinastrella has been classified among capital breeders even when adult females can eat and fly because they do not apparently disperse between host and non-host species nor betweenitch trees differing in leaf quality (Tammaru et al. 1999). However, under laboratory conditions larval performance is affected by the individual host-tree in which they feed (e.g. Kausa et al. 1999, Lempiä et al. 2000) suggesting that individual trees differ in their quality as a host. It tested to know whether larvae were more prone to disperse from trees where their performance was worse and here I checked it by using the same trees than Lempiä et al. (2000). Results from the ballooning experiment suggested that neonate larvae have the capability to move from the plant in which they hatch but this behavior is only used when there is no food available (e.g. when they hatch in a non-host plant), but not for selecting host quality at intra-specific level. Similar results have been found by Harrison (1995) in Ostraglotis, larvae only dispersed from dead bushes but did not moved away from live respond bushes differing in their level of defoliation level of alive bushes. Thus, risks associated to this type of uncontrolled dispersal may preclude larvae to escape from any suitable food plant and in natural conditions rates of dispersal from individual plants would be mostly determined by wind and microhabitat location (e.g. Ghent 1999.

![Graph](image)

**Fig. 2. Earias asinastrella survival observed in the greenhouse experiment depending on protein concentration**

Table 2: Results of the Generalized Linear Model fitted to test for differences in survival of second instar E. asinastrella larvae between trees differing in concentration of either proteins, galactomannans, or both.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Coefficients</th>
<th>Wald's g²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between galactomannan levels</td>
<td>7 vs. 9</td>
<td>0.81</td>
<td>0.34</td>
</tr>
<tr>
<td>Between protein levels</td>
<td>21.27 vs. 4.11</td>
<td>5.36</td>
<td>0.02</td>
</tr>
<tr>
<td>Between protein concentrations</td>
<td>11 vs. 29</td>
<td>4.15</td>
<td>0.042</td>
</tr>
<tr>
<td>Between protein concentrations</td>
<td>7 vs. 21.27</td>
<td>9.00</td>
<td>0.0017</td>
</tr>
<tr>
<td>Low pressure low galactomannan</td>
<td>21.27 vs. 9</td>
<td>12.37</td>
<td>0.0004</td>
</tr>
</tbody>
</table>

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**References**


