

Effects of food availability, nutritional value, and alkaloids on food choice in the generalist herbivore *Arianta arbustorum* (Gastropoda: Helicidae)

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The plant *Adenostyles alliariae* (Asteraceae) produces pyrrolizidine alkaloids (PA). These are highly toxic to mammals, but the effects on invertebrates are poorly known. Since the production of secondary compounds imposes costs on plants, they should only be produced if they provide increased protection from herbivores. To test this hypothesis, we investigated the relationship between PA and feeding preference by a naturally occurring generalist herbivore, the snail *Arianta arbustorum*.

By examining microscopically the faeces of field-collected snails, we determined what they had recently consumed. The snails' diet is very broad and it includes arthropods, wilted flowers, fresh and decayed plant material, leaf litter, and soil. We identified the species of herbaceous plants in *A. arbustorum*'s diet. The most important food items were *Adenostyles alliariae*, *Rubus* sp., leaf litter, *Festuca altissima* and *Stachys silvatica*. The proportion in the snail faeces of some of these food items changes drastically during the season, with *A. alliariae* increasing and *S. silvatica* and leaf litter decreasing with time.

We tested whether the snail consumption of the herbaceous plant species was related to their availability per unit area in the field or their nutritional value (water and nitrogen content), relative to that of other plant species. Availability of the different food items is significantly correlated with the amounts eaten. Water and nitrogen content are correlated with each other, but not with the amounts of a plant eaten by the snails.

For the most frequently eaten plant species, the seasonal changes in availability and nutritional value within each species were analyzed; they were not consistent with the feeding preferences of the snails. The PA content of *Adenostyles alliariae* leaves decreases strongly over the season, while consumption of *A. alliariae* by the snails increases. Herbivore damage to the leaves of *A. alliariae* in the field increases similarly over the season. In feeding experiments, the consumption of *A. alliariae* relative to the consumption of lettuce was also lower in May than in September.

We present evidence that *A. arbustorum* eats *A. alliariae* regularly. The negative correlation between snail feeding and PA content of *A. alliariae* strongly suggests that *Arianta* is deterred by plant PA. This snail, along with other herbivores, could provide a selection pressure on the plant favouring the production of PA.

Plant secondary compounds are generally believed to protect plants from herbivores, but the opposite can also be true. For example, *Adenostyles alliariae* (Asteraceae) containing pyrrolizidine alkaloids (PA) can be

heavily attacked by the chrysomelids *Oreina cacaliae* and *O. speciosissima*. Not only are the plant PA ineffective in deterring these herbivores, but also they provide the beetles with their defense against predators

(Pasteels et al. 1988, Pasteels et al. 1990, Ehmke et al., in press, Rowell-Rahier et al., in press). The production of secondary products imposes a metabolic cost on the plants, and this should be compensated by reduced herbivore damage (e.g. van der Meijden et al. 1988). In the example of *A. alliariae*, it is clear that the PA do not protect the plant against herbivory by *Oreina* spp. Nevertheless, other herbivores are probably deterred by these compounds. PA are well known for their high toxicity to vertebrates (Smith and Culvenor 1980), but much less is known about probable toxic effects on invertebrates.

A field survey of herbivory on *Adenostyles alliariae* showed that the generalist land snail *Arianta arbustorum* is regularly encountered on this plant together with *A. alliariae*. We decided to investigate the relationship between diet choice of this herbivore and the availability and nutritional value of the herbaceous plants at our study site. Special emphasis was put on *Adenostyles* as a food plant and the PA content of its leaves. Snails are known to change their diets often, and should therefore be able to track the changes in chemistry or availability of their actual and potential food plants.

Most theories (Feeny 1976, Rhoades and Cates 1976, Fox 1981, Coley et al. 1985) recognize two major types of plant defenses: Toxins and digestibility reducers. Plants rich in toxins are said to be unpalatable for generalists, while they are eaten by their specialists (Fox 1981). Plants rich in digestibility reducers are mainly susceptible to feeding by generalists. However, specialists and generalists are often observed feeding on the same food plants, and we know that generalists can handle many toxins (e.g. with mixed function oxidases, see Brattsten 1988).

Additionally, a third group of defenses might also be effective against generalist herbivores: the "feeding deterrents". These compounds interact with a herbivore's sensory system and inhibit feeding, without actually being toxic (Bernays and Graham 1988).

A wide range of reactions of herbivores to plant allelochemicals (with positive or negative effects on the plants) have been documented, but despite this variability, some generalizations can be made: Specialists have usually "coevolved" (sensu Ehrlich and Raven 1964) with their food plants, and therefore possess some kind of efficient counter-adaptation against the plant's toxins. Generalist herbivores interact differently with their food plants. Their evolution is thought to be "diffuse coevolution" (Fox 1981). This process leads to more universal adaptations, and this is necessary for generalists because different food plants contain different chemicals. Because of their less specialized nature, these adaptations are often assumed to be less efficient than the specialists', but this has been rarely tested. If it is true, any toxic effect of a chemical should be strongest in generalist herbivores. Therefore, the defensive function of a plant's compounds should be best testable with generalist herbivores. Recently, Masters (1991) has

found that the presence of PA in floral nectar reduces visits by generalist butterflies, but not by specialists. Additionally, if a generalist is capable of changing food plants easily, it should leave a plant whenever it is too toxic for him, or if less toxic food of comparable nutritional value is available. A change of food plants should be more easily observed than symptoms of poisoning, or a reduced growth rate. From the plant's point of view, a change of food plant is also the most desirable effect of chemical defense, and defense having this effect should be favoured by natural selection.

The following questions were investigated using the generalist snail *Arianta arbustorum*:

1. What kinds of food do belong to the natural diet of *A. arbustorum* at a particular study site, and how much *Adenostyles* is eaten by this snail, at different times of the season?
 2. How do availability and nutritional value of the different food plant species influence the snails' feeding choices?
 3. What is the seasonal pattern of consumption of the 5 most frequently eaten food items, and how does it relate to the seasonal patterns of availability and nutritional value of these items?
- To evaluate the effect of PA, we tried to answer the following questions:
4. What is the seasonal pattern of total herbivore damage to *A. alliariae* leaves in the field?
 5. What is the seasonal pattern of PA content in *A. alliariae* leaves?
 6. How much *Adenostyles* is eaten by the snails under laboratory conditions?

Materials and methods

Natural history

Adenostyles alliariae is a perennial composite growing in montane and subalpine moist habitats within forests or along streamsides. Most plants have 2–4 large leaves which develop almost synchronously in spring. It usually grows in large, dense patches. All plant parts contain pyrrolizidine alkaloids (PA); seneciphylline is the major PA (about 80% of the total), and other PA are only present in small amounts (Rowell-Rahier et al., in press). The great majority of the PA is present as N-oxides (pers. obs.). In a related species, *Senecio vulgaris*, PA are synthesized in the root and distributed over the whole plant, where they are stored as N-oxides in the vacuoles (Hartmann et al. 1989).

Arianta arbustorum (Helicidae) can be found throughout Central, Eastern and Northern Europe (Kerney et al. 1983) between 400 and 3000 m altitude (Terhivuo 1978, Burla and Stahel 1983, Meier 1987). *A. arbustorum* is found in the habitats in which *A. alliariae* is found, but also in many other habitats with a com-

pletely different plant composition. It feeds on almost everything, from arthropods to mushrooms and living or dead plant material (Frömming 1937).

The field study was carried out at Blauen in the Jura range in Northwestern Switzerland on a north-facing slope of an altitude of 780 m. *A. alliariae* grows there as an understorey plant in a mixed deciduous forest dominated by beech on calcareous soil. Along a forest path, an area of 2–3 m width and approx. 100 m length was used for plant censuses and snail collections.

Faeces examination

On rainy days between April and September in both 1989 and 1990, 203 snails were collected at the study site. These collections were not made at regular intervals, but at 12 dates when it was suitably wet. In the laboratory these snails were kept individually in plastic containers, the bottoms of which were covered with a piece of wet paper towel. All faeces produced were collected and frozen for later examination. After two d, the snails usually produced white faeces, indicating that the snails had eaten the paper which had passed the gut. The faecal string usually consists of several sections differing in colour and texture. A small portion of each section was mounted in glycerin jelly and analyzed microscopically at 40–100 × magnification.

For identification, a reference collection was built up from fresh leaves or faeces from snails fed on known food plants. Fragments of plant tissue were assigned to plant genera and sometimes species on the base of their epidermal hairs, stomata or crystals. The faeces formed by the digestive gland (fine-grained, uniformly brown particles) could not be analyzed. Five herbaceous plant species which occurred in the field contained no structures allowing identification: *Acer pseudoplatanus*, *Asperula odorata*, *Primula elatior*, *Viola* sp. and a fern; all these species were rare at the study site. Seedlings of *Acer* were often observed to suffer from snail herbivory, and all 9 snails which had been collected on *Acer* leaves produced large quantities of unidentifiable faeces, so these were assumed to be from *Acer*. In all other cases, unidentifiable faeces were recorded as “unknown plant matter”. The structures of *Rubus* sp. and those of *Corylus avellana* could not be differentiated, and the same was true for *Impatiens noli-tangere* and *Arum maculatum*. Because in the field, *Rubus* is available in larger quantities than *Corylus*, and *Impatiens* in larger quantities than *Arum*, these faeces are simply referred to as *Rubus* or *Impatiens* respectively in the text. Because faeces from *Impatiens* and *Arum* could not be differentiated from each other, the availability of these two plants was summed up, and their nutritional value averaged for the statistical analyses. The plants *Angelica silvestris*, *Phyteuma spicatum* and *Rumex* sp. were only rarely identified in the faeces. They are not found in our study plot and only rarely in its neighborhood.

To quantify the amounts eaten, the length in the faecal string of each food plant section was measured and expressed as a percentage of the total length of all food items eaten by a snail. If a section was a mixture of two foods, its length was divided between the two foods, but this was not common. Additionally, we noted whether or not each snail had eaten a specific food plant. For each of these food items, the percentage of all the snails which had consumed it was then calculated (= presence score).

Before statistical analysis, data on the amounts of foods in the faeces were log-transformed. To allow a direct comparison with plant availability and nutritional value (principal components analysis), the faeces collections of each month were pooled. One collection in September was pooled with the August data. However, for the analysis of seasonal trends, all 12 collection dates were used as separate data.

Measurements of availability and nutritional value

On five days (April 20, May 9, June 13, July 17, August 25) in 1989, samples of most species of herbaceous plants occurring at the study site and of leaf litter were collected. *Arum*, *Impatiens* and *Rubus* were collected at similar dates in August 1990 and April–July 1991. The samples were weighed and dried during two d at 40°C to determine water content and availability (g dry plant material m⁻² forest floor). The dry material was powdered, and analyzed with a Heraeus CHN-Rapid elementary analyzer to determine nitrogen and carbon content. When CHN analyses are repeated, they deviate by less than 1% from their mean. To simplify display of the availability data, all herbaceous plant species were classified as frequent (F), common (C), or rare (R). This seems justified because the rank order in availability does not change much over the season for most food items. For comparison with the results of faeces examination, relative availability was calculated dividing the values in g dry weight m⁻² by the total availability of all food items for that month. To calculate relative parameters of nutritional value, the absolute values for each plant were divided by the average nutritional value of all plants for each month. Therefore, throughout the text “availability”, “water content”, “nitrogen content” and “carbon content” refer to the relative values, unless stated otherwise. Before statistical analysis, plant availability was log-transformed.

Analysis of pyrrolizidine alkaloids in leaves of *Adenostyles alliariae*

Two g (fresh weight) of leaf material were crushed and extracted with sulfuric acid and zinc dust, to reduce alkaloid N-oxides. After addition of ammonia, PA were

extracted with dichlormethane. TLC plates were prepared with a Camag Linomat III TLC Applicator and they were run and stained as described by Mattocks (1967, 1986). On each plate, samples of 2, 4 and 8 μg pure monocrotaline (Sigma) were included as standards. Spot intensity was measured with a Shimadzu CS-930 TLC scanner. There was only one PA spot of measurable quantity which was identified as seneciphylline by comparison of its Rf value with that of purified seneciphylline (U. Zweifel, Zürich). Eleven PA-analyses were done twice, and on average the measurements deviated from their mean by 7.5%.

Each sample consisted of 10 leaves collected from 10 different *Adenostyles* individuals. Throughout 1989, the relative frequencies of young, medium-aged, and old leaves were recorded and a sample of each category analyzed separately. For each date, we then estimated average leaf PA content by calculating a weighted mean from all age classes. In 1990, only one sample was collected, including leaves of all ages. To estimate variability between individual plants, ten medium-aged leaves from 10 different plants were picked on June 14, 1990 and each leaf analyzed separately twice. Before statistical analysis, data on PA content of leaves were log-transformed.

Assessment of herbivore damage on *Adenostyles alliariae* in the field

Total herbivore damage was estimated by classifying all *Adenostyles* leaves along a transect as either "heavily damaged", if one-third or more of the leaf surface was eaten, or "less damaged". At every date, 150–520 leaves were classified this way, and the percentage of heavily damaged leaves calculated. Although the herbivores responsible for the damage were usually invisible, the nature of the damage allowed some guess about their identity. Before statistical analysis, data on herbivore damage were log-transformed.

Laboratory feeding tests

Consumption was measured in "no choice" experiments, because preceding experiments had shown that only lettuce is eaten if *Adenostyles* and lettuce are given simultaneously to a snail. Even one day after they have eaten lettuce, snails reject *Adenostyles* completely (pers. obs.). The reasons for using lettuce were that it can be used first as a model for an undefended plant, and secondly as a fairly constant standard food item, while both snails and natural food plants change over the season.

Adult and subadult snails were divided into two groups: One group was only fed *Adenostyles* and the controls only lettuce. Snails were kept individually in plastic containers with moist soil to which some calcium

carbonate had been added. The containers were placed in a climatic chamber at 18°C, L:D 18:6. To standardize the hunger level of the snails, both groups were given one standard disc (4 cm diameter = 12.55 cm²) of lettuce two d before the experiment. One d before the experiment, any remaining lettuce was removed and the snails starved for 24 h. Then, the snails were fed standard leaf discs which were cut out just before the experiment from freshly picked leaves of *Adenostyles* or lettuce. The snails were allowed to feed for 24 h. This procedure was repeated during three consecutive d in the May experiment (two in September). After each experiment, to check whether the snails were still alive, they were given one standard lettuce disc which they all consumed.

After each 24 h feeding period, the area of the leaf disc consumed was estimated. In a control experiment, the area removed and that left over were estimated independently for 80 discs; their sums deviated by less than 10% from the calculated surface of the disc. This overestimates the error, because it does not take into account the cases in which either the whole disc or nothing was eaten (which was frequent in the experiments).

In May, the experiment was carried out with snails of 14–25 mm shell diameter which had been kept in the laboratory for 9–11 d. Each snail was given two standard leaf discs per day. The experiment in September was carried out with a laboratory stock of snails which had been collected 4, 12 and 42 d previously, because snails were then difficult to find in the wild. These snails were smaller than those used in May (8–17 mm). *Adenostyles* had also become so rare by this date that only two smaller leaf discs of 2.5 cm diameter (= 9.82 cm²) could be offered to the snails, and thus only 9.82 cm² lettuce was offered to the control snails. In both experiments, *Adenostyles* consumption relative to lettuce consumption (in %) was calculated.

In another similar experiment in June, freshly collected snails were fed one standard disc of *Rubus* or *Stachys* on two consecutive days. There was no group fed with lettuce in this last experiment.

Results

Availability of herbaceous food plants and leaf litter

A list of all herbaceous plant species occurring at the study site, together with their dry weights m⁻² is given in appendix A. There are 200–300 g m⁻² dry weight of leaf litter on the forest floor throughout the season, which is about 99% composed of *Fagus sylvatica*. The total herbaceous plant dry weight accounts for roughly 40–100 g m⁻². There are no significant seasonal trends in availability (Table 2).

Table 1. Proportion (in %) of various food items found in the faeces of *A. arbustorum*, and percentage of snails which had eaten a particular food item (= presence score). Capitals indicate plant availability in the field: F = frequent, C = common, R = rare. Foods are ranked by mean amounts. Presence scores are higher than amounts and they add up to over 100%, because more than one food item is consumed per snail. Note that the ranking of each food item is almost identical, whether amounts or presence scores are used.

	Proportion (in %) of food item in faeces						Presence score
	April	May	June	July	Aug	mean	
A All foods							
All herbs (see part B)	31.6	36.1	49.2	69.7	78.9	49.4	79.8
trees	0.7	33.1	12.2	15.3	4.3	16.5	39.4
unknown plant matter	39.7	8.3	17.9	9.4	13.0	16.1	39.9
leaf litter	25.0	9.2	13.1	5.0	0.5	10.6	31.5
soil and limestone	3.0	10.9	4.6	0.6	3.3	5.8	20.7
insects and mites	0.0	2.1	3.1	0.0	0.0	1.5	18.7
B Herbaceous plants							
<i>Adenostyles alliariae</i> C	3.0	5.5	27.0	61.2	61.0	25.7	37.9
<i>Rubus</i> / <i>Corylus</i> C	9.2	18.7	9.5	2.1	5.9	11.1	29.1
<i>Festuca altissima</i> F	2.7	4.1	0.9	5.5	3.2	3.1	12.8
<i>Stachys silvatica</i> R	10.2	2.6	2.6	0.9	0.2	3.1	11.8
<i>Senecio fuchsii</i> R	0.0	3.1	0.0	0.0	6.7	2.1	3.9
<i>Circaea lutetiana</i> C	1.7	0.3	3.3	0.0	2.0	1.5	4.9
<i>Rumex</i> sp. R	0.0	0.0	3.6	0.0	0.0	0.9	1.0
<i>Hedera helix</i> C	2.7	0.8	0.0	0.0	0.0	0.7	1.0
<i>Geranium robertianum</i> R	0.0	0.1	1.1	0.0	0.0	0.3	2.0
<i>Angelica silvestris</i> R	1.9	0.0	0.0	0.0	0.0	0.3	1.0
<i>Phyteuma spicatum</i> R	0.0	0.8	0.0	0.0	0.0	0.3	0.5
<i>Oxalis acetosella</i> R	0.2	0.0	0.7	0.0	0.0	0.2	1.5
<i>Impatiens</i> / <i>Arum</i> C	0.0	0.1	0.5	0.0	0.0	0.1	1.0
Number of snails	29	67	52	22	33	Σ = 203	

Nutritional value of herbaceous food plants and leaf litter

For seasonal trends in water and nitrogen content see Table 2. In general, water and nitrogen content decreased with time. Absolute and relative values of availability and nutritional value are highly correlated ($N = 49-55$, all $r \geq 0.99$, all $p < 0.001$).

Water content (appendix B)

For most species, absolute water content is similar (between 82 and 88%), but *Festuca altissima*, *Rubus* sp. and *Hedera helix* have distinctly lower values (between 61 and 65%).

Nitrogen content (appendix C)

The absolute nitrogen content of the *Fagus* component of leaf litter varies between 1.21 and 1.47% of leaf dry weight. The other components of the leaf litter (mostly *Acer pseudoplatanus*) range from 1.41 to 1.79% N, but account only for negligible quantities. Green leaves of herbaceous plants always contain considerably more nitrogen than leaf litter, with the exception of those of *Hedera helix*. In *H. helix*, the leaves overwinter, so spring leaves are in fact from the previous year, while younger leaves are only present later.

Carbon content

Carbon content is fairly constant over the season and across food plant species (including leaf litter), and accounts on average for 42.89% of total dry weight (S.D. = $\pm 2.03\%$). Therefore, C/N-ratios closely follow the patterns of nitrogen content, and are not further discussed in this work.

Diet of *Arianta arbustorum* in the field

The diet of *A. arbustorum* is very broad. Table 1A lists the major food categories (i.e. herbaceous plants, trees, leaf litter, soil, arthropods). The species composition of the herbaceous plants category is given in Table 1B. The category "trees" consists of two food items: Wilted flower parts of *Fagus silvatica*, mainly empty anthers and bud scales, account for the majority of the observations, while leaves of *Acer pseudoplatanus* make up the rest.

Influence of availability and nutritional value on choice among food plant species

Water-, N-, and C-content are strongly correlated with each other, but not with availability of the plant or

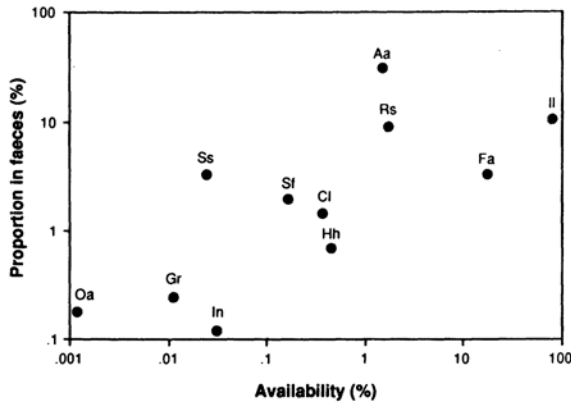


Fig. 1. Percentage of different food items in the faeces in relation to availability. Both amounts in the faeces and availability are averaged over the whole season. Species are: Aa: *Adenostyles alliariae*, Cl: *Circaea lutetiana*, Fa: *Festuca altissima*, Gr: *Geranium robertianum*, Hh: *Hedera helix*, In: *Impatiens noli-tangere* II: leaf litter, Oa: *Oxalis acetosella*, Rs: *Rubus* sp., Sf: *Senecio fuchsii*, Ss: *Stachys silvatica*.

amounts in the snail faeces. Therefore, in a first step, a Principal Components Analysis (PCA) was performed with water-, nitrogen- and carbon content only. The first principal component, which explains over 80% of the original variance, has a strong correlation with all three variables (water: 0.96, N: 0.87, C: -0.88), so we call it the plant quality factor. In a second step, the effects of this quality factor and of availability on the amounts in faeces were determined by multiple regression. The regression is significant: $r^2 = 0.291$, $DF = 43$, $F = 9.81$, $p = 0.0003$. The effect of availability is highly significant ($t = 4.28$, $p < 0.0001$), but the effect of the quality factor is not significant ($t = 1.33$, $p = 0.19$).

The three plants with the highest availability (*Festuca*, *Rubus*, *Adenostyles*) are found within the first three ranks in the snails' faeces. Out of 7 plants classified as rare, none was eaten in notable amounts and only *Stachys silvatica* was found in more than 10% of the snails. However, food consumption is far from being strictly proportional to the amounts available. Leaf litter is by far the most highly available food item in the field, but it is consumed in similar quantities to *Rubus*, which is far less available in the field. The herbaceous plant with the highest availability, *Festuca altissima*, is eaten in amounts similar to those of the rare plant *Stachys silvatica*.

The relation between availability of the various food items and their proportion in the snails' faeces averaged over the whole season, is shown in Fig. 1. One hundred % correspond to 319 g m^{-2} . The three food items (*Hedera helix*, *Festuca altissima* and leaf litter) which are found in the snail faeces in smaller amounts than expected from their availability also have low nutritional values (appendices B and C). *Adenostyles alliariae* is found more frequently in the snail faeces than

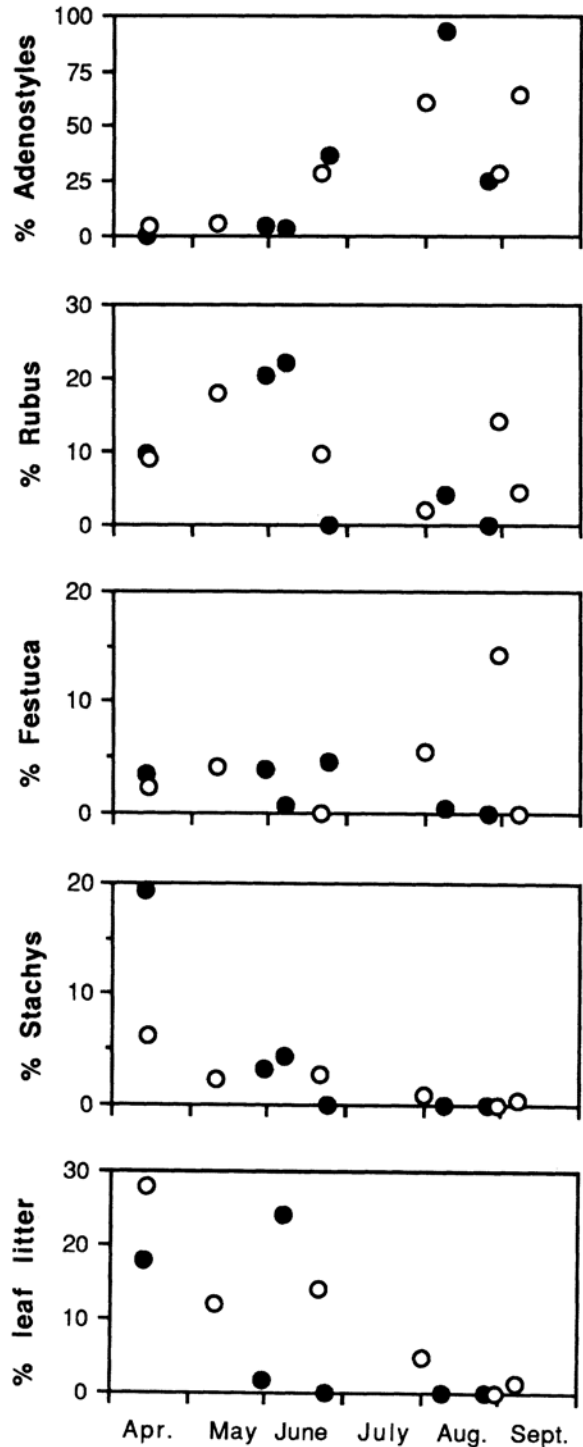


Fig. 2. Seasonal changes in the percentage of different food items in the faeces of *A. arbustorum* (in % of total food eaten). Probabilities of the regressions for the different food items are: *Adenostyles*: $r^2 = 0.63$, $df = 11$, $p = 0.0013$; *Rubus*: $r^2 = 0.029$, $df = 11$, $p > 0.27$; *Festuca*: $r^2 = 0.077$, $df = 11$, $p = 0.2$; *Stachys*: $r^2 = 0.50$, $df = 11$, $p = 0.006$; leaf litter: $r^2 = 0.40$, $df = 11$, $p = 0.016$. Filled circles represent 1989 data, open circles 1990 data.

Table 2. Correlation between season and other parameters for different food items. Correlation coefficients are given only when significant. Sample size and level of significance are given in parentheses. Levels of significance: * significant at $p < 0.05$, ** significant at $p < 0.01$, *** significant at $p < 0.001$, ns: not significant.

Parameter correlated with season	Food items				
	<i>Adenostyles</i>	<i>Rubus</i>	<i>Festuca</i>	<i>Stachys</i>	Leaf litter
amounts in faeces	$r = +0.81$ ($N = 12^{**}$)	– ($N = 12$ ns)	– ($N = 12$ ns)	$r = -0.74$ ($N = 12^{**}$)	$r = -0.67$ ($N = 12^*$)
herbivore damage	$r = +0.98$ ($N = 9^{***}$)	–	–	–	–
PA content	$r = -0.84$ ($N = 15^{***}$)	–	–	–	–
availability	– ($N = 5$ ns)	– ($N = 5$ ns)	– ($N = 5$ ns)	– ($N = 3$ ns)	– ($N = 5$ ns)
water content	– ($N = 5$ ns)	– ($N = 5$ ns)	– ($N = 5$ ns)	– ($N = 5$ ns)	–
nitrogen content	$r = -0.91$ ($N = 5^*$)	$r = +0.90$ ($N = 5^*$)	– ($N = 5$ ns)	– ($N = 5$ ns)	$r = +0.89$ ($N = 5^*$)

expected from its availability, but this is mainly due to the high consumption between June and September.

Overview of seasonal trends in consumption of the most important food items

For the 5 most important food items (*Adenostyles*, *Rubus*, *Festuca*, *Stachys* and leaf litter), the changes over the season of the amounts found in the faeces are shown in Fig. 2. For all these food items, the seasonal changes in the amounts found in the faeces, availability and nutritional value are summarized in Table 2. Correlation was used instead of regression to indicate whether the seasonal changes are positive or negative. The seasonal trends in *Adenostyles* are different from those observed in the other food items. While the percentage of *Adenostyles* found in the snails' faeces increases significantly over the season, PA- and nitrogen content decrease significantly with time. In *Rubus*, the percent-

age in the faeces does not change over the season, but nitrogen content increases. In *Festuca*, neither the percentage in the faeces nor availability or nutritional value change significantly over the season. The percentage of *Stachys* in the faeces decreases significantly over the season, but neither availability nor nutritional value change. The percentage of leaf litter in the faeces decreases over the season, while nitrogen content increases (although the absolute values are constant over the season, see appendix C). For *Adenostyles* only, PA content and herbivore damage are also included in Table 2 (see below).

All herbaceous food plants not mentioned in this paragraph are rare in the field except *Circaea lutetiana*, *Hedera helix*, and *Impatiens noli-tangere* (see Appendix A). The amounts consumed of these food items are too low for an analysis of seasonal trends.

Herbivore damage to *Adenostyles alliariae* in the field

Early in spring, a considerable portion of the rather small amount of total damage is caused by the caterpillars of *Callimorpha dominula*. These overwinter as caterpillars and pupate in May. Therefore, they do not damage *Adenostyles* later in the season.

Later in the season, most damage was probably done by some snail or slug species. Until the end of July, damage is rather slight, and then rises sharply in August. If the leaves were damaged at a constant rate, total damage would be expected to increase linearly, but the increase is much stronger. The increase in herbivore damage over the season is highly significant (Fig. 3). The high level of damage in August and September could even be an underestimate, because some leaves might have been eaten completely and therefore have escaped classification. Earlier in the season, this is unlikely.

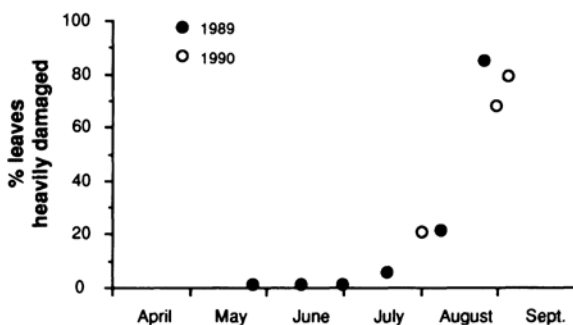


Fig. 3. Total damage on leaves of *Adenostyles alliariae* in the field. Leaves with 1/3 or more of their surface removed were scored as heavily damaged. The increase of herbivore damage over the season is significant ($r^2 = 0.95$, $df = 8$, $p < 0.0001$).

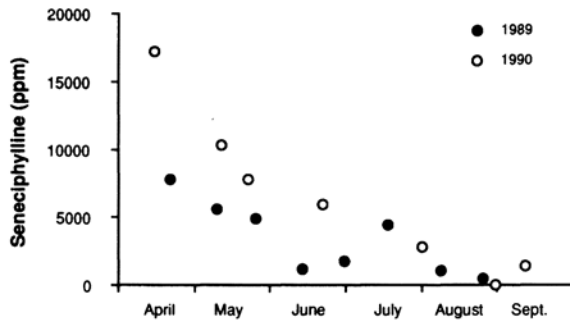


Fig. 4. Pyrrolizidine alkaloid (seneciphylline) in the leaves of *Adenostyles alliariae* during two seasons. The accuracy of the analyses is $\pm 7.5\%$ of the mean. The decrease of PA content over the season is significant ($r^2 = 0.68$, $df = 14$, $p < 0.0001$).

PA content of *Adenostyles alliariae* leaves

In spring, the leaves contain the highest amount of PA ($> 15\,000$ ppm), and there is a steady decrease over the season in both years (Fig. 4). Thus, August leaves contain only about 10% of the PA of spring leaves. The decrease in PA content over the season is highly significant. The PA content in ten individual plants ranged from 240 ppm to 19200 ppm (mean = 6961 ppm, S.D. = 5058 ppm).

Consumption of *Adenostyles alliariae* in the laboratory

In the feeding experiments, discs had been matched for surface rather than weight, and therefore results are given in cm^2 eaten. 1 cm^2 corresponds to an average of 23.6 mg *Adenostyles* or 28.4 mg lettuce. Lettuce contains 95% water in fresh weight, and 3.05% nitrogen and 39.94% carbon in dry weight. If the comparison between *Adenostyles* and lettuce is calculated with fresh weight, dry weight, or nitrogen data, the same probabilities are obtained as with surface eaten. The difference between *Adenostyles* and lettuce consumption is always

highly significant (Table 3). In May, most of the lettuce offered was eaten. In September, only about half of the lettuce offered was eaten. The relative consumption of *Adenostyles* compared to lettuce is higher in September than in May, but statistical comparisons between different experiments were not made. These experiments will be described later in the context of other similar feeding experiments not mentioned here (Speiser and Rowell-Rahier, unpubl.).

The amounts of *Rubus* and *Stachys* eaten are intermediate between those of *Adenostyles* and of lettuce: 1.64 cm^2 of *Rubus* were eaten on the first day, and 0.16 cm^2 on the second day. From *Stachys*, 3.4 cm^2 were eaten on the first day, and 1.46 cm^2 on the second day.

Discussion

The faeces analyses confirm earlier findings that *Arianta* is omnivorous (Frömming 1962, Grime and Blythe 1969, Grime et al. 1970, Mason 1970) as are other land snails and slugs (Jennings and Barkham 1975, Chatfield 1975, 1976, Williamson and Cameron 1976), i.e. that they eat both green and decayed plant material along with dead animals, soil, fungi, etc. With respect to individual plant species, snails and slugs usually exhibit distinct preferences and aversions for/against some plant species (Duval 1971, 1973, Chatfield 1973, 1975, 1976, Cates and Orians 1975, Van der Laan 1975, Dirzo 1980, Richardson and Whittaker 1982, Wink 1984, Rathcke 1985, Mølgaard 1986). The causes of this selectiveness are largely unknown, but three kinds of factors are most likely to play a role: availability, nutritional value and defenses. It is not yet known to what extent each of the three factors influences the snails' food choices.

From a plant's perspective, availability and nutritional value cannot be altered much in response to herbivory, because availability is closely linked to plant frequency, and nutritional value is constrained by physiological requirements. However, plant defenses can

Table 3. Comparison of consumption of *Adenostyles* and lettuce by *A. arbustorum* under laboratory conditions. Values are given in cm^2 .

	<i>Adenostyles</i> mean (\pm S.D.)	lettuce mean (\pm S.D.)	Mann-Whitney U-test	relative <i>Adenostyles</i> consumption
May				
number of snails	16	15		
day 1	0.041 (± 0.064)	22.2 (± 4.5)	$p < 0.0001$	0.063
day 2	0.124 (± 0.377)	17.7 (± 7.0)	$p < 0.0001$	0.701
day 3	0.078 (± 0.094)	17.6 (± 6.8)	$p < 0.0001$	0.443
September				
number of snails	17	8		
day 1	0.114 (± 0.211)	5.5 (± 2.6)	$p < 0.0001$	2.073
day 2	0.029 (± 0.020)	4.3 (± 3.0)	$p < 0.0001$	0.674

theoretically evolve to the extent that they largely control herbivores' feeding decisions. Plant availability, nutritional value and defenses are usually regarded as central to herbivores' food choice. Many authors point out that food choice is usually not based on any single plant trait, but rather on the whole complex of a plant's characteristics including the microenvironment, and the herbivores' own requirements (e.g. Barbosa 1988). Also, the effects of availability, nutritional value and plant defenses are linked. For example, a rare food will probably not be eaten unless it is of good nutritional value (see also Cates 1980). The excretion of toxins often involves a loss of nitrogen (Westoby 1978) or other nutrients (see Harborne 1988), so a food can become more toxic with decreasing nutrient content. The link between availability and defenses has been established by Feeny (1976) and Rhoades and Cates (1976).

In the following, both the seasonal trends in diet selection of *Arianta arbustorum* and the choice among food plant species will be discussed with respect to these three factors.

Effects of availability, nutritional value and defense on the choice of food plant species

Availability

There is a significant effect of availability on the percentage of a food item in the faeces (Fig. 1). Although the availability of food items other than herbaceous plants was not quantified, it is obvious that most of these are not consumed in proportion to the amounts in which they are available. For example, insects and mites, as well as wilted *Fagus* flowers make up a considerable percentage of the snails' faeces, but their availability cannot be very high.

For other snail species, it has been reported that the food plants which are frequent in the field are also eaten frequently (Chatfield 1975, 1976, Cottam 1985, Edwards and Gillman 1987). However, rarer plants are grazed disproportionately more than expected (Cottam 1985), and individual food plant species deviate in both directions from expected ingestion rates (Edwards and Gillman 1987: 304–306). The present study confirms this.

Nutritional value

The overall effect of nutritional value (quality factor) on the percentage of a food item in the faeces is not significant. In a review on several bird and mammal generalist herbivores, Bryant and Kuropat (1980) conclude that nutritional value influences food choice to a lesser extent than plant defenses. However, nutritional value may help to explain why some particular food items are eaten more (or less) than expected from their availability. For example, three poorly eaten food items, *Fes-*

tuca, *Hedera* and leaf litter also have a low nutritional value. Insects and mites are certainly an attractive food because of their high N content, and the same is probably true for wilted *Fagus* flowers, because the anthers often contain some pollen grains. Both these food items were eaten more than expected from their availability. Soil might be ingested as a food because it contains bacteria, fungi, etc., but it certainly could also supply the snail with calcium for the shell, or it could neutralize toxins in the gut (Johns 1986). Indeed, soil was abundantly eaten in May when PA content of *Adenostyles* is high, and toxin content of other herbaceous food plants is probably also at its peak. Other factors not measured here probably also contribute to nutritional value; for example, Reingold and Gelperin (1980) have shown that the slug *Limax maximus* eats more of softer foods than of harder foods of otherwise identical quality. Toughness may help to explain why leaf litter and *Festuca* are eaten much less than expected from their availability.

Defenses

A few studies show that land snails or slugs can be deterred from feeding by secondary plant compounds: Wink (1984) showed that the quinolizidine alkaloids of *Lupinus polyphyllus* repel the snail *Helix pomatia* and the slug *Arion rufus*; Gouyon et al. (1983) found that *Thymus vulgaris* is protected from herbivory by slugs through its terpenes; the slug *Ariolimax dolichophallus* feeds differentially on *Satureja douglasii*-plants which contain different monoterpenoids (Rice et al. 1979), and the anti-mollusc activity of the cyanogenic glucosides of white clover is well documented (Jones 1962, Burgess and Ennos 1987, Raffaelli and Mordue 1990). Mechanical defenses (silica crystals) active against snails have been found in grasses (Wadham and Wynn Parry 1981), and grasses are usually avoided by snails and slugs (Ingram and Petersen 1947, Pallant 1969, Grime et al. 1970, Williamson and Cameron 1976, Carter et al. 1979, Cottam 1985, Szlavecz 1986).

The only grass present at our study site, *Festuca altissima*, has extremely tough leaves with a sandpaper-like surface. This "defense" is present all year round, and indeed the consumption of *Festuca* does not show strong seasonal variation. The amount of *Festuca* eaten is also below what availability alone would predict.

We have quantified the potential defense of only one plant species, *Adenostyles alliariae*. *A. alliariae* seems to become an increasingly attractive food plant as PA content decreases (Table 1).

Seasonal trends in *Adenostyles* compared with those of other food items

The seasonal changes in the amounts of *Adenostyles*, *Rubus*, *Festuca*, *Stachys* and leaf litter found in the snail

faeces are different from the seasonal changes in the availability and nutritional value of these food items (Table 2). Therefore, it is unlikely that either availability or nutritional value alone can be the major factor explaining snails' feeding choices.

Adenostyles alliariae is the only food plant for which we have data on defenses (PA content). While both the percentage of *Adenostyles* found in the snails' faeces and the herbivore damage to *Adenostyles* leaves increase significantly over the season, PA- and nitrogen content decrease significantly with time (Table 2). In addition to what was said about availability and nutritional value in the previous paragraph, it does not seem likely that an increased consumption is caused by decreasing nutritional value. Such phenomena have recently been shown in generalist insects (Simpson and Simpson 1990), but not in snails. In August and September, *Adenostyles* has become rare because of intensive herbivory (see Fig. 3 and appendix A). This might explain the two low August values in Fig. 2.

The seasonal trends in *Adenostyles* consumption exhibited by the faeces examination and the levels of herbivore damage observed in the field are confirmed by the laboratory feeding tests. Although the absolute amounts of *Adenostyles* consumed are similar in both experiments, consumption of *Adenostyles* relative to lettuce consumption was higher in September than in May (Table 3). Also, the snails used in September were much smaller than in May. In other experiments not reported here, lettuce consumption was similar to the values obtained in May (mean = 14.86 cm², S.D. = 6.54 cm², N = 60 snails from five populations). The absolute amounts of *Adenostyles* consumed are small even in September. The relative importance of *Adenostyles* in the faeces by this date may be explained by the fact that *Adenostyles* is one of the herbaceous plants with the highest availabilities. Also, in the field many leaves of *Adenostyles* are partly decayed in September, but in the feeding experiments, only more or less intact leaves could be used.

Lettuce is certainly eaten much more than any of the plants available in the field. The consumption of *Rubus* and *Stachys* in the laboratory (in June) was higher than that of *Adenostyles* (either in May or in September). In the wild, consumption of *Rubus* is higher than that of *Adenostyles* only in April and May, and the consumption of *Stachys* is higher than that of *Adenostyles* only in April (Table 1).

For the other PA-containing plant, *Senecio fuchsii*, we also have some data on seasonal variation in PA content. However, there is absolutely no overlap in PA types occurring in *S. fuchsii* and in *A. alliariae* (Rowell-Rahier et al., in press). In *S. fuchsii*, total PA content is fairly constant through most of the season, but decreases strongly at the end (unpubl. data). This is in agreement with the somewhat higher consumption of *S. fuchsii* in August/September, but consumption was too low on most dates to allow conclusions to be drawn.

If *Adenostyles* is so well defended in spring, one might wonder why some 15% of all *Arianta* individuals still ate *Adenostyles* at that time (these individuals consumed considerable amounts of *Adenostyles*). Two explanations are likely: (1) Because of the high variability among individual plants, it is possible that the snails had fed selectively on the PA-poorest plants. This unexpectedly high variation between individual plants might account for irregularities (e.g. the peak in July 1989) via sampling error. It may also account for some of the great variability encountered in the feeding experiments. (2) A few snails in the population may be less sensitive towards PA than the majority, and these may have fed on *Adenostyles* in spring. The feeding experiments indicated that there is considerable variability among individual snails concerning the amount of *Adenostyles* they eat (Speiser et al., unpubl.).

Plant defenses may cause very different reactions in specialist and generalist herbivores. Some herbivores (often specialists) have evolved more or less efficient counter-adaptations, allowing them to feed on a plant despite its defenses. Although specialist herbivores can regularly be observed feeding on a plant species, it is difficult to assess the effects of the plant's secondary compounds on this kind of herbivore. Do the compounds handicap (e.g. via lowered growth rate, Williams et al. 1983) or benefit the herbivore (e.g. via sequestration for defense)? Other herbivores (often generalists) may change food plants partially or completely. For this kind of herbivore, it is almost impossible to assess the potential impact of secondary plant compounds. For example, Smiley et al. (1985) have found that the willow *Salix orestera* suffers more damage from the leaf beetles *Chrysomela aeneicollis* when it produces larger amounts of salicin, because this compound is utilized by *C. aeneicollis* for their own defense. It seems disadvantageous for the willows to produce salicin and thereby suffer more damage, so these authors hypothesized that salicin acts as defense against generalist herbivores such as deer, but they do not report any observations supporting this. However, there is other evidence that phenolglucosides deter vertebrate and invertebrate herbivores (review in Rowell-Rahier and Pasteels 1990). A similar problem is evident with the plant *A. alliariae* and the herbivores *Oreina cacaliae* and *O. speciosissima*: if only these herbivores are considered, it seems paradoxical that *Adenostyles* produces PA and thereby increases the survival of its herbivores. It is therefore likely that the PA defend *Adenostyles* against other herbivores, but if a herbivore is sensitive to PA, and avoids *Adenostyles*, it is not easy to show that this herbivore would eat *Adenostyles*, if it contained less PA. While in the *Salix* example, no deer could be observed, we know that the snail *A. arbustum* does eat *Adenostyles*, and with increased probability if the PA content is low. The importance of snails and slugs as herbivores compared to insects has been studied in only very few cases. However, these indicate

that snails and slugs may be important herbivores under certain conditions (Edwards and Gillman 1987: 304, Raffaelli and Mordue 1990).

Plants can only make limited investments into defense. Van der Meijden et al. (1988) showed that there is a trade-off between the investment in defense and the capacity for regrowth (i.e. reserves in the root). *Adenostyles* seems to reduce its investment in defense over the season. It seems most important for the leaves to be protected against herbivore damage in spring when the sunlight penetrates the tree canopy easily and photosynthesis is probably highest. For this reason, not only PA, but also other secondary compounds of *Adenostyles* can be expected to decrease over the season (McKey 1974).

To conclude, the negative relationship between snail feeding and PA content is in agreement with the hypothesized protective function of PA. However, this study is of a correlative nature, and experimental proof of causality is lacking as yet.

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Appendix A. Seasonal variation in availability of herbaceous plants and leaf litter (g m^{-2} dry weight). Herbaceous plant species were split into three categories: frequent (F), common (C), and rare (R).

	April	May	June	July	Aug	mean
leaf litter	286	336	125	325	180	250
<i>Festuca altissima</i> (F)	92.8	66.6	32.3	42	41.2	55
<i>Rubus</i> sp. (C)	5.3	8.2	2.2	3.8	7.0	5.3
<i>Adenostyles alliariae</i> (C)	4.4	4.5	5	5.9	1.3	4.2
<i>Hedera helix</i> (C)	5.2	0.3	1.1	0.5	0.2	1.5
<i>Circaea lutetiana</i> (C)	0.15	1	2.3	4.2	1.4	1.0
<i>Senecio fuchsii</i> (R)	0	<0.1	0.55	0.95	0.57	0.7
<i>Impatiens noli-tangere</i> (C)	0	0	0.03	0.16	0.09	0.06
<i>Stachys silvatica</i> (R)	0	0.36	<0.1	<0.1	<0.1	<0.2
<i>Oxalis acetosella</i> (R)	<0.1	<0.1	0	0	0	<0.1
<i>Geranium robertianum</i> (R)	0.03	<0.1	<0.1	<0.1	<0.1	<0.1
<i>Arum maculatum</i> (R)	0.03	<0.1	0.07	0	0	<0.02
total	394	417	169	383	232	319

Appendix B. Seasonal variation in water content of herbaceous plant species (in % of fresh weight). Plants are listed in order of decreasing mean water content. *Rumex* was not determined.

	April	May	June	July	Aug	mean
<i>Arum maculatum</i>	90	85	88	–	–	87.9
<i>Senecio fuchsii</i>	90	91	86	87	86	87.8
<i>Circaea lutetiana</i>	88	88	88	85	86	87.0
<i>Adenostyles alliariae</i>	89	86	85	85	83	85.6
<i>Oxalis acetosella</i>	81	89	85	85	88	85.5
<i>Impatiens noli-tangere</i>	–	–	90	84	82	85.3
<i>Geranium robertianum</i>	85	87	88	84	79	84.5
<i>Phyteuma spicatum</i>	87	83	85	88	–	83.2
<i>Angelica silvestris</i>	86	84	84	81	77	82.5
<i>Stachys silvatica</i>	84	80	86	82	79	82.1
<i>Festuca altissima</i>	68	61	66	68	60	64.6
<i>Rubus</i> sp.	55	59	67	64	63	61.6
<i>Hedera helix</i>	63	59	54	69	62	61.4
mean	80.5	79.3	80.9	80.2	76.8	79.9

Appendix C. Seasonal variation in nitrogen content of herbaceous plant species and leaf litter (in % of dry weight). Plants are listed in order of decreasing mean nitrogen content. *Rumex* was not determined.

	April	May	June	July	Aug	mean
<i>Senecio fuchsii</i>	4.84	4.66	3.71	3.12	3.39	3.94
<i>Impatiens noli-tangere</i>	–	–	3.63	3.95	4.14	3.91
<i>Arum maculatum</i>	3.79	3.62	3.54	–	–	3.65
<i>Stachys silvatica</i>	3.72	4.02	3.81	3.3	3.05	3.58
<i>Phyteuma spicatum</i>	3.85	4.09	3.4	2.79	–	3.53
<i>Circaea lutetiana</i>	3.69	3.53	3.77	3.03	2.95	3.39
<i>Adenostyles alliariae</i>	3.63	4.0	3.09	2.81	2.54	3.21
<i>Geranium robertianum</i>	3.41	3.2	2.98	3.94	2.31	3.17
<i>Angelica silvestris</i>	3.97	3.33	–	2.79	2.56	3.16
<i>Oxalis acetosella</i>	2.29	3.35	2.28	2.46	2.94	2.66
<i>Rubus</i> sp.	2.18	1.97	2.51	2.62	2.6	2.38
<i>Festuca altissima</i>	2.12	1.63	2.25	2.27	2.08	2.07
<i>Hedera helix</i>	1.31	1.37	1.43	1.71	1.71	1.51
leaf litter (<i>Fagus</i>)	1.21	1.23	1.3	1.47	1.32	1.31
mean	3.08	3.08	2.90	2.79	2.63	2.96