Interaction between willow species and their caterpillar grazers

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A Dissertation submitted for the Degree of Master of Science in Ecology

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Abstract

The first aim of this investigation was to determine the effect of leaf removal either by grazing or hand cutting on the photosynthetic ability of the *Salix* species. The second aim was to investigate any change of leaf quality to feeding insect larvae which occurred as a consequence of the removal. Thirdly, the selectivity of the larvae between different *Salix* species and its effect on the larval development were studied.

The leaf removal by grazing or hand cutting did not decrease the leaf fresh weight in *Salix viminalis* (submitted to two intensities of treatment) or in *S. vitellina*, after a period of recovery. The total leaf production in both species was similar to the control. In *S. cinerea* the grazing reduced the leaf weight and the total leaf production. The leaf size was reduced also.

The leaves of previously grazed or hand cut *Salix viminalis* plants had no depressive effect on the growth of the Geometridae larvae "*G*". A similar result was obtained with the larvae of the sawfly *Amauronematus sagmarius* feeding on *S. rotundifolia*.

The Geometridae larvae "*G*" selected *Salix viminalis* (58% of the total food consumption) rather than *S. cinerea* in a choice experiment. *S. viminalis* promoted a faster growth of the larvae "*G*" when transferred to it from their previous food plant *S. cinerea*.

The growth of the sawfly larvae was faster on *S. fragilis*, the species selected by the female for oviposition, than on *S. rotundifolia*. The death rate of the larvae of *Amauronematus sagmarius* was higher on both *S. viminalis* and *S. cinerea* than on *S. vitellina*, selected by the adult female for egg laying.

Finally, the young leaves of *S. rotundifolia* promoted a higher death rate on the first generation of *Amauronematus sagmarius* larvae than the old leaves. The time required for pupation was shorter on the diet of young leaves in the first and second larval generations.

Introduction

The effect of grazers feeding on plants in natural ecosystems often passes unnoticed apart from extreme cases of defoliation. Grazers consume less than 10% of the production in terrestrial ecosystems (Owen 1976). Therefore, plants must be able to regulate the biomass of consumers (Owen 1976).

Rather than a "one-way" producer to consumer relationship, plants and insects are viewed, nowadays, as co-evolving competing and often dependent systems (Southwood 1971).

The evolutionary competition between higher plants and their invertebrate grazers (mainly higher insect orders) has led to the innovation of means of defence in the plants. Apart from an avoidance "tactic" in time, these could be divided in physical and chemical ways.

As physical defences, the thickened plant cuticles which prevent or reduce feeding can be cited (Bernays and Chapman 1970). Hairs and spines on the epidermis seem to play a similar role.

Furthermore, plants have evolved a wide range of biochemical compounds known as secondary compounds. They are considered as primordial in the plant defence mechanisms against grazing and competition. Some workers think of them as the major criterion in host selection in insects (Fraenkel 1969). These compounds seem at the origin of the specialisation in the insects' diet, as these latter have had to evolve means of detecting them or inhibiting their effect. The large insect community feeding on the highly toxic bracken *Pteridium aquilinum* illustrates very well the specialisation (Lawton 1982).

Polyphagy is considered as a luxury possible under certain circumstances (Dethier 1954). Even so, there are often severe limits and polyphagous species often have an order of preference between two genera of the same family or even two species of the same genus. The beetle larvae *Gastrophysa viridula* feed three times as much on the dock *Rumex obtusifolius* than on *R. crispus* (Bentley and Whittaker 1979). The larvae of the emperor moth *Saturnia pavonia* grow better on *Salix atrocinerea* than on *S. alba* (Craggs 1978).

Within the same plant species the quality and palatibility of the food plant may change. A plant already grazed can become less nutritious in comparison to a non-grazed; i.e. allows grazers to grow less well. This is the case of the larvae of the moth *Oporinia autumnata* which feed on *Betula pubescens* in Fennosandinavia. The pupae of the larvae fed on leaves from plants which had been partially defoliated were lighter (Haukioja 1980).

In this work the relationship between some species of the genus *Salix* and their caterpillar grazers has been studied. To test the effect of the grazers on the plant productivity and photosynthetic ability, the leaf weight of grazed willow cuttings has been examined in comparison with control plants. The impact of the grazing on the cuttings has been studied; whether it increases the plant resistance, i.e. lowers the nutrient availability. The caterpillar growth was taken as the criterion of the plants' palatability.

The selectivity within the genus *Salix* has been investigated by studying the growth of the larvae on different species.

Methods

A. Methods of analysing the development of the larvae studied

Two species were used to study the effects of the diet on their growth and pupation: larvae of a Geometridae and larvae of the sawfly *Amauronematus sagmarius*.

I - Geometridae larvae

The larvae of this species were reared from eggs. The adult was not obtained and a specific identification has not been made. It will be referred to as species "*G*". The larvae "*G*" grew to 500-600mg. By the end of August they all pupated and entered diapause. The larvae were used on the experiments of the Section II (1) and Section III (1 and 2). Their growth rate was studied under different conditions (see previous Sections). In each case a graph was drawn of the mean larval weight plotted against days. In most cases the relationship was non-linear (Fig. 1a). The mean larval weight was transformed to a logarithmic scale and this gave a close fit to a straight line (Fig. 1b), allowing the calculation of a regression line from which the slope and its standard error could be determined.

II - *Amauronematus sagmarius* larvae

The larvae of this sawfly were first found by mid-June on the bushes of the horticultural species *Salix rotundifolia* on the Science Site. Their development has been studied under different conditions in Sections II (2), IV (2) and V.

Larvae of a sawfly believed to be the same species were found on *Salix fragilis*. These were studied in Section IV (1).

The life span of the larvae is very short. In two weeks they accomplish their larval growth and pupate. The largest individuals weigh between 25-35mg by then. However, the mean pupal weight was usually much smaller.

Unlike the Geometridae species "*G*", the larval growth rate has a linear relationship when plotted against days (Fig. 2), i.e. a constant increase in weight occurs irrespective of body size. During the experiments the larvae were weighed every two or three days. In the results their weight increase is expressed as a daily weight increase per larva during the growth period until maximal weight was reached. Loss of weight preceded pupation.

The mean live pupal weight (mg) is used as a measure of growth. The initial mean larval weight is also given in order to justify the attempt to obtain similar sized larvae in the experimental and control groups. In no case was there a significant difference between the larval weight of the experimental and the control groups at the start of an experiment.

A further method of considering the suitability of the diet for the larvae has been to compare their death rate during experiments.

B. Methods used during the experiments

I - Effect of grazing on the photosynthetic ability of cuttings of the 3 willow species: *Salix viminalis, S. vitellina* and *S. cinerea*

To study the effect of the grazing by the insect larvae on the photosynthetic ability and productivity of the three *Salix* species, experiments were carried out on cuttings under natural conditions.

For each *Salix* species, a group of plants was grazed by caterpillars, another was hand cut. A control group was also used.

1. *Salix viminalis*

The rooted cuttings from the same tree were grown in separate pots. Each treatment, i.e. grazed or hand cut, was divided into two sub-groups, giving two levels of intensity of treatment.

In the grazed group of plants, the heavily grazed sub-group had 30-40% of their original leaf area removed by Geometridae larvae. Some of the larvae were recognised as *Hydriomena furcata*. All the larvae had been found feeding on willow trees. The grazing was started on 1 June and stopped 4 weeks later. In the other sub-group 10-15% of the leaf area was grazed. Moreover, the mode of grazing was different, i.e. no leaves were completely eaten as in the previous sub-group. The grazers were of the Lymatriidae: *Orgyia antiqua*. Grazing lasted six weeks. The intensity of the grazing was controlled by eye. The group submitted to leaf removal by hand cutting was divided in a similar way to parallel the natural grazing. The fresh weight of the leaves removed from each individual plant was recorded.

On 20 August the fresh weight of the leaves on all the plants was determined.

2. *Salix vitellina* and *S. cinerea*

For each of these species the grazed plants had 30-40% of their original leaf area removed. The grazers were larvae of species "*G*" and, later on, larvae of *Amauronematus sagmarius*. The grazing lasted six weeks, starting at the end of June. Similarly, a group of plants of each species was hand cut, simulating the larvae grazing.

On 25 August the fresh weight of the leaves of all the plants was determined.

No other treatment was given to any of the plants of the three *Salix* species apart from spraying some of them against a Red Spider mite infestation.

II - Effect of grazed willow on larvae growth

Two experiments were carried out to test whether a grazed willow plant became less nutritious and had a depressive effect on the growth of larvae.

1. Larvae "*G*" fed on *Salix viminalis* plants

Four larvae "*G*", kept separately at 15°C, were fed on the new shoots of the heavily grazed *Salix viminalis* cuttings, 20 days after all grazing had stopped. Four others were given shoots from the heavily cut *S. viminalis* plants. Four larvae used as control were fed with leaves of the control plants. The larvae were weighed every three or four days from 13 July to 2 August. The food was renewed at each weighing.

2. *Amauronematus sagmarius* fed on *Salix rotundifolia*

A similar experiment was carried out using leaves from bushes of *Salix rotundifolia*. Leaves from bushes grazed by the first generation of the larvae of *Amauronematus sagmarius* were given to larvae of the second generation. Two sets of six larvae, all of them kept in separate tubes at 15°C, were used consecutively between 2 August and 23 August. Two other sets fed with leaves from ungrazed bushes were used as control.

III - Food selection and differential growth rates of the larvae "*G*" on two *Salix* species

1. Food selection

This experiment was carried out to determine whether the larvae "*G*" have any preference for *Salix viminalis* or *S. cinerea* leaves. For this study four larvae were kept separately at 15°C. Each was offered equal surface areas of *Salix viminalis* and *S. cinerea* leaves. A similar amount of both plants was used as a control for the water loss. Every three or four days, for a fortnight, the remaining food was weighed, then a new amount provided.

2. Differential growth rates

The aim of this experiment was to study the growth rate of the larvae "*G*" on either *Salix viminalis* or *S. cinerea* leaves. For this purpose, two sets of four larvae, each reared on either *S. viminalis* or *S. cinerea* leaves, were kept separately at 15°C and fed on their previous diet. Two other sets of four larvae were kept in similar conditions, but with the change from their previous *Salix* diet to the other species. The larvae were weighed every three or four days and had their food renewed for a total of 12 days.

IV - Effect of the change from the *Salix* species selected for oviposition by the adult on the larval development

To study whether a *Salix* species chosen by the adult sawfly as an oviposition site is the best diet for the larval growth and pupation, two experiments were made.

1. Sawfly on *Salix fragilis*

Sawfly larvae found on *S. fragilis* (see Method A II) were fed on *Salix rotundifolia*. Two sets of six replicates, each kept at 15^{o}C, were used as experimental and control groups. In each replicate several larvae were kept together. The weight of the larvae was recorded every two or three days.

2. *Amauronematus sagmarius* on three *Salix* species

Adults of the first generation of *Amauronematus sagmarius* laid more eggs on *Salix vitellina* plants than on *S. cinerea* and none on *S. viminalis*. Three sets of six larvae, kept separately, were fed consecutively between 30 July and 30 August on each of the willow species. The larvae were fed for 2 days on the experimental food before starting the experiment. The larvae were weighed regularly every two or three days.

V.- Specific selection of *Salix rotundifolia* leaves by *Amauronematus sagmarius* larvae

Amauronematus sagmarius larvae feed on the older leaves of *Salix rotundifolia* rather than on the young leaves near the shoot tips (as most moth caterpillars do). To investigate the effect of the young leaves on the larval development, nine replicates of five to six larvae each were fed exclusively on young leaves at 15^{o}C between 16 June and 3 July. A similar set was used as a control.

Six larvae of the second generation of *Amauronematus sagmarius*, kept separately at 15^{o}C, were submitted to the same treatment. Six others were used as a control.

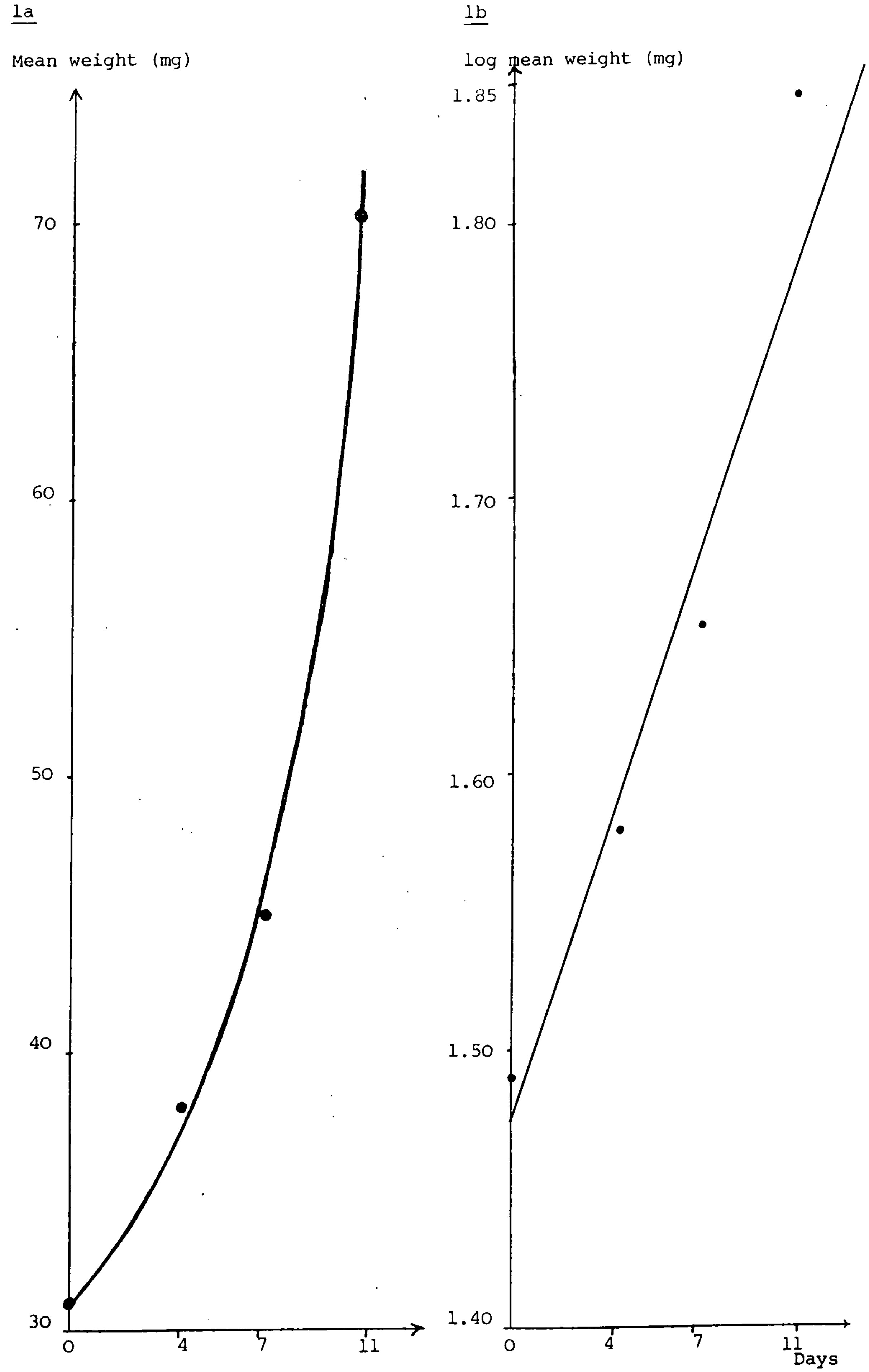
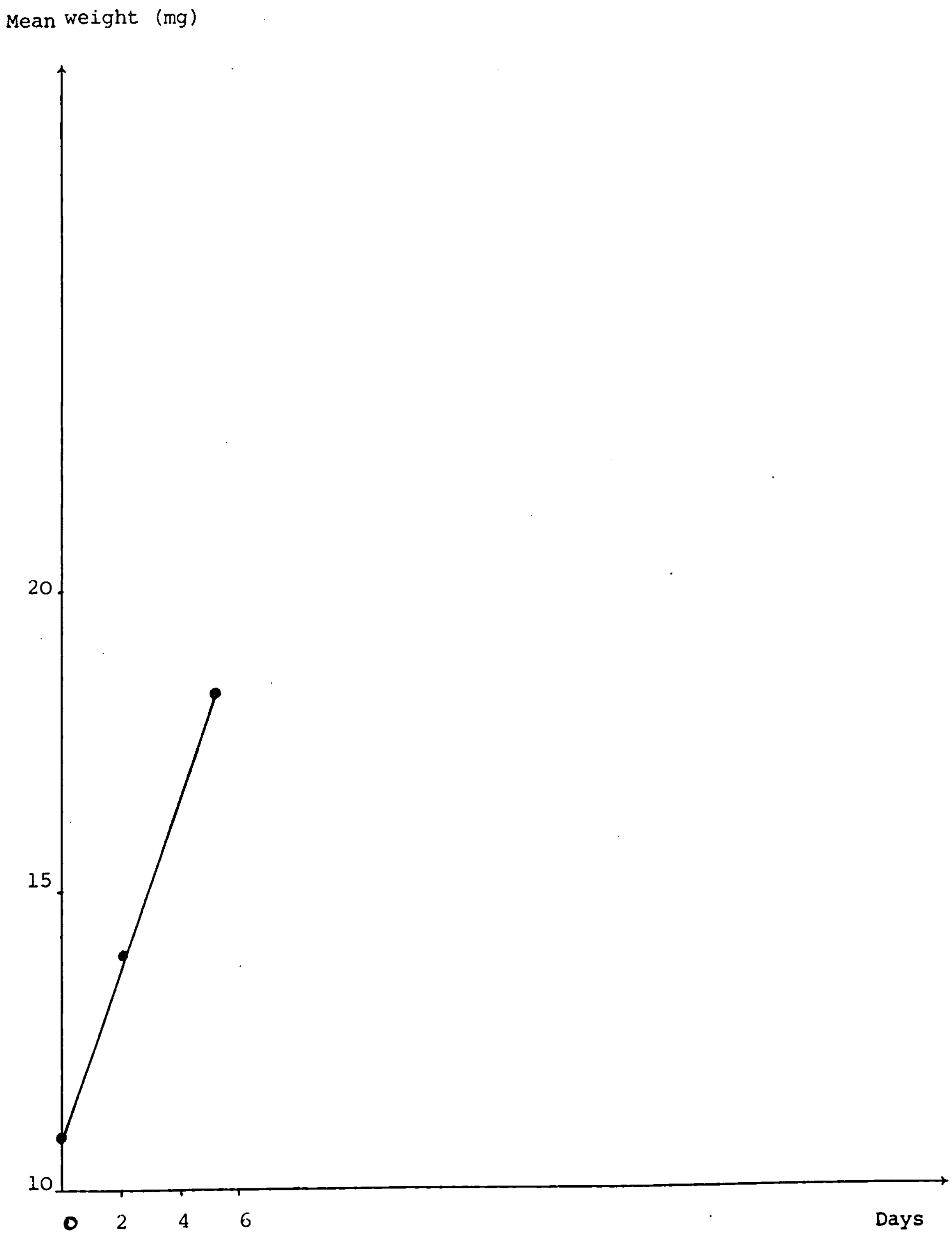


Figure 1. Mean larval weight (mg) (Fig.1a) and log mean larval weight (Fig.1b) of the larvae "*G*" against days feeding on *Salix viminalis* leaves after being reared on *S. cinerea* leaves

Figure 2. Mean larval weight (mg) plotted against days of *Amauronematus sagmarius* larvae (n=6) feeding on *Salix vitellina* leaves



Results

Section I - Effect of grazing on the photosynthetic ability of cuttings of the 3 willow species: *Salix viminalis*, *S. vitellina* and *S. cinerea*

Cuttings belonging to the willow species: *Salix viminalis*, *S. vitellina* and *S. cinerea* were either grazed by larvae or cut by hand. The aim was to study the effect of the leaf removal by either methods on the plant photosynthetic ability and its productivity during the experiment. A total leaf weight production (i.e. adding the amount removed), greater than the control, will be considered as a compensation by the plant.

At the end of each experiment the mean leaf weight of the plants of each group has been determined and then compared with the control. All plant groups had an initial leaf weight comparable with their controls.

For *Salix viminalis* plants, two intensities of treatment were used in each group (see Methods). The mean leaf weight of each group is presented in Table 1.

The mean leaf weights of the 10% cut and both grazed groups were higher than the control. None of the values found is significantly different, however. This implies that the amount of leaf removed by grazing or hand cutting at two intensities did not significantly decrease the leaf area of the plant, i.e. its photosynthetic ability. Presumably the plants have compensated for the leaf removal.

The mean leaf weights, after adding the amount removed, have been calculated (Table 1). Three experimental groups have a higher total leaf weight than the control throughout the experiment.

These increases in productivity (or compensation) are not significantly different from the control, but it should be noted that they all suggest a degree of compensation.

The plants of *Salix vitellina* were divided into two groups and a control (see Methods). The mean leaf weights are presented in Table 2. The mean values of the leaf weight at the end of the experiment are lower than the control value. None of these is significantly different from the control. After adding the amount removed during the treatment, the mean production values are higher than the control. None of these is significantly higher either. This implies that the leaf removal did not decrease significantly the leaf area of the plants. On the other hand, the productivity of the plant throughout the experiment is higher, but not significantly from the control.

The plants of *Salix cinerea* were also divided into two groups (see Methods). The mean leaf weights are presented in Table 3. The values at the end of the experiment of the treated groups are lower than the control. This difference is significant in the case of the grazed group only (Table 4).This suggests that the grazed plants have a lower leaf weight than the control and the hand cut groups. After adding the weight removed by the treatment, the mean weights remain smaller than the control (Table 3). Moreover, the difference between the grazed group and the control is significant (Table 4). This suggests that the grazed group has a lower total productivity during the experiment.

The comparison between the mean weight of a leaf of the grazed and the non-grazed plants gives a significant value in the case of *Salix cinerea* only ($p < 0.01$) (Table 5). In *S. viminalis* or *S. vitellina* the leaves of the grazed and the non-grazed plants have the same mean weight, while in *Salix cinerea* the grazing affects the leaf size, reducing the leaf area.

Table 1. Mean leaf fresh weight (g) of *Salix viminalis* plants submitted to different treatments (± *S.E.*) on 20 August and the mean of the total leaf weight production

	Control	10% cut	Lightly grazed	30% cut	Heavily grazed
	(n = 5)	(n = 8)	(n = 9)	(n = 8)	(n = 8)
Leaf weight at end of experiment	8.7687 ± 0.958	9.5097 ± 2.015	10.3191 ± 1.329	7.3377 ± 0.7787	9.8312 ± 1.2978
Weight removed by hand cutting or estimated grazed	0	0.4414 ± 0.0118	0.625 ± 0.059 (10%)	0.8105 ± 0.1533	1.2628 ± 0.119 (35%)
Total leaf weight production	8.7687 ± 0.958	9.9511 ± 2.0268	10.9441 ± 1.388	8.1482 ± 0.9320	11.0940 ± 1.4168

Table 2. Mean leaf weight (g) ± S.E. of *Salix vitellina* plants, submitted to grazing or hand cutting, on 25 August and the mean of the total leaf weight production

	Control (n = 6)	Grazed (n = 6)	Hand cut (n = 6)
Leaf weight at end of experiment	6.6213 ± 0.9593	5.5703 ± 0.4841	5.3798 ± 0.4503
Weight removed by hand cutting or estimated grazed	0	1.5596 ± 0.1544 (35%)	1.7687 ± 0.5134 (36%)
Total leaf weight production	6.6213 ± 0.9593	7.1299 ± 0.6385	7.1485 ± 0.9637

Table 3. Mean leaf fresh weight (g) ± S.E. of *Salix cinerea* plants, submitted to grazing or hand cutting, on 25 August and the mean of the total leaf weight production

	Control (n = 5)	Grazed (n = 5)	Hand cut (n = 5)
Leaf weight at end of experiment	7.7621 ± 0.8626	3.0750 ± 0.3502	6.1489 ± 0.7455
Weight removed by hand cutting or estimated grazed	0	2.1529 ± 0.3632 (40%)	0.9031 ± 0.0167 (30%)
Total leaf weight production	7.7621 ± 0.8626	5.2279 ± 0.6134	7.0520 ± 0.7622

Table 4. Values of "t" test applied to the mean leaf weight of *Salix cinerea* plants submitted to grazing or hand cutting and to their total leaf weight production

Mean weight at end of experiment	Difference between control and grazed	$t_8 = 5.03$	$p < 0.01$
	Difference between grazed and hand cut	$t_8 = 3.73$	$p < 0.01$
Total leaf weight production	Difference between control and grazed	$t_8 = 2.39$	$p < 0.05$
	Difference between grazed and hand cut	$t_8 = 1.86$	not significant

Table 5. Mean weight (g) of a leaf of grazed or non-grazed plants (control and hand cut) of *Salix viminalis*, *S. vitellina* or *S. cinerea* (± S.E.)

	Mean weight of a leaf of		
	Non-grazed plants	Grazed plants	
S. viminalis	0.082 ± 0.0066 (n = 26)		
S. vitellina	0.191 ± 0.010 (n = 86)		
S. cinerea	0.1169 ± 0.0073 (n = 107)	0.0592 ± 0.0044 (n = 68)	$t_{173} = 6.77$

Results

Section II - Effect of grazed willow plants on larvae growth rates

1. Larvae "*G*" fed on *Salix viminalis* plants

Two sets of four larvae "*G*" were fed on *Salix viminalis* leaves from grazed or hand cut plants to test whether the plants once submitted to leaf removal react by decreasing their palatibility (see Methods). Four larvae were used as a control.

The daily weight change (mg) per larva is presented in Table 6 using a logarithmic transformation. The mean daily weight change of the larvae fed on grazed plant leaves is lower than the two others. The larvae fed with the control plants have the highest daily weight increase. However, none of these differences is significant. This suggests that the plants, whether grazed or hand cut, have the same effect on the larvae "*G*" growth as the control plants.

2. *Amauronematus sagmarius* larvae fed on *Salix rotundifolia*

The second generation of the sawfly larvae *Amauronematus sagmarius* were fed on leaves from previously grazed *Salix rotundifolia* bushes and on control leaves from ungrazed plants.

The daily weight increase of the larvae on both diets is reported in Table 7. The larvae growing on the ungrazed bushes leaves have a higher weight increase than the experimental group. This difference is not significant.

The mean weight at pupation is higher on the experimental larvae, starting with a similar larval weight (Table 8). This difference is not significant.

There is no evidence to show that a grazed plant has a depressive effect on the *Amauronematus sagmarius* larvae growth rate or on their pupal weight.

Table 6. Log weight change (mg) per day per larva "G" feeding on *Salix viminalis* leaves from grazed, hand cut or control plants

Larvae on Control plants

Time	larva 1	larva 2	larva 3	larva 4
13-16 July	0.056	-0.0014	-0.0353	-0.0094
16-20 July	0.0132	0.0708	0.0312	0.0441
23-26 July	-0.0028	0.0458	0.0638	0.0534
26-29 July	0.0387	-0.0054	0.0663	0.0713
29- 2 August	0.0522	0.0266	0.0380	0.0180

Mean ± S.E. = + 0.0362 ± 0.0055

Larvae on Grazed plants

Time	larva 1	larva 2	larva 3	larva 4
13-16 July	0.0535	0.0560	0.0367	0.0417
16-20 July	0.0476	0.0275	0.0502	0.0495
20-23 July	0.0182	0.0339	0.0361	0.0048
23-26 July	0.0273	0.0016	0.0031	0.0246
26-29 July	-0.0097	0.0119	0.0116	0.0537
29- 2 August	0.0329	0.0357	0.0379	0.0336

Mean ± S.E. = + 0.0299 ± 0.0037

Larvae on hand cut plants

Time	larva 1	larva 2	larva 3	larva 4
13-16 July	0.0762	0.0529	0.0463	0.0364
16-20 July	0.0532	0.0238	0.0399	0.0640
20-23 July	0.0262	0.0321	-0.0011	0.0329
23-26 July	-0.0064	-0.0042	0.0148	0.0204
26-29 July	0.0475	0.0550	0.0411	0.0086
29- 2 August	0.0456	0.0320	0.0128	0.0448

Mean ± S.E. = + 0.0331 ± 0.0067

Table 7. Daily weight increase (mg) of *Amauronematus sagmarius* larvae feeding on leaves of grazed or ungrazed *Salix rotundifolia* bushes

Daily weight increase (mg)	Frequency of larvae fed on Control leaves (n=9)	Grazed leaves (n=16)
0.1	0	1
1.3	0	1
2.1	2	0
2.3	0	1
2.8	0	1
2.9	1	0
3.4	1	0
3.5	1	0
3.6	0	1
3.8	0	2
3.9	0	1
4.1	0	1
4.2	0	1
4.5	1	0
4.7	0	1
5.0	0	1
5.1	0	1
5.6	1	0
6.1	0	1
6.2	0	1
6.3	1	0
6.6	0	1
8.6	1	0
Mean ± S.E.	4.3 ± 0.7	3.9 ± 0.4

Table 8. Mean weight (mg) ± S.E. of the larvae of *Amauronematus sagmarius* at the start of the experiment and their pupal weight on leaves of grazed or ungrazed *Salix rotundifolia* bushes

	Initial larval weight	Pupal weight
Control leaves diet	15.2 ± 1.87 (n=12)	17.3 ± 2.28 (n=12)
Grazed leaves diet	15.9 ± 2.14 (n=12)	19.1 ± 2.51 (n=12)

Results

Section III - Food selection and differential growth rates of the larvae "*G*" on two *Salix* species

1. Food selection

Four larvae "*G*" were given the choice between equal surface areas of *Salix viminalis* and *S. cinerea* leaves (see Methods). The amount consumed of each species was calculated after correcting for water loss (Table 9).

The mean weights of both leaves consumed (Table 10) give a higher consumption of *Salix viminalis* leaves throughout the experiment. This consumption is significantly higher during the first period of time ($p < 0.05$) and the third ($p < 0.01$). On the whole, the percentage of *Salix cinerea* consumed is 41.45% of the total consumption (Table 10). This indicates a preference for *Salix viminalis* leaves by the larvae "*G*" when given the choice between them and *Salix cinerea*.

2. Differential growth rates

To test the effect of *Salix cinerea* or *S. viminalis* on the larvae "*G*" growth, larvae were kept on their previous diet or fed on the other willow species (see Methods). The regression line of the mean weight plotted against days has been calculated in each case (see Methods A - I). The mean weights of the larvae feeding on either their previous diet or when changed experimentally to the other willow species are reported consecutively in Tables 11 and 12. The regression lines of the mean weight against days of the larvae on their previous diet (Fig. 3) show a different slope on each diet. The comparison of the slopes (Table 13) shows no significant difference.

Regression lines:

Salix cinerea diet: $y = 0.0336x + 1.2073$

S. viminalis diet: $y = 0.0429x + 1.2451$

When changing the larvae from their previous food to the other *Salix* species, their growth is different (Fig. 4). The comparison of the slopes gives a "t" value = 2.74. This can be considered as a one-tailed test for the larvae "*G*" when given the choice preferred *Salix viminalis* to *S. cinerea* (see Section III - 1) and their growth rate on *Salix viminalis* is higher than on *S. cinerea* (see previous results). The "t" value is significant ($p < 0.05$), entering the table as a one-tailed test.

Regression lines:

Salix cinerea diet: $y = 0.0128x + 1.4816$

S. viminalis diet: $y = 0.0316x + 1.4685$

The comparison of the growth rates of larvae "*G*" feeding previously on *Salix cinerea* leaves and fed experimentally on either species (Table 13) gives no significant difference. The comparison of the growth rates of the larvae "*G*" reared on *Salix viminalis* and fed experimentally on either species (Table 13) gives a significant difference, $t_4 = 4.09$, ($p < 0.05$). The larvae "*G*" grew slowly when changed from their previous food *Salix viminalis* to *S. cinerea*.

Table 9. Proportion of the weight remaining of *Salix cinerea* or *S. viminalis* leaves used as a control for the leaves water loss (± S.E.)

	30 June - 3 July	3 July - 7 July	7 July - 10 July
Salix cinerea leaves (n = 3)	0.50 ± 0.006	0.45 ± 0.036	0.59 ± 0.008
S. viminalis leaves (n = 3)	0.51 ± 0.011	0.37 ± 0.002	0.62 ± 0.010

Table 10. Mean weight (mg) of both *Salix cinerea* and *S. viminalis* leaves consumed by the larvae "*G*" after correcting for water loss (±S.E.)

	30 June - 3 July	3 July - 7 July	7 July - 10 July	Mean percentage of total consumption
Salix cinerea leaves (n = 4)	113.37 ± 16.05	107.59 ± 8.32	124.19 ± 3.89	41.45 ± 0.63
S. viminalis leaves (n = 4)	166.41 ± 4.22	153.47 ± 21.25	166.90 ± 6.42	58.54 ± 0.63
t_6	3.21	2.01	5.69	

Table 11. Mean weight (mg) of larvae "*G*" feeding on their previous food either *Salix cinerea* or *S. viminalis* leaves (± S.E., n = 4)

Food Days	*Salix cinerea*	*S. viminalis*
0	16.1 ± 0.22	16.5 ± 0.55
3	19.9 ± 0.95	25.0 ± 1.8
7	29.0 ± 3.3	38.0 ± 1.7
10	34.0 ± 3.0	44.0 ± 2.9

Table 12. Mean weight (mg) of larvae "*G*" when changing from their past food and feeding on either *Salix cinerea* or *S. viminalis* leaves (± S.E., n = 4)

Food Days	*Salix cinerea*	*S. viminalis*
0	32.0 ± 2.0	31.0 ± 1.7
4	33.0 ± 1.5	38.0 ± 0.75
7	34.0 ± 1.6	45.0 ± 1.2
11	45.0 ± 3.3	70.0 ± 2.9

Table 13. Slopes ± S.E. of the growth rates of larvae "G" feeding on their past food or changing it to either *Salix cinerea* or *S. viminalis* leaves

Past food	*Salix cinerea*		*S. viminalis*	
Experimental food	*S. cinerea*	*S. viminalis*	*S. cinerea*	*S. viminalis*
Slope ± S.E.	0.0366±0.0022	0.0316±0.0047	0.0128±0.0050	0.0429±0.005

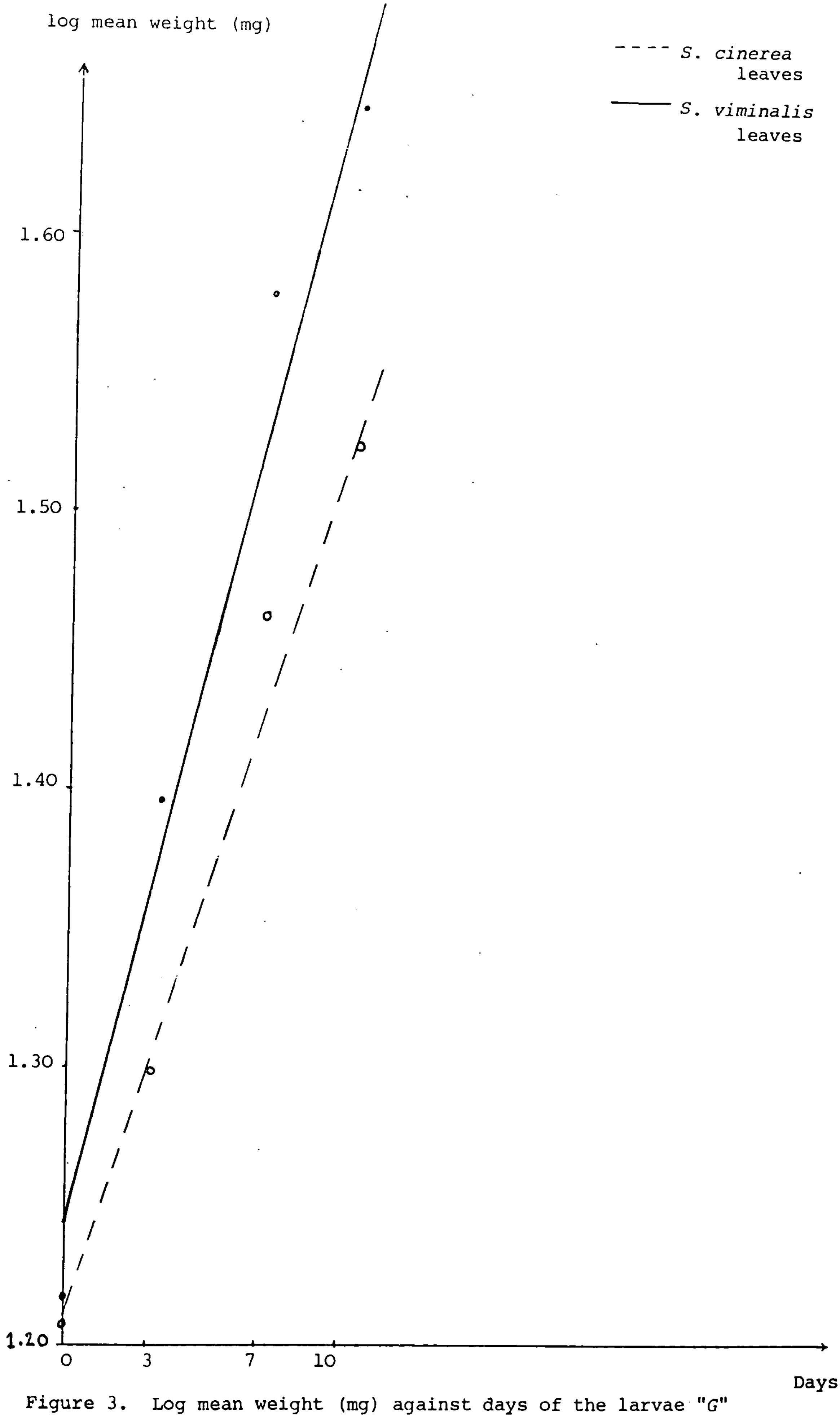


Figure 3. Log mean weight (mg) against days of the larvae "*G*" feeding on their previous food, either *Salix cinerea* or *S. viminalis* leaves.

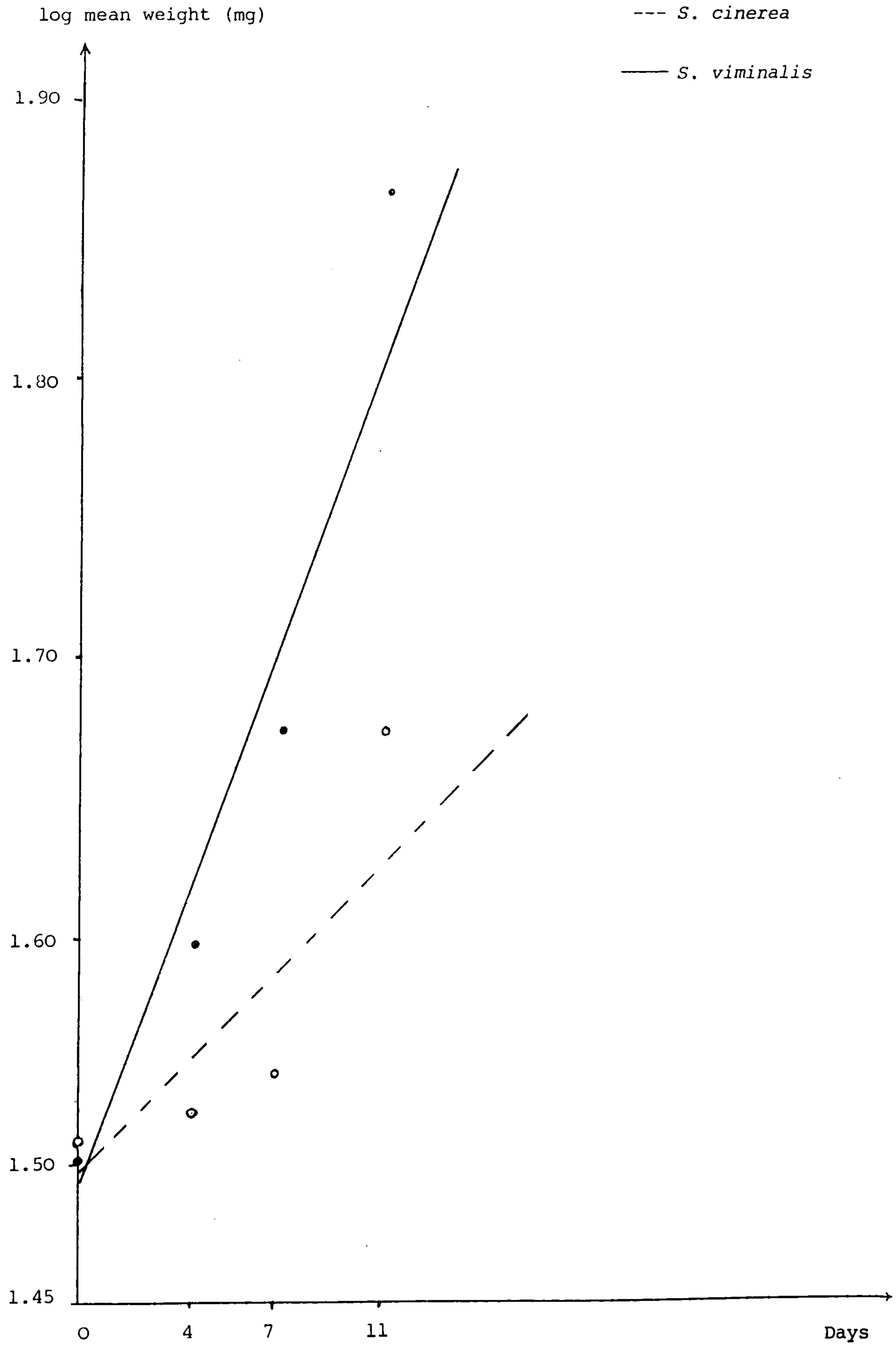


Figure 4. Log mean weight (mg) against days of the larvae "*G*" when changed from their previous food *Salix cinerea* or *S. viminalis* to the other *Salix* species

Results

Section IV - Effect of the change from the *Salix* species selected for oviposition by the adult on the larval development

1. Sawfly on *Salix fragilis*

The sawfly larvae which hatched on *Salix fragilis* were fed on *Salix rotundifolia* leaves at a constant temperature (see Methods).

The daily weight increase of the larvae of the experimental group and the control is reported in Table 14. The mean daily growth is twice as high on the *Salix* species where the oviposition occurred than on the experimental diet. The difference between the daily growths is significant ($p < 0.01$). The larvae grew better on the plant species selected by their female parent than on the other willow species.

The mean pupal weight is given in Table 15. The larvae feeding on the control diet were heavier at the pupation time. This difference is not significantly higher than the experimental pupae weight.

The death rates (Table 16) are not significantly different between the larvae raised on the two *Salix* species ($\chi^2_1 = 2.54$) after applying Yates correction).

2. *Amauronematus sagmarius* on three *Salix* species

The first generation of the adult sawflies had the possibility to lay eggs on plants of the following *Salix* species: *S. vitellina*, *S. cinerea* and *S. viminalis*. The percentage of plants where eggs were laid is different between the three species (Table 17), *Salix viminalis* having the highest number of plants available had no eggs laid on at all.

To test whether the growth of the larvae is different on each of these *Salix* species, larvae were fed on *Salix cinerea* or *S. viminalis* leaves, with the control fed on *S. vitellina* (see Methods).

The daily weight increase of the larvae on the three species (Table 18) shows no significant difference between them. The larvae grew at the same rate on any of the three *Salix*.

The mean pupal weight (Table 19) shows no significant difference between the three *Salix* species. However, the larvae feeding on the control *Salix vitellina* have the highest weight increase in relation to their original larval weight.

The larvae kept on *Salix viminalis* had the highest death rate (Table 20), followed by those on *S. cinerea*. The death rate between the two is not significantly different. The comparison of the death rate on *Salix viminalis* with the control *S.vitellina* gives a significant value: $t_{41} = 3.15$ ($p < 0.01$). The comparison of the death rates between *Salix cinerea* and the control is significant too: $t_{43} = 2.13$ ($p < 0.05$). This suggests that the *Salix* species with a low percentage of oviposition have a higher death rate than the control species chosen by the adults for oviposition.

The comparison of the initial weight of the dead larvae between *Salix cinerea and S. viminalis* gives a significantly different value: $t_{13} = 2.90$ ($p < 0.05$). This suggests that the larvae dying on *Salix viminalis* are heavier than on *S. cinerea*.

Larvae feeding on *Salix viminalis* have the highest death rate in comparison with the two other species. There is no difference in either the larval growth rate or the pupal weight.

Table 14. Daily weight increase (mg) of the sawfly larvae on either *Salix rotundifolia* or *S. fragilis* leaves diet

Daily weight increase (mg)	Frequency of larvae on *Salix fragilis* diet	Frequency of larvae on *S. rotundifolia* diet
0.5	2	2
0.8	0	2
0.9	5	0
1.0	3	3
1.2	6	0
1.4	0	3
1.5	5	9
1.6	0	1
1.7	0	5
1.8	0	8
1.9	4	0
2.0	0	3
2.5	1	6
2.6	5	0
3.0	7	4
3.2	1	0
3.5	3	0
4.0	1	0
4.5	2	0
6.0	2	0
7.0	3	0
10.0	1	0
Total	51	46
Mean ± S.E.	3.5 ± 0.26	1.7 ± 0.09

$t_{95} = 6.66$

Table 15. Mean weight (mg) ± S.E. of the larvae of *Amauronematus sagmarius* feeding on *Salix fragilis* or *S. rotundifolia* leaves at the start of the experiment and at the pupation time

	Initial larval weight	Pupal weight
Salix fragilis diet	8.85 ± 0.63 (n=23)	14.9 ± 2.2 (n=14)
S. rotundifolia diet	8.77 ± 0.70 (n=22)	12.0 ± 0.67 (n=16)

Table 16. Number of dead *Amauronematus sagmarius* larvae feeding on either *Salix rotundifolia* or *S. fragilis* leaves

	Dead larvae	Initial number of larvae
Salix fragilis diet	9	23
S. rotundifolia diet	3	22

$$\chi^2_1 = 2.54$$

Table 17. Percentage of *Salix viminalis, S. cinerea* and *S. vitellina* plants where *Amauronematus sagmarius* adults laid eggs to the total number of plants

Species	Plants with eggs laid on	Total number of plants	Percentage
S. vitellina	14	26	53.84
S. cinerea	2	24	8.33
S. viminalis	0	38	0

Table 18. Daily mean weight increase (mg) ± S.E. of *Amauronematus sagmarius* larvae feeding on *Salix vitellina, S. cinerea* or *S. viminalis*

Food	*Salix vitellina* (n=37)	*S. cinerea* (n=21)	*S. viminalis* (n=18)
Mean weight increase	2.66 ± 0.35	2.03 ± 0.44	3.03 ± 0.53

Table 19. Original mean larval weight and subsequent mean pupal weight (mg) ± S.E. of *Amauronematus sagmarius* larvae feeding on *Salix vitellina, S. cinerea* or *S. viminalis*

Food	Original larval weight	Pupal weight
Salix vitellina	12.2 ± 7.5 (n=19)	17.2 ± 8.2 (n=19)
S. cinerea	16.6 ± 6.2 (n=19)	16.0 ± 6.6 (n=19)
S. viminalis	15.1 ± 4.9 (n=14)	18.2 ± 6.6 (n=14)

Table 20. Proportion of the dead larvae and their initial mean weight (mg) ± S.E. of *Amauronematus sagmarius* feeding on *Salix vitellina, S. cinerea* or *S. viminalis*

Food	Dead larvae	Initial number of larvae	Proportion dying ± S.E.	Initial weight (mg) ± S.E. of dead larvae
Salix vitellina	1	20	0.05±0.048	16.3
S. cinerea	6	25	0.24±0.085	6.1±1.0
S. viminalis	9	23	0.39±0.101	10.3±1.1

Results

Section V - Specific selection of *Salix rotundifolia* leaves by *Amauronematus sagmarius* larvae

a. First generation

The larvae of *Amauronematus sagmarius* were always found feeding on the older leaves of *Salix rotundifolia* twigs. When some larvae were removed and put experimentally on the young leaves near the shoot tips, they all moved away. The following day, three out of the eight larvae were found on the older leaves. An experiment was carried out to find the reason and consequences of this preference.

Larvae were fed either on older leaves or young shoots. The daily weight increases of the larvae fed on these diets are given in Table 21. They show no significant differences. The mean pupal weight of the larvae reared on the young leaves diet (Table 22) is lower than those on the old leaves diet. This difference is not significant either. The number of days spent by larvae on either diet before pupation is different (Table 22). This difference is significant ($p < 0.05$). This suggests that the larvae feeding on *Salix rotundifolia* young leaves required less days before pupating.

The death rates of the larvae on the two diets are different (Table 23). It is four times higher on the young shoot diet than on the older leaves. The difference is significant ($p < 0.01$). Comparing the initial weight of the dead larvae with the initial weight of the larvae used for each diet (Table 24) shows that the dead larvae were initially the smaller ones. The difference between the initial weight of the larvae and the dead on each diet is significant (Table 24).

Starting with a comparable larval weight on both diets, the dead larvae on the experimental diet are not significantly heavier than on the control.

b. Second generation

The experiment has been repeated with two sets of six larvae of the second generation of *Amauronematus sagmarius* (see Methods) between 9 August and 23 August.

Their daily weight increase (Table 25) is different. The larvae feeding on the old leaves have a higher growth rate than the experimental ones, but not significantly so.

The pupal weight of the control (Table 26) is not significantly higher than that of the experimental larvae. The mean number of days required before pupation on either diet is presented in Table 26. The difference is significant ($p < 0.05$). This suggests that the larvae feeding on the old leaves take longer to pupate.

No deaths were recorded amongst the larvae on either diet.

Table 21. Daily weight increase (mg) of *Amauronematus sagmarius* larvae feeding on young or older *Salix rotundifolia* leaves

		0.5	1.0	1.5	2.0	2.1	2.5	3.0	3.4	3.5	4.0	4.5	5.0	6.0	6.5	7.0
Daily weight increase		0.5	1.0	1.5	2.0	2.1	2.5	3.0	3.4	3.5	4.0	4.5	5.0	6.0	6.5	7.0
Frequency of larvae on	Young leaves diet	0	0	11	5	0	0	2	3	0	0	4	1	0	2	0
	Old leaves diet	10	7	1	0	5	20	0	0	10	1	0	6	2	3	1

Mean ± S.E.

Young leaves diet: 2.8 ± 0.2 (n=28)

Old leaves diet : 2.7 ± 0.2 (n=66)

Table 22. Mean initial larval weight (mg) ± S.E. and pupal weight and the number of days before pupation of *Amauronematus sagmarius* larvae feeding on young or old *Salix rotundifolia* leaves

Food	Initial larval weight	Weight at pupation	Days before pupation
Young leaves	25.3 ± 1.9	29.2 ± 1.89	4.82 ± 0.58
	(n=58)	(n=30)	(n=23)
Old leaves	25.5 ± 1.8	30.2 ± 1.60	6.36 ± 0.43
	(n=60)	(n=42)	(n=36)
			$t_{57} = 2.13$

Table 23. Death proportion of *Amauronematus sagmarius* larvae feeding on young or old *Salix rotundifolia* leaves

Food	Number of dead larvae	Initial number	Proportion dying
Young leaves	25	58	0.43 ± 0.065
Old leaves	6	60	0.1 ± 0.038

$t_{116} = 4.38$

Table 24. Initial mean weight (mg) ± S.E. of the total larvae used and of the dead larvae of *Amauronematus sagmarius* feeding on young or older leaves of *Salix rotundifolia*

Food	Total larval weight	Dead larvae weight	"t" values
Young leaves	25.3 ± 1.9 (n=58)	18.9 ± 2.2 (n=25)	$t_{82} = 2.2$
Old leaves	25.5 ± 1.8 (n=60)	11.2 ± 4.3 (n=6)	$t_{64} = 3.06$

Table 25. Daily weight increase (mg) of *Amauronematus sagmarius* larvae feeding on the young or old leaves of *Salix rotundifolia*

Weight increase		1.0	1.4	1.6	1.7	2.1	2.3	2.6	2.9	3.4	3.5	4.5	6.3	7.7	8.6
Frequency on	Young leaves diet	1	1	1	2	0	1	1	0	0	0	0	0	1	0
	Old leaves diet	0	0	0	0	2	0	0	1	1	1	1	1	0	1

Mean ± S.E.

Young leaves diet: 2.5 ± 0.74

Old leaves diet : 4.1 ± 0.78

Table 26. Mean initial weight and pupal weight (mg) ± S.E. and the mean number of days before pupation ± S.E. of *Amauronematus sagmarius* larvae feeding on young or old *Salix rotundifolia* leaves

Food	Initial larval weight (n=6)	Pupal weight (n=6)	Days before pupation (n=6)
Young leaves	16.9 ± 1.0	16.1 ± 1.8	7.0 ± 0.44
Old leaves	14.8 ± 1.1	19.3 ± 3.3	8.83± 0.65
			$t_{10} = 2.33$

Discussion

Section I - Effect of grazing on the photosynthetic ability of cuttings of the 3 willow species: *Salix viminalis, S. vitellina* and *S. cinerea*

The effects of the leaf removal by natural grazing or hand cutting on the three *Salix* species: *S. viminalis, S. vitellina* and *S. cinerea* were different. In *S. viminalis,* the leaf weight at the end of the experiment in three of the four groups treated was higher (but not significantly so) than the control. Given time to recover from the effect of the leaves removal, the leaf weight of the plant was the same in the grazed, hand cut and control plants. The leaf removal did not decrease the plants photosynthetic ability for very long. The effect was unnoticeable a few weeks later. Adding the amount removed by the treatments did not increase the total leaf production significantly above the control levels. It is suggested that when the plant is submitted to a grazing stress it increases its productivity in an attempt to compensate for leaf loss.

There is no evidence to show that the grazers have any effect on the plant apart from the strict leaf area removal; i.e. there is no difference between the groups submitted to grazing or hand cutting. It must be noted that the mode of leaf removal was different between the different larvae used. The small *Orgyia antiqua*, used on the 10-15% grazed group, removed a small part from the leaves edges, while the bigger Geometridae used on the 30% grazed group removed the leaves entirely. The simulation of the grazing was sometimes difficult because of the larvae behaviour.

There is evidence that moderate grazing induced a change in the plant reproductive strategy; e.g. towards a sexual reproduction in the plants of the leek *Allium porrum* grazed by the specialised larvae of the moth *Acrolepiopsis assectella* (Boscher 1979). The effect on the plant production and vegetative growth depends on the timing and the mode of the leaf attack (Harris 1971). Grazing of the young leaves early in the season (as most moth caterpillars do) is more stimulating; it increases the photosynthetic rate of the plant by removing the young leaves considered as an "energy drain".

The results found in *Salix vitellina* suggest that the leaf removal did not have a depressive effect on the plant leaf weight.

The total leaf production is slightly higher than the control, suggesting a certain degree of compensation.

The intensity of leaf removal is important in both cases and the amount of the leaves removed before the non-recovery point is reached remains unanswered.

In *Salix cinerea*, the grazed group had a significantly lower leaf weight and total leaf production than the control and hand cut groups. The mean weight of a leaf from a grazed plant had a smaller weight, i.e. leaf area, than those from the two other groups. In this case the hand cut was less damaging to the plant than the grazing, or the time allowed for the plants to recover was not enough (14 days). The 10% difference between grazing and hand cut intensities could be crucial. The other reason could be that *S. cinerea* responds to the grazing by decreasing its shoot/root ratio, while the others increase it (Bentley and Whittaker 1979, working on two *Rumex* species).

Section II - Effect of grazed willow on larvae growth

The investigation of the change in the leaf quality when grazed or hand cut was done throughout the study of the larvae "*G*" growth rates. The larvae feeding on the leaves from grazed plants had a lower growth rate than those on the hand cut or the control plants. This suggests that the leaves submitted to a stress are less nutritious and induce a slower growth rate (Haukioja 1980). However, the difference between the growth rates was not significant in this case, and further work is required. It is possible that the stress had ended or been reduced when the experiments started. A more significant deterioration in the leaf quality may be detected a few days after the leaf damage occurred, but I could not afford plant material for experimental use on two occasions.

Similarly, the growth of the second generation of *Amauronematus sagmarius* larvae fed on the leaves of *Salix rotundifolia* from grazed plants did not differ from the control. In this species three generations have been observed this year, so quick and efficient growth is vital. The likelihood that the larvae feed on grazed plants is high. However, the time separating the first two generations was 30 days, which could explain the absence of depressive effect of the leaves or the larval growth or pupal weight.

Section III - Food selection and differential growth rates of the larvae "*G*" on two *Salix* species

The larvae "*G*", when given the choice, preferred *Salix viminalis* to *S. cinerea* since 58% of the leaf weight consumed was *S. viminalis* leaves. The study of the larval growth on each species separately might explain this preference. The transfer of the larvae "*G*" from their accustomed diet of *S. cinerea* leaves to *S. viminalis* leaves did not change their growth rate, while the larvae transferred from *S. viminalis* to *S. cinerea* had a significantly lower growth rate. When the larvae were kept on their accustomed food, either *S. cinerea* or *S. viminalis*, their growth rates were comparable. Fraenkel (1969) claimed that plants can "equally" well serve as food provided they are eaten in sufficient amounts and "no adverse chemical or mechanical factors are operating". The difference in the physical texture of the leaves between the two species could affect the consumption. In *S. cinerea* the leaves are hairy on both sides and have a tougher feel than *S. viminalis*. The chemical composition of the leaves could be different. A reduced water content can induce a slower growth (Scriber 1977), but the water content is not different between the two species. The balance between the main classes of nutrients could be different (House 1965). Soo Hoo and Fraenkel (1966) found that the larvae of polyphagous armyworm *Prodenia eridania* selected the food plant species with the highest protein content. The selection (even if not very marked) of *S. viminalis* leaves by the larvae "*G*" is explained by the fact that it promotes a faster growth, i.e. is more nutritious.

Section IV - Effect of the change from the *Salix* species selected for oviposition by the adult on the larval development

Fraenkel (1969) stated that, in general, both the adult female and the larvae have the ability to recognize the host plant. If the larvae do not leave the plant they show a reduced ability to recognize it and depend on adult selection. The sawfly larvae are very sedentary.

In this case, the *Salix* species selected by the adult female should be most beneficial. The sawfly larvae feeding on *S. rotundifolia* leaves or on *S. fragilis* leaves, the species where the oviposition occurred, had a comparable pupal weight. However, their daily growth rate was twice higher on *S. fragilis* than on *S. rotundifolia*. The species selected by the adult female did seem more suitable for the larvae.

When all three *Salix* species (*S. viminalis, S. cinerea* and *S. vitellina*) were present, the adult sawflies *Amauronematus sagmarius* selected *S. vitellina* in preference to *S. cinerea* for egg laying and avoided *S. viminalis* completely. Larvae, put experimentally on *S. viminalis* plants, moved away searching for other food sources. This behaviour is unusual as the larvae normally have a sedentary feeding habit. It is possible that this willow species has the presence of a "deterrent" (Jermy 1966). The study of the daily weight increase and the pupal weight of the larvae feeding on one of the three species gave no evidence of greater suitability of one of the species. The death rate was, however, much higher on *S. viminalis* and *S. cinerea* than on *S. vitellina* where most egg clusters were laid. The mortality rate of larvae fed on either *S. viminalis* or *S. cinerea* was higher in the smaller individuals. It is possible that the small larvae had a lower resistance to the plant toxic material, a higher nutrient requirement, or were infected (e.g. by a virus) at the start of the experiment. The physical structure of the leaves of *S. viminalis* (species inducing the highest death rate) and *S. vitellina* is unlikely to cause this difference in larval mortality as this is similar in both plant species. The high death rate of larvae on *S. cinerea* leaves, in comparison with *S. vitellina,* could have been caused partially by the difference in the leaf structure between the two, as the leaves are more hairy and tougher in *S. cinerea*. The death rate found on *S. cinerea* was lower (even if not significantly) than on *S. viminalis*. This could be the selective advantage in the preference of adults to lay their eggs on *S. cinerea* (8% of plants contained eggs) but no eggs were laid on *S. viminalis* plants.

Section V - Specific selection of *Salix rotundifolia* leaves by *Amauronematus sagmarius* larvae

The leaf quality could differ within the same plant species between young and old or mature leaves. A deterioration of the quality with the advance of the season has been observed in many cases. It would be related, as discussed earlier, to a change in the physical quality, e.g. a thickened plant cuticle (Feeny 1970); or in the chemical composition, e.g. water content (Scriber 1977) or protein content due to an increase in a secondary compound (Feeny 1970).

This difference can be present, at a time, between the young and old leaves of the same plant. The development of *Amauronematus sagmarius* larvae was different when fed on the young and older leaves. Neither the daily weight increase nor the pupal weight were different on either of these diets. However, the larvae feeding on the diet of young leaves pupated earlier. This suggests that the young leaves are more nutritious, but this is not confirmed by the daily weight increase nor by the pupal weight on both food diets.

However, the death rate of the larvae of the first generation was four times higher in those fed on the young leaves. This could be related to a difference in the components of the leaves, i.e. a higher concentration of a toxic compound or simply a lower availability of nutrients. In this case too, the mortality rate was higher in smaller individuals. The reason could be, as discussed in the previous section, a lower resistance to the plant toxic compounds maybe stressed by an infection of these smaller larvae.

A change of leaf quality with the season could explain the absence of mortality in the larvae of the second generation.

Conclusions

There was no decrease in the leaf weight of the treated plants of *Salix viminalis* and *S. vitellina* contrary to *S. cinerea*. The intensity of the treatment as well as the mode of removing are important. The response to this stress could differ between the different plant species of the same genus.

There was no conclusive evidence of a decrease in palatibility of the leaves from grazed plants in either case studied. A further investigation could be fruitful, particularly if the time between the removal and the subsequent feeding is shortened.

The adult females or the larvae appear to select the most nutritious food species available. The species selected promoted either a faster growth or a higher survival rate. Within the same *Salix* species, larvae fed on the leaves which resulted in a higher survival rate.

References

Bailey N.T.J. (1980) Statistical methods in Biology. 2nd Ed. Hodder and Stoughton.

Bentley S. and Whittaker J.B. (1979) Effects of grazing by a chrysomelid beetle, *Gastrophysa viridula,* on competition between *Rumex obtusifolius* and *R. crispus*. Journal of Ecology 67, 79-90.

Bernays, E.A. and Chapman, R.F. (1970) Experiments to determine the basis of food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera : Acrididae) in the field. J. Anim. Ecol. 39, 761-776.

Boscher, J. (1979) Modified reproductive strategy of leek *Allium porrum* in response to a phytophagous insect, *Acrolepiopsis assectella*. Oikos 33, 451-456.

Chinery, M. (1973) A field guide to the insects of Britain and Northern Europe. Collins, London.

Clapham, A.R., Tutin, T.G. and Warberg, E.F. (1962) Flora of the British Isles (2nd Edition). Cambridge.

Craggs, S.E. (1978) Selective grazing of willow species by invertebrate herbivores. M.Sc. dissertation, Durham University.

Dethier, V.G. (1954) Evolution of feeding preferences in phytophagous insects. Evolution, Lancaster, Pa. 8, 33-54.

Edwards, P.J. and Wratten, S.D. (1980) Ecology of Insect-plant Interactions. Studies in Biology. No. 121.

Feeny, P.P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51, 565-581.

Fraenkel, G. (1969) Evaluation of our thoughts on secondary plant substances. Ent. exp. and Appl. 12, 473-486.

Harris, P. (1971) Insects in the population dynamics of plants. R.E.S. Symposium 6. Insect/Plant Relationships.

Haukioja, E. (1980) On the role of plant defences in the fluctuation of herbivores. Oikos 35, 202-213.

House, H.L. (1965) Effects of low levels of the nutrient content of a food and of nutrient imbalance on the feeding and the nutrition of a phytophagous larva, *Celerio euphorbiae* (Linnaeus) (Lepidoptera : Sphingidae). Can. Ent. 97, 62-68.

Imms, H.D. A general textbook of Entomology. 9th ed. (1957) Methuen.

Jermy, Y. (1966) Feeding inhibitors and food preference in chewing phytophagous insects. Entomologia exp. appl. 9, 1-12.

Lawton, J.H. (1982) Vacant niches and unsaturated communities : a comparison of bracken herbivores at sites on two continents. J. Anim. Ecol. 51, 573-595.

Owen, D.F. and Wiegert, R.G. (1976) Do consumers maximize plant fitness? Oikos 27, 488-492.

Polunin, O. and Everard, B. (1976) Trees and Bushes of Europe. Oxford University Press. London.

Price, P.P. (1975) Insect Ecology. John Wiley and Sons, New York.

R.E.S. of London Handbooks for the identification of British Insects. Vol. VI - Hymenoptera.

Scriber, J.M. (1977) Limiting effects of low leaf - water content on the nitrogen utilization, energy budget and larval growth of *Hyalophoro cecropia* (Lepidoptera : Saturniidae) Oecologia 28, 269-87.

Soo Hoo, C.F. and Fraenkel, G. (1966) The selection of food plants in a polyphagous insect, *Prodenia eridania* (Cramer). J. Insect Physiol. 12, 693-709.

South, R. (1908) The moths of the British Isles. Frederick Warne and Co. London.

Southwood, T.R.E. (1971) The insect/plant relationship - an evolutionary perspective. R.E.S. Symposium 6. Insect/Plant Relationships.