A Study of the relative quality of various species of the Cruciferae as foodplants for the larvae of Pieris brassicae and Artoqeia napi (Lepidoptera)

Wendy Jane Salmon

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Species named in the text

Plants

Alliaria petiolata (Bieb.) Cavara and Grande.
Barbarea vulgaris R.Br.
Brassica napus L.
Brassica oleracea L.
Brassica rapa sylvestris (L.) Jachen
Cardamine pratensis L.
Erysmium asperum L.
Hesperis Matronalis L.
Lupinus L.
Reseda luteola L.
Sisymbrium officinale (L.) Scop.
Thlaspi arvense L.

Animals

Anthocharis cardamines L.
Artogeia napi Kudrna (= Pieris napi L.)
Artogeia napi Macdunnoughii Remington
Artogeia rapae Kudrna (= Pieris rapae L.)
Papilio Macheon L.
Pieris brassicae L.
Plebejus icariodes Bdv.

INTRODUCTION

Background

Larvae of the Pieridae butterfly family will only feed, in natural situations, on plant tissues which contain mustard oils-glucosinolates. These plants are members of the Cruciferae, Rosedaceae, Capparidaceae and Tropaeolaceae families (Vers'chaffelt 1910). Mustard oils are referred to as secondary metabolic compounds as they have no known physiological function within a plant. Within the plant kingdom there are a host of different secondary compounds, often strong smelling and tasting, characteristic of different families, genera, and in some cases, species. One hypothesis for a functional role is that they play a part in defence against herbivore attack, primarily against insectiverous herbivores, (Ehlich & Raven 1964, Fraenkel 1966). In order to feed on plant structures, insects have had to become immune, or detoxify the chemical defences a plant possesses, i.e. to become physiologically adapted to their food plant. Such adaptations place a metabolic load on an insect, and rather than maintaining mechanisms for detoxification of a wide range of chemicals, the majority of insects are restricted to feeding on those plants which contain one particular secondary compound. The adaptation has become so fine that what was previously a chemical repellent has, in some instances, become an attractant and feeding stimulus to the adapted insect (Whittaker & Feeny 1971). For those animals which specialize on particular plants, the secondary compounds of other (non-host) plants remain repellent and/ or toxic in many cases (Blau, Feeny and Contardo 1978).

Mustard oils are a feeding stimulant to Pieridae larvae, and caterpillars of Pieris brassicae can be induced to feed on a semi-synthetic diet if a mustard oil is included in the ingredients (Verschaffelt 1910, David and Gardiner 1966). Adult Pieridae are also sensitive to mustard oils, this is advantageous, as the adult female has to lay her eggs on a suitable foodplant, so that the larvae on hatching will be in contact with a plant bearing the necessary chemical constituents to stimulate feeding. Mustard oils stimulate oviposition in female Pieridae; David and Gardiner, 1962, found that a green paper treated with a 0.2% sinigrin solution (a mustard oil) stimulates oviposition in Pieris brassicae females.

In Northern temperate latitudes, crucifers are the main foodplants of the larvae in the subfamily Pierinae (Whites and Orange Tips) of the Pieridae butterfly family. However not all crucifer species are acceptable as host plants by the butterflies, and species within the Pierinae group differ as to which crucifers the adults will oviposit upon, and on which the larvae will feed (Chew 1975, 1977, Shapiro 1975). In many cases use of different foodplants can be explained by the length of time the butterflies and plants have coexisted; and the predictability of the occurrence of the food plant resource (Bowden 1970). Chew (1975) found that six crucifers growing in meadows in the Rocky Mountains of Colorado were suitable as larval food for the butterfly Artogeia napi macdunnoughii which lives in this area. But there were two other crucifers on which the larvae could not develop Erysmium asperum, which the larvae would not eat, and Thlaspi arvense, which the larvae ate but later died. The adults avoided oviposition on E. asperum, but T. arvense was still used despite lethal consequences. This behaviour may be explained by the fact that E. asperum contains toxic cardenolides (cardiac glucosides) which the larvae may recognise and so refuse to eat. In evolutionary time this may have proved a strong enough selection pressure to remove any tendency to oviposit on E. asperum from the population. T. arvense is thought to have been introduced into the Rocky Mountains less than one hundred years ago, and in this case not enough time may have elapsed to allow the evolution of avoidance in the adults, or those of tolerance in young larvae.

Chew measured the survival, pupal weights and time taken to develop to pupation of P.n. macdunnoughii larvae when feeding on different crucifers. Pupal weight is correlated with the number of eggs a female carries. The speed of development determines the period of time a larva is exposed to possible predation and paratisation. A rapid development may also benefit a larva by allowing pupation before the first frosts of Autumn in the Rocky Mountains, and is especially critical for the offspring of late emerging adults. She found no significant difference between pupal weights or survival on the different crucifers but a significant difference ($P < 0.001$) in larval development times.

Chew 1977 showed that the relative proportions of plants chosen as oviposition sites by female butterflies of A.n. macdonoughii tended to reflect their suitability as larval food in terms of development times. It is believed that the adults can distinguish between different crucifer species by their glucosinolate profiles (Hovanitz & Chang 1963, Hicks 1974, Chew 1979).

For my research project I wanted to find out whether there were any differences between the crucifers growing on the banks of the River Wear in Durham, in terms of suitability as Pierid larval food, indicated by larval growth rates, survival, pupal weights and time taken to complete development. Lees and Archer (1974) have studied the ecology of Artogeia napi (one of my study animals) in Britain, and they have listed the relative preferences of this species for food plants using the likelihood of finding eggs when searching the leaves of crucifers. I shall refer to their work later in my thesis, in order to compare the adult oviposition preferences with the larval food preferences of A.napi which I have found in the laboratory.

Study Area

This was mainly a laboratory based study. The crucifers I chose for my feeding experiments were some of those which grow on the banks of the river Wear in Durham, one plant Cardamine pratensis, which grows in wet meadows near the river, and also the cultivated cabbage. Four species of Pieridae fly along the river banks and nearby meadows.

Cruciferae

Alliaria petiolata	Hedge Garlic, Garlic Mustard, Jack-by-the-Hedge Biennial or perennial.
Barbarea vulgaris	Winter Cress, Yellow Rocket. Biennial or perennial.
Brassica rapa sylvestris	Wild Turnip. Annual or biennial.
Brassica oleracea	The Cultivated Cabbage. This plant will be referred to as Cabbage throughout the thesis.
Cardamine pratensis	Cuckoo Flower, Lady's Smock. Perennial.
Hesperis matronalis	Dame's Violet. Biennial or perennial. A garden escape.
Sisymbrium officinale	Hedge mustard. Annual or overwintering herb.

Pieridae

Pieris brassicae	Large Cabbage White.
Artogeia napi	Greenveined White.
Artogeia rapae	Small Cabbage White.
Anthocharis cardamines	Orange Tip.

The food plants show a successional appearance with the seasons. A. petiolata, B. Vulgaris and C. pratensis are vernal species followed later in the year by H. matronalis, B. rapa and S. officinale. Many of the plants are ruderal species growing on bare ground as primary colonizers. The provision of bare ground is determined by the flooding of the river, human trampling and agricultural practices in the near-by fields and so the number of crucifers varies from year to year (Courtney 1980).

Pieris brassicae

Eggs of this species were obtained from Dr. B. O. C. Gardiner of Cambridge University. They were from a permanent culture he maintains. In the wild state in Durham the species has two flight periods, the first in late May and early June, butterflies emerging from over-wintering pupae. The later emergence in July and August is reinforced with continental migrants. In Britain the food plant predominantly used is the cultivar of *Brassica oleracea* - cabbage, though there are records of the species feeding on wild crucifers (South 1944), e.g. *Brassica napus*.

Artogeia napi

Adults from two populations of *A.napi* were used in the study. Female adults were caught flying along the banks of the river Wear in Durham; I also obtained some from an upland population from Garrigill near Alston, S. Tynedale, (courtesy of S. Courtney). The females caught laid eggs and from these the larvae hatched which were used in the experiment. Lees and Arthur (1974) have found that *A.napi* larvae will accept more than 30 species of crucifer in the laboratory, as well as other exotic species containing mustard oils.

Anthocharis cardamines

I had hoped to work with the larvae of *A.cardamines*, and collected eggs from the Wear banks. Unfortunately all those collected died through disease. However, as feeding experiments formed one aspect of S. Courtney's work (1980) on the ecology of this species in Durham, this area has already been studied. It will be interesting to compare the relative suitability of the crucifers as larval food for this species and A.napi.

Artogeia rapae

This species uses both cabbage and wild foodplants and therefore comes into competition with both A.napi and P.brassicae. I did not work with this species.

METHODS

Pieris brassicae

Larval growth when feeding on different crucifers

Two feeding experiments were carried out, one at 15°C and one at 10°C. The larvae used had hatched on, and been initially reared on Cabbage.

Batches of larvae were given the foodplants B.vulgaris, C.pratensis and cabbage when four days old, and one batch received A.petiolata when thirteen days old. This group of animals were kept at 15°C and no attempt was made to distinguish between individual animals, and all the caterpillars eating a particular food plant were kept together.

The larvae kept at 10°C were fed on Cabbage, B.vulgaris, B.rapa, H.matronalis and A.petiolata. The animals were placed on the different food plants when thirteen days old. In this experiment the animals were kept singly in petri dishes, so that the growth of individuals could be monitored, and as a precaution against the spread of disease.

At each temperature the food was renewed or changed as necessary, and the containers cleaned of frass at regular intervals.

The larvae were weighed individually at frequent intervals, usually every three days, in order to monitor their weight gain as an indication of the relative growth rates supported by the different foodplants. The survival, the time taken to complete development and the pupal weights of the larvae on the different food plants were recorded.

The difference between the plants used in the 10°C and 15°C trials was due to their availability at the times of the experiments. The 10°C trial was run later in the year when Cardamine pratensis was difficult to obtain in sufficient quantities in the Durham area, and when Hesperis and Brassica rapa were in greater abundance than they had been when the 15°C trial had been run. From the experiment below some indication of larval weight gain can be ascertained on H.matronalis and B.rapa at 15°C.

Larval weight gain and food intake

This experiment was conducted to see whether there were differences between the intake of each foodplant by individual larvae which may account for any differences between their weight gains.

The larvae in this experiment were kept individually in petri dishes. They were weighed and then given a known wet weight of one crucifer, kept fresh with moist cotton wool. A representative sample of each crucifer was weighed wet, and then reweighed after having been dried at 40°C for seven days. From the sample weights a wet/dry weight ratio could be calculated. This ratio was used to find out how much of a crucifer a larva had eaten during the experimental period. Using the ratio, the initial wet weight of the crucifer given to an animal was converted to a dry weight; the amount of food left at the end of the trial was weighed when dry and this amount subtracted from the dry weight of the food given initially.

This experiment was run over three periods of two days each using the crucifers: cabbage, A.petiolata, B.vulgaris, B.rapa and H.matronalis.

Larval food preferences

This experiment was carried out to discover whether the larvae showed a preference for any crucifer when given a choice, and whether their preference was related to the suitability of the foodplants in terms of the rapidity of development they supported.

Individual larvae of known weight were placed in petri dishes containing known wet weights of H.matronalis, B.rapa, B.vulgaris, A.petiolata and cabbage. The food plants were overlapping and kept fresh with moist cotton wool. At the end of the experimental period the amount of each crucifer eaten was calculated using the wet/dry weight ratio (as outlined above). This experiment was repeated three times using the same caterpillars. In this way it could be determined whether individual caterpillars kept at the same food preferences over an extended period, or whether their food choice became more catholic in taste as the period of exposure to a number of crucifers increased.

In the above experiments the P.brassicae larvae had all hatched on cabbage B.oleracea, and had been eating this plant for at least four days before they were transferred to wild plants. It was wondered how much affect the foodplant on which a larvae hatched and completed its first instar had on its initial growth. To gain this information, eggs of

Pieris brassicae were hatched on *H.matronalis*, *A.petolata*, *B.vulgaris* and cabbage and their weights after nine days were recorded.

Artogeia napi

The larvae from the Alston population were used in similar experiments to those carried out with Pieris brassicae, to gain information on larval development on the different crucifers; larval weight gain and the amount of each crucifer eaten, and larval food preferences. Similar methods were employed. The animals were kept at 15°C for the duration of each experiment. The food plants used were A.petiolata, B.vulgaris, B.rapa, H.matronalis and S.officinale. The larvae were transferred from A.petiolata when thirteen days old.

Experiments were started to measure survival, development time and pupal weight of larvae from the Durham population of A.napi on different crucifers. However, the majority of animals died through disease, but I have a few results from these experiments.

Results

and

Interpretation

Larval growth on the different foodplants

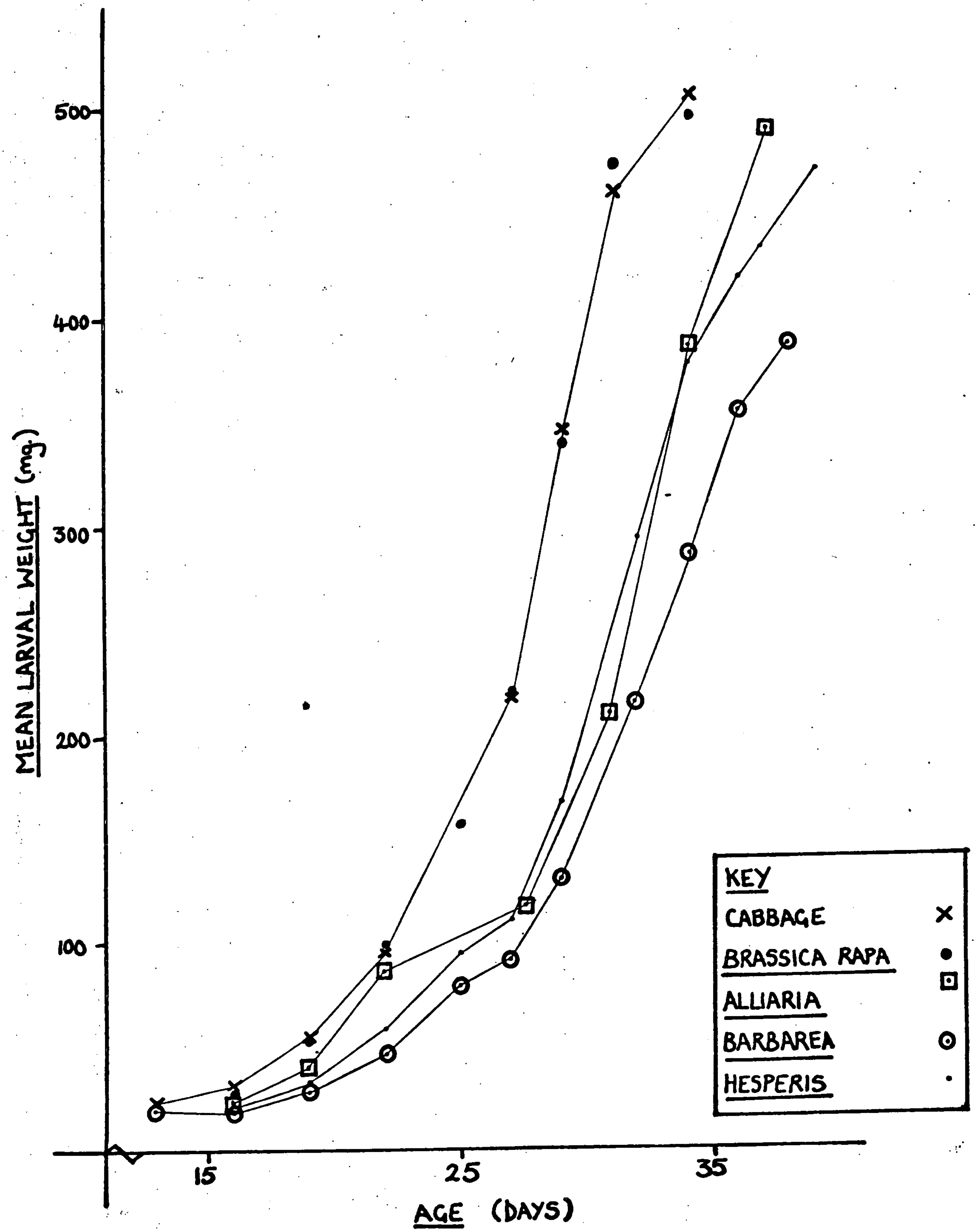
Pieris brassicae

Graphs 1 and 2 show the arithmetic plot of the relative mean weight gain of the larvae of Pieris brassicae when feeding on different crucifers at 10°C and 15°C, and these mean weights are listed in Tables 1 and 2. Although the larvae are transferred onto the wild foodplants at the same initial weight it can be seen that the weights of the larvae on the different foodplants diverge during the experiments. In the 10°C experiment, during the first three days after they were introduced to the new foodplants, the larvae given Alliaria, Hesperis and Barbarea showed little increase in weight, in fact there was a decrease in weight of the larvae feeding on Hesperis. The larvae ate very little of the wild crucifers during this period, seeming to be reluctant to accept the new crucifers of unfamiliar glucosinolate profiles. The larvae of P.brassicae accepted Brassica rapa immediately, a plant of the same genus as cabbage. It would seem that there are some chemical characteristics of the other new plants which either repel the larvae or fail to elicit the feeding response. However, after the first three days the larvae accept and feed on the wild crucifers (see also 'Larval weight gain and food intake').

Graphs 1 and 2 form an S-shaped curve, the characteristic shape of logistic growth curves. A property of steady geometric increase in weight is that it will generate a straight line when the mean weights are graphed on a logarithmic scale - Graphs 3 and 4. Graph 3 shows a linear relationship between the logarithm of the larval mean weights and their age except

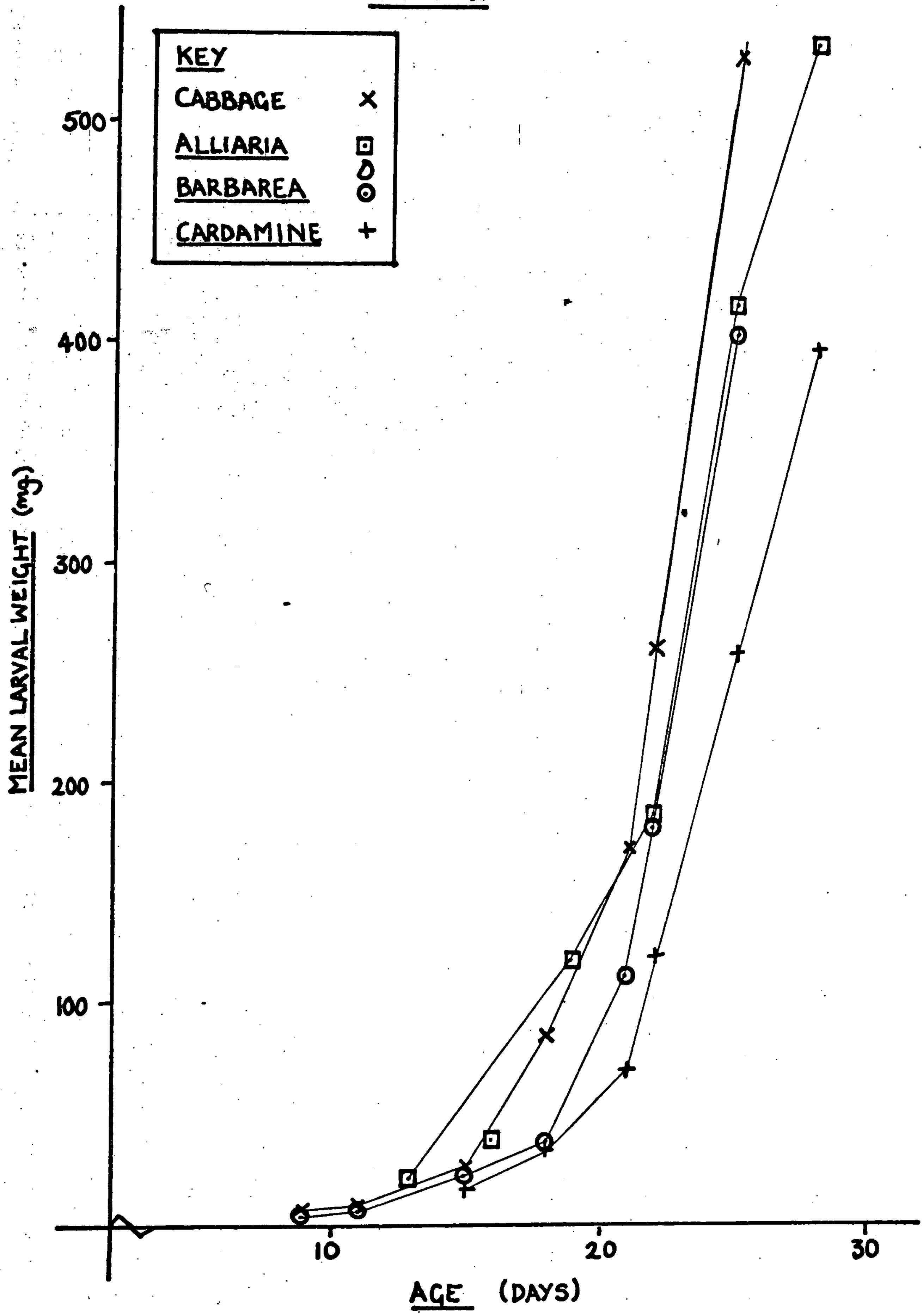
THE WEIGHT GAIN OF LARVAE OF *PIERIS BRASSICAE* FEEDING ON DIFFERENT CRUCIFERS AT 10°C

GRAPH 1



THE WEIGHT GAIN OF LARVAE OF PIERIS BRASSICAE FEEDING ON DIFFERENT CRUCIFERS AT 15°C

GRAPH 2



The mean weights (mg) of larvae of *Pieris brassicae* feeding on different members of the Cruciferae at 10°C, (Standard deviations and sample size shown).

Table 1

Age (days)	Cabbage	*Brassica rapa*	*Barbarea vulgaris*	*Alliaria petiolata*	*Hesperis matronalis*
13	M=25.01 SD= 3.25 n=15	M=22.0 SD= 5.38 n=10	M=22.22 SD= 3.24 n=10	M=21.72 SD= 5.5 n=18	M=20.03 SD= 5.05 n=10
15	M=30.11 SD= 7.71 n=15	M=28.81 SD= 7.11 n=10	M=28.1 SD= 9.23 n= 8	A* M=22.65 16 SD=3.97 n=17	M=18.87 SD= 5.08 n= 7
19	M=59.91 SD=15.87 n=15	M=54.63 SD=20.68 n= 9	M=28.1 SD= 9.23 n= 8	M=43.19 SD=11.71 n=17	M=30.4 SD=10.95 n= 7
22	M=97.71 SD=22.05 n=14	M=100.56 SD= 32.38 n= 9	M=44.89 SD=19.04 n= 8	M=85.94 SD=22.87 n=16	M=58.56 SD=24.60 n= 7
25		M=158.4 SD=43.06 n= 8	M=77.71 SD=34.48 n= 8		M=95.81 SD=28.24 n= 7
27	M=221.21 SD=74.73 n= 9	M=224.11 SD= 64.74 n= 8	M=90.6 SD=22.45 n= 6		M=109.56 SD= 26.88 n= 7
29	M=348.6 SD= 84.90 n= 6	M=339.2 SD= 65.14 n= 7	M=130.93 SD= 54.31 n= 4	A M=120.33 28 SD=29.66 n=16	M=167.6 SD= 65.19 n= 7
32	M=464.07 SD= 60.63 n= 6	M=476.47 SD= 45.87 n= 7	M=210.73 SD= 89.68 n= 4	M=207.26 31 SD=63.24 n=15	M=296.21 SD=112.21 n= 7
34	M=506.13 SD= 48.56 n= 6	M=499.84 SD= 52.81 n= 7	M=287 SD=112.51 n= 4	M=384.23 SD=74.81 n=15	M=377.67 SD=130.11 n= 7
36			M=355.22 SD= 94.65 n= 4	M=493.4 37 SD=53.09 n=15	M=422.21 SD=107.91 n= 7
38			M=385.83 SD= 77.43 n= 4		M=472.3 SD= 13.14 n= 4

Key
M = mean
SD = standard deviation
n = sample size

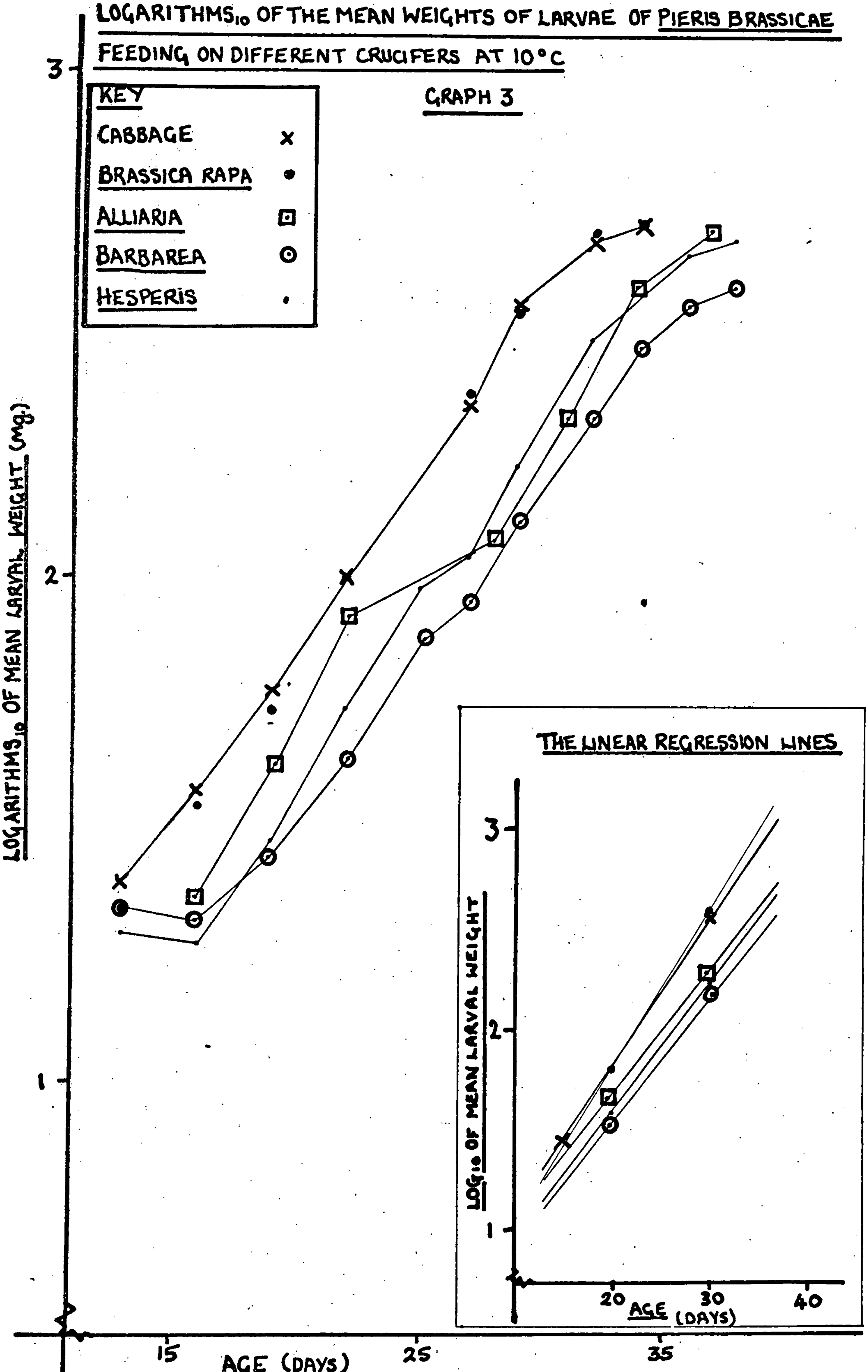
The mean weights (mg) of larvae of *Pieris brassicae* feeding on different members of the cruciferae at 15oC, (Standard deviations and sample sizes also shown)

Table 2

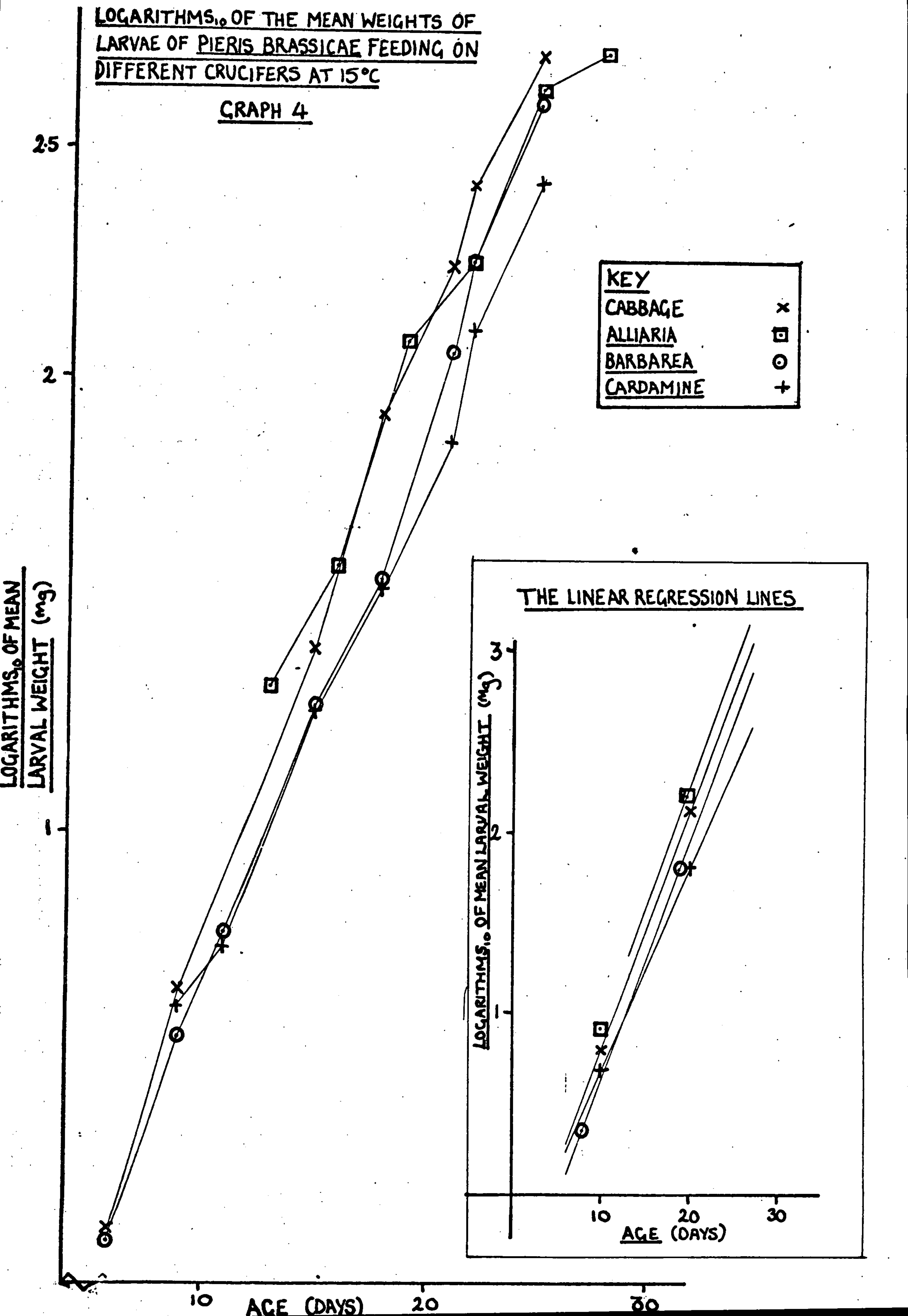
Age (days)	Cabbage	*Barbarea vulgaris*	*Cardamine pratensis*	*Alliaria petiolata*
6	M=1.32 SD=0.37 n=40	M=1.29 SD=0.25 n=25	M=1.31 SD=0.31 n=28	
9	M=4.50 SD=1.05 n=25	M=3.65 SD=1.16 n=22	M=4.14 SD=1.10 n=25	
11	M=5.9 SD=1.37 n=25	M=5.98 SD=1.62 n=22	M=5.4 SD=1.20 n=24	
13				M=21.29 SD= 3.02 n=17
15	M=25.4 SD= 4.37 n=25	M=19.2 SD= 6.84 n=17	M=18.4 SD= 6.59 n=17	
16				M=37.76 SD= 7.2 n=17
18	M=84.12 SD=24.51 n=25	M=37.0 SD=18.16 n=15	M=34.6 SD=13.98 n=16	
19				M=120.46 SD= 13.31 n= 16
21	M=172.5 SD= 50.02 n= 25	M=113.3 SD= 24.62 n= 15	M=70.0 SD=22.22 n=17	
22	M=268.7 SD= 65.68 n= 25	M=188.0 SD= 62.16 n= 14	M=124.9 SD= 57.25 n= 16	M=182.2 SD= 23.56 n= 16
25	M=505.6 SD= 52.08 n= 19	M=402.5 SD= 99.6 n= 13	M=259.57 SD=112.21 n= 12	M=418.91 SD= 52.1 n= 16
28		M=480.98 SD= 43.14 n= 7	M=391.0 SD=153.0 n= 6	M=511.58 SD= 24.51 n= 14

Key
M = mean
SD = Standard deviation
n = sample size

at the extremes of the plot, when the larvae are first introduced to the new plants, and when the larvae are mature and preparing for pupation. Graph 4, however, shows a linear relationship throughout the experiment; because of the higher temperature the growth rates of the animals were higher and any delays in accepting the new food plants not as obvious as they were with the animals kept at 10°C. The linear relationship indicates that the larvae are putting on weight at a constant rate. The value of plotting the mean weights as logarithms is that the linear regression lines can be calculated - Graphs 3 and 4 insets. The gradients of these regression lines are an expression of the rate of weight gain the larvae are achieving on the different food plants. By calculating the standard deviation of the gradients they can be compared. It was found that there was no significant difference between the growth rates as measured by the gradients of the regression lines, i.e. after the initial delay in eating the larvae do not differ in growth rate whatever plant they are feeding on. This implies that the differences in mean weight between animals feeding on different food plants, which are found to occur if they are compared at any point during the experiment, are due to the initial delay in feeding when first introduced to the novel food plants at 10°C. This may also have been the case when the larvae were kept at 15°C, however differences in mean weight did not appear until the larvae were 15 days old, 11 days after being given new foodplants. The larvae were very small before 11 days old, and had to be handled with great care. It may be



LOGARITHMS10 OF THE MEAN WEIGHTS OF LARVAE OF PIERIS BRASSICAE
FEEDING ON DIFFERENT CRUCIFERS AT 10°C
GRAPH 3
KEY
CABBAGE
BRASSICA RAPA
ALLIARIA
BARBAREA
HESPERIS
3
2
1
LOGARITHMS10 OF MEAN LARVAL WEIGHT (mg.)
15
25
35
AGE (DAYS)
THE LINEAR REGRESSION LINES
LOG10 OF MEAN LARVAL WEIGHT
20
30
40
AGE (DAYS)


LOGARITHMS10 OF THE MEAN WEIGHTS OF LARVAE OF PIERIS BRASSICAE FEEDING ON DIFFERENT CRUCIFERS AT 15°C
GRAPH 4
LOGARITHMS10 OF MEAN LARVAL WEIGHT (mg)
2·5
2
1
10
20
30
AGE (DAYS)
KEY
CABBAGE ×
ALLIARIA
BARBAREA
CARDAMINE +
THE LINEAR REGRESSION LINES
LOGARITHMS10 OF MEAN LARVAL WEIGHT (mg)
3
2
1
10
20
30
AGE (DAYS)

that the method of weighing the larvae when very young did not reveal small differences in individual weights. Or perhaps there were differences in growth rate not revealed by the above method of analysis. In order to investigate this possibility the geometric growth rates between each weighing date were calculated.

The geometric rate of increase in weight over any unit period of time is the weight at the end of that period divided by the weight at the beginning. The geometric rates of weight increase between each weighing date for the groups of larvae feeding on the different crucifers were calculated (Table 3 and 4), and the means of these can be compared using Students' t-tests. The geometric growth rates show some variation which can be attributed to individual variability; the cessation in feeding when the animals are moulting, the time of which varied from individual to individual, and perhaps human error in the case of the animals feeding on *Alliaria* at 10°C (see page 20). No significant difference was found between the growth rates of the larvae. The greatest difference between the growth rates of the larvae feeding on different food plants was between those on Cabbage and those on *Cardamine* at 15°C. This difference gave a t value of 2, which at 10 degrees of freedom gives a probability of 90% that there is a real difference between the two growth rates. It can be seen from Table 4 that the animals feeding on *Cardamine* never achieve the highest growth rates shown by those feeding on Cabbage and are consistently low, and a real difference in growth rate may be present.

The geometric growth rates per day of the larvae Pieris brassicae feeding on different crucifers at 10°C

Table 3

Age (days)	Foodplant: cabbage	Brassica rapa	Barbarea	Hesperis	Alliaria
13					
	0.401	0.424	No growth	No growth	No growth
16					
	0.663	0.632	0.445	0.537	0.636
19					
	0.544	0.614	0.533	0.642	0.663
22					
		0.525	0.577	0.545	
25	0.453				
		0.707	0.583	0.572	0.233*
27					
28	0.788	0.757	0.723	0.765	
					0.574
29					
31	0.444	0.468	0.536	0.589	
					0.618
32					
	0.545	0.525	0.682	0.638	
34					
			0.618	0.559	0.428
36					
37			0.543	0.559	
38					
	M=0.573 SD=0.132 n=6	M=0.604 SD=0.105 n=7	M=0.576 SD=0.077 n=9	M=0.601 SD=0.072 n=9	M=0.584 SD=0.093 n=5

*The growth rate of larvae feeding on Alliaria between age 22-27 days old has not been included in the calculation of the mean.

The geometric growth rates per day of larvae of *Pieris brassicae* feeding on different crucifers at 15°C

Table 4

Age (days)	Foodplant			
	cabbage	*Barbarea*	*Alliaria*	*Cardamine*
6				
	1.135	0.943		
9				
	0.656	0.820		0.653
11				
13	1.076	0.803		0.852
15			0.591	
16	1.104	0.642		0.627
18			1.063	
19	0.684	1.021		0.674
21			0.504	
22		0.714	0.766	
	0.627			0.693
25				
				0.493
28				
	M=0.880 SD=0.247 n=6	M=0.824 SD=0.140 n=6	M=0.731 SD=0.247 n=4	M=0.665 SD=0.116 n=6

However, at the 0.05% level of probability the two methods of analysis of the geometric growth rate substantiate one another, in showing that during the middle growth phase the larvae show no significant difference in growth rate.

However, over the duration of the growth experiment at 10°C the initial delay in feeding by the larvae on certain foodplants produced significant differences between the mean weights of the animals feeding on different foodplants. When 34 days old the animals feeding on cabbage and Brassica rapa were significantly heavier than those larvae feeding on Alliaria ($P<0.05$), Hesperis ($P<0.01$) or Barbarea ($P<0.001$). There was no significant difference between the mean weights of the animals feeding on the latter three wildplants. However on studying Graph 3 it can be seen that between the age of 22 days to that of 28 days there was a drop in growth rate of the larvae feeding on Alliaria, in comparison with the weight gains both before and after this period. It is thought that this might be due to an error in the feeding regime, i.e. that the animals were left without food for some time during this period. Had this not been so the mean weight of the larvae feeding on Alliaria may well have remained significantly greater than those on Hesperis and Barbarea, as it was before the aberrent drop in growth rate.

Graph 4 shows the relative mean weight gain (expressed as logarithms) of the larvae of Pieris brassicae when feeding on different crucifers at 15°C, and these mean weights are listed in Table 2. A similar situation as shown in Graph 3 is apparent with the larvae showing better growth on cabbage than on the wild plants. At 25 days old the mean weights of the animals feeding on cabbage is significantly heavier than the mean weights of the larvae feeding on Alliaria (P 0.05) Barbarea (P 0.01) and Cardamine (P 0.001). The larvae feeding on Alliaria and Barbarea show no significant difference in mean weight but both are significantly heavier than the mean weight of the larvae feeding on Cardamine (P 0.01).

From the 'Larval weight gain and food intake' experiment Table 9 which was conducted at 15°C, weight gains of the larvae feeding on Brassica rapa, and Hesperis, are comparable with those of larvae (initially of the same mean weight) feeding on Cabbage at this temperature. Larvae feeding on B.rapa showed no significant difference in weight from those on Cabbage. However the larvae given Hesperis did not eat for the first two days then fed and gained weight.

The results shown in Graphs 1 and 3 and those from the 'larval weight gain' experiment show that although the growth rates of larvae of Pieris brassicae that the different food-plants will support, are not significantly different, a delay in feeding when presented with some of the wildplants produces differences in mean weights during the experiment. The delay is less obvious at 15°C. At both temperatures there is a lag in weight gain by the larvae feeding on Alliaria, Barbarea, Hesperis and Cardamine when compared with larval weight gain on cabbage and Brassica rapa. From the magnitude of lag in weight gain behind that achieved on cabbage an order of suitability of the crucifers as larval foodplants can at this stage be tentatively proposed as:-

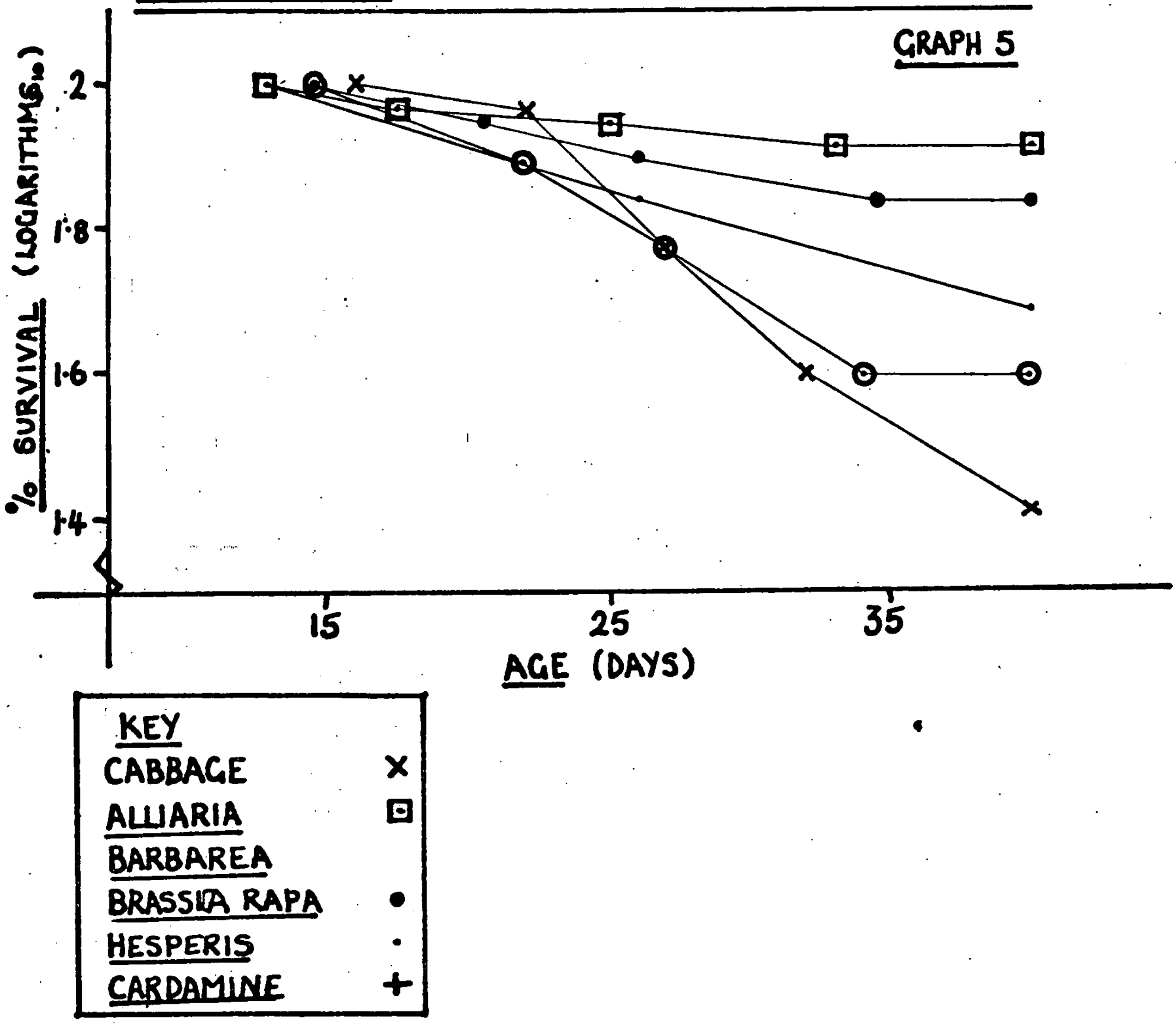
1. cabbage and Brassica rapa
2. Alliaria
3. Barbarea and Hesperis
4. Cardamine

Survival

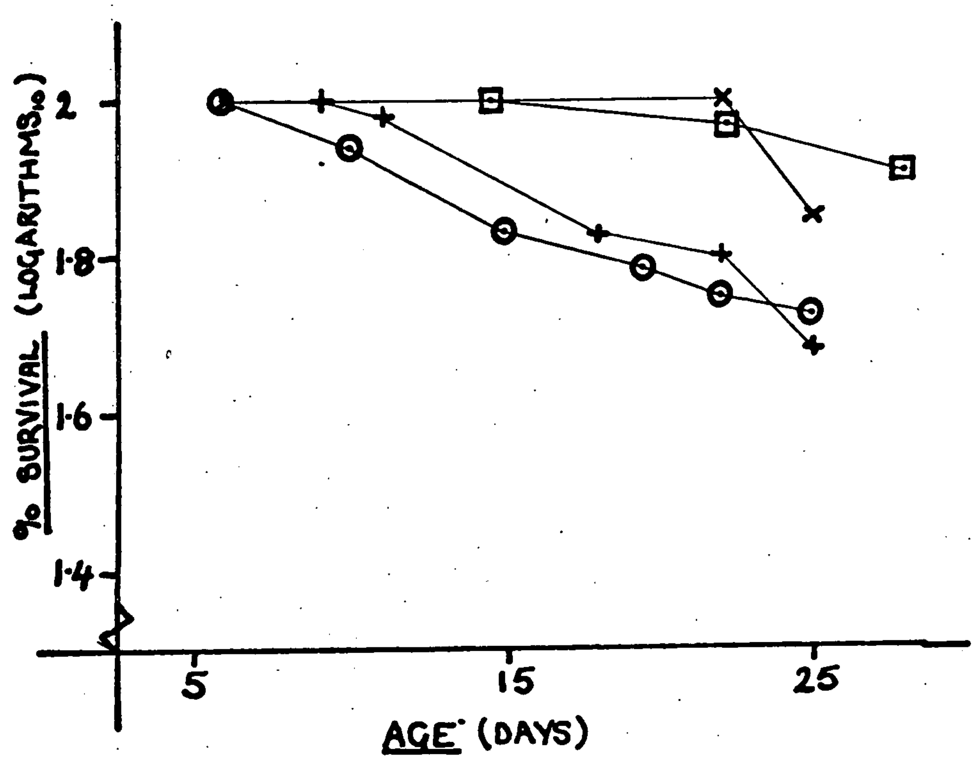
Graphs 5 and 6 (plotted as logarithms) and Tables 5 and 6 show the percentage survival of the larvae on the different crucifers at 10°C and 15°C respectively. Survival is in general better at the higher temperature on any specific foodplant. It may be that the lower temperature puts the larvae under some degree of physiological stress, under which they have less ability to overcome disease. Alliaria petiolata supports the highest percentage survival of larvae at both temperatures. However cabbage which would be expected to support good survival of larvae, and does so at 15°C, shows very poor survival at 10°C, lower than all the other crucifers. Due to this inconsistency by the larvae feeding on cabbage the survival graphs do not give any conclusive evidence with regard to the suitability of the crucifers as foodplants for Pieris brassicae larvae. But again Alliaria appears to be a better foodplant than Hesperis, Barbarea or Cardamine in terms of larval survival.

From the logarithmic plots (Graph 5 and 6), it can be seen that there is some evidence of a linear relationship between percentage survival and larval age, which indicates a constant death rate throughout the experiment. For those batches of larvae which did seem to die at a constant rate, the mortality rate per unit time can be calculated and the results are shown in Table 6, Alliaria petiolata supporting

THE PERCENTAGE SURVIVAL (EXPRESSED AS LOGARITHMS$_{10}$) OF LARVAE OF *PIERIS BRASSICAE* FEEDING ON DIFFERENT CRUCIFERS AT 10°C



THE PERCENTAGE SURVIVAL (EXPRESSED AS LOGARITHMS$_{10}$) OF LARVAE OF *PIERIS BRASSICAE* FEEDING ON DIFFERENT CRUCIFERS AT 15°C



The survival of *Pieris brassicae* larvae feeding on different crucifers at 15°C, shown as a percentage

Table 5a

Age (days)	cabbage	*Barbarea*	*Cardamine*	*Alliaria*
6	100	100	100	
9	100	88	100	
11	100	88	96	
13	100			100
15	100	68	68	
16	100			100
18	100	60	68	
19	100			94
21	100	60	68	
22	100	56	62	94
25	100	52	48	94
28	76	52	48	94

The survival of *Pieris brassicae* larvae feeding on different crucifers at 10°C, shown as a percentage

Table 5b

Age (days)	cabbage	*Brassica*	*Alliaria*	*Barbarea*	*Hesperis*
13	100	100	100	100	100
16	100	100	94	100	70
19	100	90	94	80	70
22	93	90	88	80	70
25		80			
27	60	80		60	70
28	40	70	88	40	70
31			83		70
40	27	60	72	40	50

The mortality rate of larvae of *Pieris brassicae* when feeding on different crucifers at 15°C

Table 6a

Crucifer	Proportion of animals which died in 28 days	Deathrate/10 days
Barbarea	0.72	0.9079
Cardamine	0.76	0.9225
Alliaria	0.18	0.6039

The mortality rate of larvae of *Pieris brassicae* when feeding on different crucifers at 10°C

Table 6b

Crucifer	Proportion of animals which died in 34 days	Deathrate/ 10 days
Brassica rapa	0.3	0.7018
Barbarea	0.6	0.8605
Alliaria	0.167	0.5907
Hesperis	0.5	0.8156

a relatively low mortality rate compared with the other foodplants at each temperature.

Pupal weights

Tables 7 and 8 list the pupal weights of the larvae fed on the different crucifers at 10°C and 15°C respectively. At 10°C there is no significant difference between the mean pupal weights of the larvae which had been feeding on cabbage, Brassica rapa, Alliaria or Hesperis but all are significantly heavier than the mean pupal weight of the animals which had been feeding on Barbarea. These aninals showed a reduction in mean pupal weight of 30% compared with those feeding on cabbage.

At 15°C pupal weights on Alliaria are significantly heavier than those which had fed on cabbage ($P<0.05$) a 4% relative decrease in weight, and are heavier than those animals which had been feeding on Barbarea ($P<0.001$) a 10% relative decrease in weight.

Pupal weight is positively correlated with size of the adult, and in the females with the number of eggs she carries, thus influencing her fertility. A reduction in weight of 30% and 10% as shown by the animals which had fed on Barbarea compared with those feeding on the plants which supported greatest pupal weight, may well represent a significant reduction in fertility in the adult females reared on Barbarea. Thus Barbarea again appears low in the hierachy of suitability as a food plant for larvae of Pieris brassicae.

Development Times

The animals feeding on cabbage and Brassica rapa develop to pupation faster than the larvae feeding on the other plants at 10°C, shown in Table 7. This is consistent with the faster larval growth on these two plants, i.e. the animals may have to reach a certain stage of development before they can pupate and where there is a time lag in this development as expressed as weight gain, this is followed by a delayed pupation relative to those animals which did not delay in feeding. However some animals on Barbarea and Hesperis show a delay in pupation much longer than the three or so days which they delayed in feeding. At 15°C, Table 8 the larvae which had fed on cabbage and Alliaria have the same development time, both faster than the animals which had fed on Barbarea.

A delayed pupation and prolonged development time may be unfavourable for a caterpillar, especially in the later stages of development. When approaching pupation the caterpillars are relatively large, and at their most visible, they are also very sluggish becoming still before spinning the threads which attach the larvae to a solid substrate. During this period they can offer little resistance to would be parasites or predators. A food plant which supports rapid larval development gives an animal an increased chance of survival, over one which allows only slow development.

A delay in pupation appears to be negatively correlated with pupal weight. However this assertion must be treated with caution as the sample sizes here are small and do not give

The pupal weights and development times of the larvae of *Pieris brassicae* reared on different Crucifers at 10°C

Table 7

Alliaria petiolata	Cabbage	*Brassica rapa*	*Barbarea vulgaris*	*Hesperis matronalis*
Weight (mg)	Weight	Weight	Weight	Weight
M=396.7 SD= 32.0 n= 13	M=422.4 SD= 24.0 n= 4	M=422.44 SD= 24.0 n= 6	M=298.45 SD= 33.21 n= 4	M=401.0 SD= 32.65 n= 5
Development Time	Development Time	Development Time	Development Time	Development Time
46-49 days	41-44 days	41-44 days	44-52 days	41-52 days

The pupal weights and development times of the larvae of *Pieris brassicae* reared on different Crucifers at 15°C

Table 8

Cabbage		*Alliaria*		*Barbarea*	
Weight	Development Time	Weight	Development Time	Weight	Development Time
M=422.64 SD= 18.87 n= 17	31-33 days	M=439.69 SD= 26.18 n= 16	31-32 days	M=395.89 SD= 21.97 n= 7	33-36 days

statistically significant correlations. Thus animals feeding on Barbarea are doubly handicapped by a slow development when vunerable to danger, and small pupal weights producing small adults with relatively reduced female fertility.

A tentative explanation for the correlation between delayed pupation and pupal weight could be that during the growth of a larva, weight gain, and hormonal or other physiological development proceed together, but that any delay in feeding retards weight gain to a greater extent than the physiological development. Thus the animals reach a readiness for pupation at a lower weight. This may be the case where pupation is delayed by the same period of time as feeding was delayed. Where, however, there was a longer delay, the foodplants, i.e. Barbarea and Hesperis, may be retarding development and preparation for metamorphosis itself.

The larval weight gain and food intake of Pieris brassicae larvae

In Tables 9 and 10, the dry weight of plant food eaten by an individual larva over the period indicated is recorded next to the weight gained by that larva over the same period. The frass produced was not collected and weighed because in many cases the animals feeding on the wild plants produced loose watery faeces which became smeared over the sides of the dishes, thus being impossible to adequately collect. (It is of interest that this was especially so when the animals were feeding on Cardamine pratensis (larval growth experiment at 15°C) where growth rate was the lowest recorded. It may be that the state of the frass gives an indication of the suitability of the plant as larval food.

Comparing the larval weight gain and food intake between the 7 and 9 July and the 9 and 11 July for each plant, it can be seen that the larvae feeding on Alliaria, Hesperis and Barbarea between 7 and 9 July gained little or no weight. As had also happened when the larvae were first introduced to those three crucifers in the 10°C larval growth experiment (Table 1). By recording the weight gain next to food intake it can be seen that the low weight gains can be accounted for by low food intake over this period, rather than any internal physiological inability to digest and utilize the plant matter. The asterisks (*) indicate that a larva has moulted during that period and this will cause a pause in consumption. Many of the animals moulted during 7-9 July, however this alone cannot account for the low weight gain, as four out of five of the

The weight gain and food intake of larvae of *Pieris brassicae* feeding on different crucifers at 15°C

Table 9

23-26 June		26-29 June		
Amount eaten dry wt. (mg)	Weight gain wet wt. (mg)	Amount eaten dry wt. (mg)	Weight gain wet wt. (mg)	dry weight eaten : wet weight gain ratio
Cabbage				
17.0	22.2	22.1	63.7	2.197
15.8	21.2	27.6	66.3	2.016
17.5	23.2	18.6	23.7	1.299
13.2	22.2	29.0	61.9	1.993
		12.9	44.9	
Barbarea vulgaris				
11.8	21.7	46.5	46.9	1.177
8.8	20.1	54.5	52.2	1.142
3.8	17.7	28.2	37.7	1.731
9.2	26.2	46.7	48.5	1.336

The weight gain and food intake of larvae of Pieris brassicae feeding on different crucifers at 15°C

Table 10

7-9 July Amount eaten dry wt. (mg)	7-9 July Weight gain wet wt. (mg)	9-11 July Amount eaten dry wt. (mg)	9-11 July Weight gain wet wt. (mg)	7-11 July Amount eaten : Weight gain
Cabbage				
30.0	110.1	122.0	154.6	1:1.741
35.1	60.2 *	100.0	120.0	1:1.334
44.9	89.1 *	117.2	165.9	1:1.526
54.1	37.0 *	101.7	189.8	1:1.327
25.4	67.1 *	117.4	206.0	1:1.918
Brassica rapa				
27.0	85.3	103.0	153.3	1:1.835
39.1	56.2	96.4	134.4	1:1.407
21.2	35.0	95.1	164.4	1:1.715
22.6	21.8	65.0	144.1	1:1.894
23.0	47.3	108.4	155.2	1:1.541
Barbarea vulgaris				9-11 July
5.4	loss *	49.5	76.0	1:1.535
3.4	loss *	59.1	101.5	1:1.717
30.2	32.0	0	loss	
11.3	3.2 *	79.7	113.0	1:1.418
16.2	12.1 *	81.8	110.5	1:1.351
Alliaria petiolata				
0	loss *	46.0	128.5	
23.0	33.4		Dead	
3.8	loss	65.2	114.3	
72.0	133.0			
27.8	17.6	21.5	70.7	
Hesperis matronalis				9-11 July
17.6	1.5 *	126.0	73.4	
10.3	22.2 *	88.4	140.4	1:1.588
11.1	0.3 *	47.8	75.8	1:1.586
22.4	7.0	18.4	17.4	
28.5	54.0			

* Animal moulted during this period

caterpillars on cabbage also moulted but still gained a substantial amount of weight. The reluctance to eat may be regarded as the reason for the low weight gains on certain cruciferous foodplants. This reluctance was, however, only evident during the first period, perhaps it is increased hunger which finally makes the larvae overcome their distaste for the new foodplant, or sharpens their response to its novel and/or weaker feeding stimulus.

Although the sample sizes in this experiment are small, the data produced may be used to emphasize the findings of the first experiment:- 'Larval growth' at 10°C. If the caterpillars are of comparable starting weight and have been in the presence of the "new" plant for at least three days they show no significant difference in growth rate whatever the foodplant. But consumption is delayed when the animals are first introduced to Alliaria, Barbarea or Hesperis.

On the righthand side of Tables 9 and 10, the ratios of the dry weight of foodplant eaten to the wet weight gain by the individual larva is recorded, for periods when the larvae were eating. The means of these ratios were calculated and compared.

The results from the June experiment, where cabbage and Barbarea were the only crucifers used, show that the animals feeding on cabbage put on a greater wet weight gain per unit dry weight of plant material than do the animals feeding on Barbarea. However, the standard deviations are high and the difference between the means gives a t value of 2.304 which at 6 degrees of freedom gives a probability of 90% that the difference between the means is not due to chance. The results from the July experiment show no statistically significant differences for the ratio of food eaten to weight gain between the larvae feeding on different crucifers. Indicating that the crucifers used in this experiment show no difference in digestibility and usefulness in terms of weight gain by the larvae. However, the sample sizes are small, and differences may have been revealed by working with larger samples.

The food preferences of *Pieris brassicae* larvae

Table 11 records how much a larva of *P.brassicae* ate of each foodplant when placed in a petri dish with the leaves of five crucifers: cabbage, *Alliaria*, *Hesperis*, *Barbarea* and *Brassica rapa*. From these results it can be seen which crucifers were preferred by individual larvae. By combining all the results from the 18 separate trials, Table 12, and scoring the data as shown below that table, the relative popularity of the foodplants can be found. The crucifers are preferred (in terms of amount eaten) by the larvae of Pieris brassicae in the order:- cabbage, *Alliaria*, *Hesperis*, *Brassica rapa*, and *Barbarea*. An order reflected in the first choice preferences of the larvae.

Cabbage is by far the most frequently eaten food, never being totally ignored, this is the food plant on which the larvae were feeding prior to the experiment. But if, at the start of the experiment, larvae were merely choosing food-plants with a familiar taste (i.e. mustard oil profile), it would be expected that *Brassica rapa* (of the same genus as cabbage) would be eaten more often than it was. However, *Hesperis* and *Alliaria* were chosen as often, if not more frequently than *Brassica rapa*. The larvae do seem to show an aversion to *Barbarea vulgaris* and it scores a relatively low mark compared with the other plants, and is very often not touched by the larvae at all. This is also the case with *Artogeia napi* larvae, when given a choice they often do not eat *Barbarea vulgaris* leaves.

Considering individual larvae there is a tendency for

The order of preference of *Pieris brassicae* larvae for crucifers as food, measured as the relative weight of each foodplant eaten

Table 11

Date	7-9 July	9-11 July	11-14 July
Larva Order of food preference Amount eaten (mg)	a Cab Ap Br Hm Bv 35 15 12 0	a Br Cab Ap Hm Bv 20 19 18 16 0	a Cab Hm Ap Br Bv 135 66 59 40 16
Larva Food preference Amount eaten	b Ap Hm Br Cab Bv 27 17 14 12 7	b Ap Hm Cab Br Bv All 35 17 0	b Cab Hm Ap Br Bv 165 106 67 62 8
Larva Food preference Amount eaten	c Cab Br Bv Hm Ap 17 0 0 0 0	c Hm Cab Br Ap Bv 23 20 14 0 0	c Cab Br Ap Hm Bv 154 70 29 0
Larva Food preference Amount eaten	d Cab Br Bv Hm Ap 17 6 0 0 0	d Cab Ap Br+Bv 20 13 0 0	
Larva Food preference Amount eaten	e Ap Br Cab Hm Bv 23 20 10 8 8	e Ap Cab Br Hm Bv All 34 21 9 0	
Larva Food preference Amount eaten	f Cab+Hm Br Bv Ap 10 8 0 0	f Br Cab Bv Ap 22 20 10 6	
Larva Food preference Amount eaten	g Cab Hm Ap Br Bv 18 15 8 0 0	g Ap Hm Cab Bv Br All 46 6 5	g Ap Cab Hm Bv All 155 110 59

Key
- Cab - Cabbage
- Ap - *Alliaria petiolata*
- Br - *Brassica rapa*
- Hm - *Hesperis matronalis*
- Bv - *Barbarea vulgaris*

Amount eaten measured as dry weight.

The order of preference of *Pieris brassicae* larvae for crucifers as food, combining all data from Table 11

Table 12

Preference in terms of amount eaten	1st Choice	2nd Choice	3rd Choice	4th Choice	5th Choice	Little or none eaten
Cabbage	14	2	1	1		
Hesperis	3	6	2	2		3
Alliaria	6	2	5	1		4
Barbarea		2	2		4	11
Brassica rapa	2	5	4	2		3

Scoring the data so that :- 1st choice = 5
2nd choice = 4
3rd choice = 3
4th choice = 2
5th choice = 1

Scores:- Cabbage = 83
Alliaria petiolata = 55
Hesperis Matronalis = 49
Brassica rapa = 46
Barbarea vulgaris = 18

a larva to choose the same foodplants throughout the experiment though over the three periods the range of crucifers eaten is often increased. In only one case was only one foodplant eaten (C July 7-9), all the other larvae sampled more than one plant, in the majority of cases changing plants before they had totally consumed a particular plant.

The weights of *Pieris brassicae* larvae at 9 days old, having hatched on different crucifers

Table 13

Plant	Mean Weight (Mg)	Standard deviation	Sample size
Cabbage	4.04	0.53	8
Alliaria	1.90	0.61	8
Barbarea	0.94	0.14	8
Hesperis	0.92	0.23	8

Eggs of *Pieris brassicae* were hatched on the different crucifers in order to introduce the larvae to the wild plants as early in their life as possible. All the animals started eating immediately on hatching. However, by observation more frass was produced by the larvae on cabbage than on the other plants, and the animals on *Barbarea* ate noticeably less than the animals on cabbage in terms of leaf damage. By 9 days old the hierarchy of weight gained had already been established as:-

1. Cabbage
2. *Alliaria*
3. *Hesperis* and *Barbarea*

and these differences were statistically significant (P 0.001).

The mean weights (Mg) of larvae of *Artogeia napi* (the upland population) feeding on different crucifers at 15°C (standard deviations and sample sizes are also shown).

Table 14

Age (days)	*Alliaria*	*Brassica*	*Barbarea*	*Hesperis*	*Sisymbrium*
13	M=42.2 SD=11.98 n= 6	M=46.1 SD=10.8 n= 6	M=49.8 SD= 8.5 n= 6	M=37.4 SD= 8.2 n= 6	
15	M=50.3 SD= 6.3 n= 6	M=51.8 SD=10.4 n= 6	M=45.3 SD= 8.0 n= 6	M=49.2 SD= 7.6 n= 6	M=108.1 SD= 37.28 n= 3
17	M=85.1 SD=27.0 n= 4	M=94.0 SD=26.1 n= 5	M=74.9 SD=29.0 n=5	M=63.9 SD=22.5 n= 6	M=140.7 SD= 42.69 n= 3
20	M=150.5 SD= 18.6 n= 3	M=165.8 SD= 29.4 n= 4	M=122.1 SD= 45.9 n= 5	M=100.3 SD= 53.6 n= 5	
22	M=185.0 SD= 18.8 n= 3	M=197.6 SD= 30.1 n= 3	M=143.8 SD= 61.8 n= 5	M=160.5 SD= 56.7 n= 3	
24			M=177.6 SD= 15.3 n= 3		

Key
m = mean
SD = Standard deviation
n = sample size

The geometric growth rates of the larvae of *Artogeia napi* (the upland population) feeding on different crucifers

Table 15

Foodplants	Alliaria	Brassica	Barbarea	Hesperis	Sisymbrium
Age (days)					
13					
15	0.596	0.562	loss	0.658	0.619
17	0.846	0.907	0.827	0.649	
20	0.884	0.882	0.815	0.785	
22	0.615	0.596	0.588	0.800	
			0.615		
	M=0.735 SD=0.151	M=0.730 SD=0.19	M=0.712 SD=0.127	M=0.723 SD=0.081	

The pupal weights and development times of the larvae of *Artogeia napi* (the upland population) reared on different crucifers

Table 16

Alliaria	Brassica	Hesperis	Barbarea
Weight (mg)	Weight	Weight	Weight
142.8 158.5 144.4	143.4 166.2	137.8 178.0	166.6 130.8 143.6
Development time	Development time	Development time	Development time
29-30 days	29 days	29 days	29-31 days

The pupal weights and development times of the larvae of *Artogeia napi* from the Durham population reared on different foods

These animals were the few survivors of a disease which killed many animals in the earlier batches.

Hatched 20-21 May

Table 17

Alliaria leaves		*Barbarea* leaves		*Alliaria* seedpods	
Weight (mg)	Development Time	Weight	Development Time	Weight	Development Time
167.6	28-29 days	150.4	28 days	178.5	31 days
155.7		154.2			

Hatched 11 June

Table 18

Alliaria	
Weight (mg)	Development time
144.8	25 days
159.0	
158.0	
134.2	
115.6	
137.3	

Food preferences of Artogeia napi larvae

Table 19 records how much a larva ate of each food plant, when placed in a petri dish with leaves of five crucifers:- Alliaria, Hesperis, Barbarea, Brassica and Sisymbrium. From these results it can be seen which crucifers were preferred as food by individual larvae. By combining all the results from the 26 separate trials (Table 20) and then scoring the data as shown below that table, the relative popularity of the foodplants can be found. The crucifers are preferred (in terms of amount consumed), by larvae of Artogeia napi, in the order:-

Sisymbrium, Hesperis, Alliaria, Brassica and Barbarea.

It is interesting that Sisymbrium and Hesperis are preferred to Alliaria on which the larvae were feeding prior to the experiment. It cannot merely be that the larvae are choosing foodplants with which they are most familiar, in which case one would expect Alliaria to be the preferred choice of food. As found with Pieris brassicae larvae, the larvae of A.napi avoid eating Barbarea when given a choice.

Considering individual larvae there is a tendency for a larva to choose the same foodplants throughout the experiment, though towards the end of the experiment a wider range of plants may be eaten.

The order of preference of *Artogeia napi* larvae for crucifers as food, measured as the relative weight of each plant eaten

Table 19

Larva Order of food preference Amount eaten (mg)	A So Ap Hm Br Bv 15 5 0 0 0	A So Hm Br Ap Bv 20 15 13 11 0	A Br So Ap Hm Bv 21 10 0 0 0	A Hm Br Ap So Bv 13 12 6 0 0	A Hm So Br Ap Bv 53 42 21 10 5	A
Larva Order of food preference Amount eaten (mg)	B Hm So Br Ap Bv 22 15 10 0 0	B So Hm Bv Ap Br 30 12 0	B Ap Hm So Br Bv 25 10 0 0 0	B Br So Hm Ap Bv 17 10 9 0 0		
Larva Order of food preference Amount eaten (mg)	C So Hm Ap Bv Br 20 8 0 0 0	C Bv So Hm Ap Br 25 24 18 14 0	C Br Hm Ap So Bv 16 11 0 0 0			
Larva Order of food preference Amount eaten (mg)	D So Ap Hm Br Bv 12 0 0 0 0					
Larva Order of food preference Amount eaten (mg)	E So Ap Hm Br Bv 10 0 0 0 0	E So Hm Ap Br Bv 13 5 0 0 0	E Ap Hm Bv Br So 6 0 0 0 0			
Larva Order of food preference Amount eaten (mg)	F So Ap Hm Br Bv 9 0 0 0 0	F So Hm Ap Br Bv 11 0 0 0 0	F Ap Br So Bv Hm 16 7 5 0 0	F Ap Br Hm So Bv 9 8 6 5 0		F Ap Hm Br So+Br 20 12 7 0 0
Larva Order of food preference Amount eaten (mg)	G So Hm Ap Br Bv	G Hm So Ap Br Bv	G So Ap Hm Br Bv		G Ap+Hm Br Bv So 15 15	G So Ap Hm Br Bv 20 13 0 0 0

The order of preference of *Artogeia napi* larvae for crucifers as food, combining all the data from Table 19

Table 20

Preference in terms of amount eaten	1st Choice	2nd Choice	3rd Choice	4th Choice	5th Choice	Little or none eaten
Alliaria	6	3	2	3		11
Hesperis	6	6	3			9
Sisymbrium	12	6	1	1		5
Brassica	2	3	4			18
Barbarea	1	1			1	20

Scoring the data so that - 1st choice = 5
2nd choice = 4
3rd choice = 3
4th choice = 2
5th choice = 1

Scores - *Sisymbrium officinale* = 89
Hesperis matronalis = 63
Alliaria petiolata = 56
Brassica rapa = 34
Barbarea vulgaris = 10

DISCUSSION

Hovanitz (1969), working with the larvae of *Artogeia rapae*, has said that the ability of larvae to survive on different foodplants, is not an all or nothing phenomenon, but is based on the relative ability to survive, and that plants may be placed in order of desirability with regard to the ability of the larvae to survive, or to grow satisfactorily, on plants which they may accept only reluctantly. This is certainly true of *Pieris brassicae* larvae feeding on different members of the Cruciferae plant family. The mean weights, growth curves, pupal weights and development times of the larvae together produce a hierarchy of suitability:-

	at 10°C	at 15°C
1.	cabbage and *Brassica rapa*	cabbage
2.	*Alliaria*	*Alliaria* and *Barbarea*
3.	*Hesperis*	*Cardamine*
4.	*Barbarea*	

These hierarchies were not produced just by a delay in eating novel crucifers but are substantiated by the results of the experiment in which the larvae were hatched on different crucifers. After nine days a significant difference in growth was measurable, and the hierarchy:

1. cabbage
2. *Alliaria*
3. *Barbarea* and *Hesperis*

was again produced.

The larvae of *Artogeia napi* showed no significant difference in terms of mean weights, growth rate, survival, pupal weights and the time taken to complete development. However small sample sizes were used and the amount of variation between the larval weights was high. These results, however, are supported by the work of Dowdeswell and Wilcox (1961) also working with Artogeia napi. They found that the growth rates of larvae were similar when feeding on either Alliaria petiolata or Cardamine pratensis, also the time of pupation and the duration of the pupal period were unrelated to the food of the larvae. Whereas Wicklund (1974) working with the larvae of Papilo macheon the Swallowtail butterfly, and Chew (1975) with those of A.n.macdunnoughii felt that their results enabled a hierarchy of foodplant suitability to be drawn up, Courtney (1980) working with Anthocharis cardamines larvae in Durham used some of the foodplant that I have used in feeding experiments and found a similar order of suitability for that species as I have found with Pieris brassicae.

From the larval weight gain and food intake experiment I had hoped to be able to elucidate whether any differences in weight gain were due to a low rate of consumption or to a low nutritional and/or toxic content of the plant food. This experiment (and also the Growth Experiment at 10°C) showed that the larvae were at first reluctant to eat the new foodplants Alliaria, Hesperis and Barbarea, and a low initial weight gain was due to this fact. This reluctance to eat may be due to a weaker glucosinolate profile or perhaps a peculiar chemical constituency of the plant which repels the larvae. David and Gardiner (1966) feeding larvae of P.brassicae on a semi synthetic diet found that increasing the glucosinolate concentration did not increase the rate of consumption, and concluded that the stimulus to eat provided by glucosinolates is a qualitative rather than a quantitative response. It may be that when the larvae refused to eat for two days but then finally resumed eating, starvation had lowered their threshold of response. Feeny and Slansky (1977) believed that the growth of P.rapae larvae on different plants could be explained best in terms of stabilization (and probably maximization) of the nitrogen accumulation rate, and that glucosinolates affect growth to a much lesser extent than do the nutritional characteristics of food plants. In the 15°C Growth experiment (Graph 2a) where the larvae were introduced to the new food-plants at four days old, significant differences in mean weight did not occur until the larvae were over eleven days old. I have no evidence that this reduction in mean weight by the larvae feeding on Barbarea and Cardamine, as compared with those feeding on cabbage was due to low consumption rates, and therefore feel that poor nutritional qualities of the wild foodplants must be playing a part in producing lower growth rates of P.brassicae larvae. It would be understandable if the larvae are reluctant to eat these foodplants because they recognize their nutritional deficiencies.

Hovanitz (1962) has said that the food previously eaten by some Pieris rapae larvae directly influences their choice of food in the direction of the previously eaten food plants. My results from the 'Food preference' experiment using P.brassicae larvae agrees with this view to some extent. Cabbage was the foodplant the larvae were reared on and this was the foodplant eaten in greatest quantity when the larvae were given a choice. From this experiment I wanted to determine whether the larvae could recognise the relative suitability of the plants they were offered:-

Pieris brassicae

Food plant suitability	Food plant preference
1. cabbage and Brassica rapa	1. cabbage
2. Alliaria	2. Alliaria
3. Hesperis	3. Hesperis and Brassica rapa
4. Barbarea	4. Barbarea

The hierarchies are very similar. It is surprising that Brassica rapa is not higher in the preference hierarchy as this plant supports good growth, and also, presumably has similar chemical characteristics to cabbage.

Artogeia napi chose foodplants in the order

1. Sisymbrium
2. Hesperis
3. Alliaria
4. Brassica rapa
5. Barbarea

Contrary to Hovanitz's findings the larvae preferred foodplants Sisymbrium and Hesperis, to that on which they had previously been feeding, i.e. Alliaria. Both my experimental animals avoid Barbarea vulgaris as a foodplant, which supports only poor larval development of Pieris brassicae and also slow development of Anthocharis cardamines in Durham. It may be that this species possesses peculiar chemical properties that both repel and cause slow growth of the larvae.

Lees and Archer (1974) studying Artogeia napi in Britain listed the plants it most commonly used as foodplants which were:- Cardamine pratensis, Alliaria petiolata, Sisymbrium officinale and Rorippa nasturtium-aquaticum (L) Hayek, Artogeia napi females were frequently and regularly observed to ovipositit on, and larvae could be regularly obtained from, these plants. They listed species less frequently utilized containing plants I did not use in my experiment. A third category listed species for which the authors only had one or two isolated observations of female oviposition and from which it was virtually impossible to recover larvae. One of these latter plants was Barbarea vulgaris. Thus the oviposition preferences of the adults reflect the larval foodplant preferences. This phenomenon has also been found by other workers in this field (Chew 1975, Wicklund 1973). Wicklund (1974) has discussed how the suitability of various plant species as food for the larvae is interrelated with the oviposition preferences of the adults. He proposed that either (1) larval food is "remembered" by the female adult and predisposes her to lay her eggs on that plant (after Hopkins (19), or (2) larval foodplant suitability and the adult oviposition preferences are determined by the same gene complex, or (3) larval food suitability and the adult oviposition preferences are determined by different gene complexes. Hovanitz and Chang (1964) found that they could condition strains of Pieris rapae larvae to prefer a particular foodplant and the adults produced by those larvae preferentially used this plant for oviposition. However this is the only butterfly in which the larval food-plant has been demonstrated to influence the adult oviposition preference. Wicklund (1974) in experiments with Papilio macheon found that in no case had the oviposition preferences of the adults been influenced substantially by the larval food. He also concluded from his work, and that of others, that larval food suitability and oviposition preferences are determined by different gene complexes. There are many recorded cases where adult females have oviposited on plants on which their larvae could not complete development, or even refused to eat (Chew 1975, Bowden 1970, Straatman 1962). In Durham (1980) females of Anthacharis cardamines were seen to oviposit on plants of Reseda luteola (a plant in the Resedaceae family which also contain glucosinolates) and many eggs were found on these plants. In no case, in the field, did the larvae survive their first instar of Reseda luteola plants and were either found dead on the inflorescences or not recovered at all.

Butterfly larvae will eat plants which are never oviposited on in nature. The Blue butterfly Plebejus icarioides larvae are restricted to feeding on species of plant in the genus *Lupinus*. In any area where more than one species of *Lupinus* occurs, the females only oviposit on one species, usually the most pubescent species. However the larvae of any particular population will accept twentyeight different species of *Lupinus* as foodplants in the laboratory (Downey and Durn 1964). Singer in 1971 concluded that "larval food-plant preference is not related to adult oviposition preferences in any predictable way".

Although perhaps determined by separate gene complexes in natural situations the oviposition preferences and larval food-plant preferences do seem to be related, and this is probably due to natural selection acting on species, sub-species and populations of butterflies and their larvae in any particular area. Wicklund (1974) believes that as host plant choice is exercised by the adults, natural selection will act on the oviposition preference system of the adults to direct egg laying towards the most suitable plant species. It would then be expected that by females ovipositing preferentially on a host plant which conferred above average survival to larvae this would lead to a monophagic strategy. However in the case of many butterflies, including *Artogeia napi* and, to a lesser extent, *Pieris brassicae*, on oligophagic strategy is adopted by the adults and their larvae (there may be a hierarchy of suitability but larvae are able to complete development on a number of crucifers). Oligophagy is said to be intermediate between mono and polyphagy and occurs when a limited number of taxonomically related host plants are used in a limited number of habitats. The reason for the adoption of a oligophagic strategy, or it may be said the non-occurrance of monophagy in the four British Pierids living in Durham, can be accounted for by the nature of their cruciferous host plants and the habitats in which they live.

The majority of crucifers along the banks of the River Wear in Durham are annuals or biennials and this unpredictable in space, and in numbers. This unpredictability has led to a vagrant mode of life: *Artogeia napi*, *A.rapae* and *Pieris brassicae* are all highly mobile animals and the females of *Anthocharis cardamines* are also known to move away from the river and travel over wide distances presumably in search of host plants. This vagrent mode of life does not allow the butterflies to become locally adapted. The crucifers, also grow in a number of different microhabitats by the river: wet meadows and dry bare waste areas, also at different heights on the banks. In different years with different weather conditions, there microhabitats differ in suitability for larval growth. In wet years the meadows may be sodden and the river banks flooded, whereas in dry years the plants in high, bare areas may become desiccated. Thus, because the foodplants are adapted to different habitats, they also vary in their relative degree of suitability as larval food. Thus natural selection, in an unpredictable climate, and with unpredictable provision of conditions for crucifer germination, may never favour the same host plant species, in terms of suitability for larval food, in consecutive years. Thus, and the inability to utilize the same plant regularly, forces the butterflies to utilize a number of host plants in the habitats used by the species. Accounting for the ability of the larvae of Pieris brassicae and Artogeia napi to utilize a number of different crucifers in the laboratory.

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