NUTRITIONAL STUDIES OF EASTERN SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

I. SOLUBLE SUGARS

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Abstract   *Can. Ent.* 106: 353–365 (1974)

An absolute requirement for sugar could not be shown but laboratory rearing experiments using artificial diets have demonstrated a definite increase in weight of adult spruce budworm (*Choristoneura fumiferana* (Clem.) Freeman) with increasing dietary levels of certain sugars. Males exhibit a threshold of 0.9% soluble sugars above which higher sugar levels produce no further increases in size. Females respond with an increase in size up to 4.0%, the highest level tested. Generally, faster development rates accompany greater mature weights on diets with higher nutrient levels.

Maltose, raffinose, glucose, sorbitol, sucrose, and fructose are all good sugar sources. Galactose and trehalose are only slightly inferior. Lactose, ribose, melibiose, xylose, mannose, arabinose, and melezitose in the diet are little different from the sugarless control. Sorbose is somewhat inhibitory.

Results of transfer experiments confirm the importance of sugar particularly during late larval development. They also indicate that a high protein diet during early instars has a significant effect on development rates. These results suggest that departure from the normal synchrony of development in the insect and its host can affect both rate of development and mature size of the insect.

Introduction

The eastern spruce budworm (*Choristoneura fumiferana* (Clem.) Freeman) feeds principally on current growth of balsam fir (*Abies balsamea* (L.) Mill.) or white spruce (*Picea glauca* (Moench) Voss) (Freeman 1967; Stehr 1967). Miller (in Morris 1963) pointed out the need for careful study of the effect of food quality on the survival and fecundity of the budworm. Although food quality changes have been shown to play a part in the collapse of outbreaks of this insect, the part that they may play in the early build-up phases of outbreaks, if any, has yet to be determined. As part of an investigation of these factors, we have undertaken studies of the nutrition of the spruce budworm, and of the relationship of its nutritional needs to foliage constitution of the host trees.

Soluble sugars are utilized by most insects and are important for their growth, but they are not essential dietary components for many insects (Altman and Dittmer 1968). Sugars are common constituents of plant materials, including balsam fir (Little 1970) and white spruce (Chalupa and Fraser 1968) and have been shown to influence budworm feeding (Heron 1965). To evaluate the importance to the insect of soluble sugars of host tissues, it was first necessary to determine which, if any, of the soluble sugars is used and/or required by the developing budworm. If soluble sugars are used we must know what relationship exists between levels of those sugars present in the host plants and insect performance as expressed in survival, mature size, and fecundity.

Materials and Methods

Spruce budworm for all experiments were first-laboratory-generation families produced by late-instar larvae collected from several locations in eastern Canada.

In each experiment several such families were represented, usually from at least three locations.   Second-instar diapause was fulfilled by storage at 1°C for 25–35 weeks (Harvey 1958).

Larvae were reared on artificial diet in petri dishes or ¾-oz (approximately 22-ml) translucent plastic creamers closed with paper lids, at 21°C and 71% R.H., with overhead fluorescent lights providing a 17-h photophase and a 7-h scotophase (Stehr 1954; Grisdale 1970).   Post-diapause second-instar larvae were collected daily and placed on the diet surface, usually five to a creamer, and allowed to develop on the same diet until pupation.   In "transfer" experiments larvae were started with five to 25 per creamer, then moved to a second creamer (five per creamer) containing the same or a different diet when the insects had reached the late third or early fourth instar.   During the early larval stages rearing containers were examined semi-weekly but in later stages pupae were removed daily from rearing containers and weighed (within 24 h of pupation).   Development times were calculated in half days from placement on the diet to the day of pupation. Survival during establishment was calculated as the percentage of larvae that started to feed after being placed on a diet.   Rearing survival was calculated as the percentage of feeding larvae completing their development to the pupal stage.   The product of these two values yields the overall survival value (as presented in Table II).

Mortality in the pupal stage was low throughout the rearings and all adults were apparently normal and fertile on all diets.   Weight of pupae has been shown to be directly related to adult fecundity (Miller 1957) and this obviates the need for the more laborious fecundity measurements to evaluate response to experimental diets.   Thus, overall survival to the pupal stage, mean weight of pupae, and larval development time satisfactorily express the collective effects of the dietary differences and have been used as measures of insect performance.   Developmental performance sometimes varied considerably between experiments (see Tables VII and VIII) because of differences in the source, population history, etc. of the insects.   Where survival on the control diets differed in this way, all values in divergent experiments were weighted to permit pooling of the data and yet maintain proportional differences among the test diets.   To assist in evaluating insect performance, the interrelated measures of mean pupal weight and mean development times have been combined by calculating mean daily weight-gain values (initial second-instar weight of 0.1 mg ignored in this calculation).

The McMorran (1965) diet was used in this study, except that Bacto-agar (Difco) was substituted for nutrient agar.   Larvae reared in the laboratory on this diet attain average female pupal weights of 121.7 mg, with a range from 93.5 to 154.0 mg (McMorran 1965); our results are in general agreement with these values.   Field-collected female pupae, however, generally weigh from 70 to 140 mg and average close to 100 mg (Miller 1957; Harvey unpublished).   It was desirable in the present studies to obtain weights close to the natural average; consequently concentrations of sugar, casein, and salt mixture were used at one-half the standard levels ('control' Table I).   Previous studies (Harvey unpublished) had shown that weights of insects reared on such diets averaged very close to those of field-collected insects, and that the adults were normally vigorous and fertile; on such diets larval survival was slightly greater, development rates slightly lower than on the standard diet.   To limit fungal growth all exposed surfaces inside the creamer were sprayed with a 95% ethanol solution of 4% sorbitol and 3% methyl *p*-hydroxybenzoate

Table I.   Composition of diets used in spruce budworm nutrition studies
(g/100 g diet)

Ingredient	Standard[1]	Control	Basic
Water (ml)	22	22	22
Casein	3.5	1.75	3.5
KOH, 4M	0.5	0.5	0.5
Alphacel	0.5	0.5	0.5
Salt mixture W[2]	1.0	0.5	0.5
Sucrose	3.5	1.75	0
Wheat germ	3.0	3.0	0
Wheat-germ residue[3]	0	0	1.02
Wheat-germ oil[2]	0	0	0.40
Choline chloride	0.1	0.1	0.1
Vitamin solution (ml)	1.0	1.0	1.0
Ascorbic acid	0.4	0.4	0.4
Methyl 4-hydroxy benzoate	0.15	0.15	0.15
Aureomycin (chlortetracycline HCl)	0.03	0.03	0.03
Formaldehyde (37% solution)	0.05	0.05	0.05
Bacto-agar solution 4% w/v (ml)	62	62	62

[1]McMorran (1965), with bacto-agar replacing nutrient agar.
[2]ICN Nutritional Biochemicals Corporation, Cleveland, Ohio.
[3]Free of fats and soluble carbohydrates.

(after Grisdale 1970; Chawla and Howell 1967).   After evaporation of the alcohol the creamers were capped and refrigerated until needed.

Utilizability of various sugars was studied by substituting them for sucrose in the meridic diet.   All of the sugars tested were of the highest purity available from ICN Nutritional Biochemicals Corporation or Calbiochem and had the D-configuration, except for L-sorbose and L-arabinose.   Wheat germ[1] present in the McMorran diet contains unspecified quantities of carbohydrates, lipids, etc.   Commercial wheat germ products are reported to contain 16.2% soluble sugars, consisting of 62.3% sucrose and 37.7% raffinose, and 14.0% starch (Fraser and Holmes 1959).   In diets containing 3.0 g wheat germ and 1.75 g other sugar per 100 g fresh weight of diet (Table I, II, etc.) the level of soluble sugars, including the 486 mg present in the wheat germ, amounted to 2.24 g (= 187 mg/g dry wt.).   Total sugars in the diets have been calculated to include those present in the wheat germ.   It should be noted that the amount of sugar added was not increased to compensate for water of hydration present in several sugars (see Table III).

To study the effects of sugar-free diets, sugars present in the wheat germ were reduced to a minimum in the following manner.   Wheat germ, ground in a Wiley mill (1-mm screen) was extracted (Sohxlet) for 6 h with diethyl ether to remove lipids to facilitate sugar extraction.   The residue was dried and extracted with 80% ethanol for 7 h to remove sugars.   After a final 1-h extraction with diethyl ether the residue was dried at 50°C.   The residue representing 57–62%, and the lipid fraction 15–17% of the original wheat germ have both been found to contain substances essential for budworm growth on this diet (Harvey unpublished).   In the 'basic' diet 1.02 g of the dried residue and 0.40 g of wheat germ oil (NBC) were added (Table I); these amounts are approximately equivalent to 1.75 g/100 g of fresh wheat germ.   In addition to being virtually sugar-free, the basic diet differs from the control diet in the level of casein and wheat germ; hence, insect performance on basic or basic plus sugar diets is not strictly comparable with those on control diets (see Tables II and III).

[1]Nu-Age Biorganic Products of Canada Ltd., Toronto.

Soluble sugars in frass and foliage samples were extracted, separated chroma-tographically (Little 1970), and measured using anthrone (Ebell 1969). Total nitrogen was measured with a micro modification of the Kjeldahl technique (A. G. Gordon, pers. comm.).

Results

Sugar Concentration

Diets containing extracted wheat germ and no other added sugar (basic, Table I) are virtually free of soluble sugars. Spruce budworm reared on such diets have low pupal weights, long development times and relatively poor survival (Table II), but substantial numbers survive to mate and lay fertile eggs (Harvey unpublished). Therefore, this insect's requirement, if any, for dietary sugars must be very low. The slow development rates on the basic diet are attributable to differences between basic and control diets other than in sugar level.

The responses of male and female budworm to increasing sucrose levels were similar (Fig. 1). Pupal weights and development rates of males were significantly greater at 0.9% sugar than with no sugar (Table II). However, there was no further improvement in male performance with increasing sugar concentration up to 4.0%. Females showed no significant improvement up to 1.6% sugar. In contrast to males, however, they responded to increases in sugar concentration with substantially increased weights and reduced development times from this level at least up to 4.0% (Fig. 1).

Frass from larvae fed diets containing 2.2% soluble sugars or less contained only trace amounts of sugar, indicating almost total utilization. Appreciable sucrose was present in frass from larvae fed on the diet containing 4.0% sugar. The presence of sugar in the frass indicates that the sugar level in this diet was
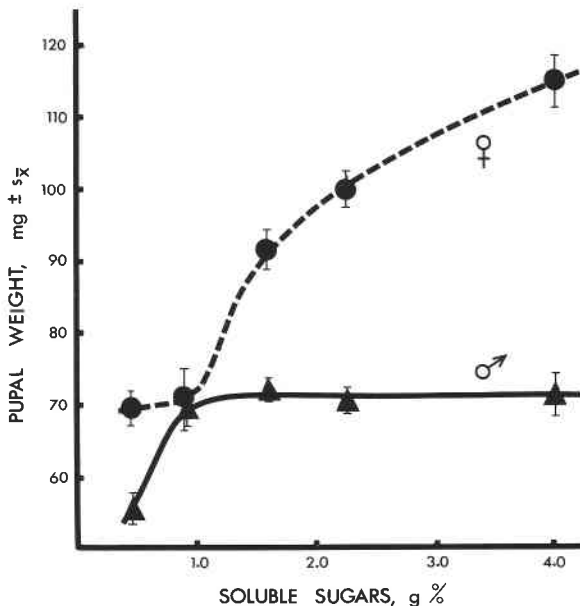

FIG. 1. Relationship between spruce budworm pupal weight and dietary sucrose level expressed in terms of fresh weight of diet.

Table II. Insect performance on diets containing different levels of added sucrose

Diet	Sugar[1] (%)	No. of expts.	Survival[2] (%)	Females			Males		
				No.	Pupal wt. (mg)	Dev. time (half days)	No.	Pupal wt. (mg)	Dev. time (half days)
Basic[3]	None	5	17.9	191	71.6±1.5	66±1.1	94	48.8±1.3	68±1.6
Control (= C)	0.5	3	29.6	29	69.4±2.6	52±0.7	38	56.2±2.3	52±1.1
C + sucrose	0.9	1	46.6	15	71.0±4.3	54±1.6	31	69.5±2.3**	44±0.9**
C + sucrose	1.6	2	38.2	45	91.8±2.9**	51±1.0	49	72.1±1.7	44±0.5
C + sucrose	2.2	4	38.0	88	100.2±2.8*	48±0.7*	88	70.8±1.9	44±0.7
C + sucrose	4.0	2	40.0	43	114.9±3.8**	46±1.4	47	71.9±3.2	42±1.5

[1]Calculated total soluble sugars, including 0.5% in wheat germ.
[2]Average percentage survival among experiments receiving the same treatment.
[3]Effects of basic diet (Table I) were studied in separate experiments; hence, results are comparable only in a general manner (see Methods).

NOTE: Where applicable, mean values are followed by ±$s_{\bar{x}}$. Asterisks show where t-tests with next lower sugar concentration indicated significant differences at 1% (**) and 5% (*) levels.

Table III. Insect performance on diets containing various sugars as the principal carbohydrate source

Sugar added	No. of expts.	Survival (%)	Females			Males		
			No.	Pupal wt. (mg)	Dev. time (half days)	No.	Pupal wt. (mg)	Dev. time (half days)
Maltose.H_2O	1	36.3	19	104.8±4.1 a	47±0.9 abcfi	9	71.0±3.9 ab	45±1.1 a–d,g
Raffinose.$5H_2O$	1	43.4	19	103.1±4.1 a	48±1.1 abcefi	23	82.0±2.3 ab	41±0.8 a
Sucrose (= Control)	4	43.1	88	100.2±2.8 a	48±0.7 acf	88	70.8±1.9 bc	44±0.7 ab
Glucose	3	48.7	61	98.1±3.1 a	50±1.1 abcefi	85	68.4±2.0 abc	46±1.0 abc
Fructose	3	45.1	54	93.5±3.8 ab	51±1.3 b–f,i	79	65.3±2.2 bcd	49±1.3 cdfg
Trehalose.$2H_2O$	2	40.1	20	88.3±4.2 bc	52±1.6 c–i	33	70.3±2.7 bcd	48±1.2 bcdg
Galactose	3	41.3	47	90.1±2.8 bc	55±1.2 d–i	51	67.6±2.4 bcd	49±1.1 c–f,g
Lactose.H_2O	2	37.3	23	80.3±2.5 cd	53±1.4 e–i	33	64.4±2.2 b–e	50±1.4 defg
Ribose	1	36.0	13	79.8±3.5 cd	53±1.2 f–i	19	64.9±2.9 b–e	45±0.9 a–d
Melibiose.H_2O	1	48.0	8	74.3±7.4 de	59±3.9 g–j	11	52.3±3.9 b–e	54±2.2 a–d,g
Mannose	1	29.5	7	74.0±3.6 de	58±3.7 g–j	10	60.9±3.0 b–e	48±1.6 a,c–g
Melezitose.H_2O	1	30.0	17	74.0±4.6 de	56±3.2 h–j	13	65.3±3.5 e	46±3.1 ef
None	3	32.6	29	69.4±2.6 de	52±0.7 ij	38	56.2±2.3 e	51±1.1 efg
Sorbose	1	31.3	17	62.3±3.7 e	60±1.9 j	12	53.2±3.4 c,e	55±2.8 e
Sucrose + basic[1]	2	29.2	103	105.20±2.8 p	55±1.0 p	94	77.8±1.8 p	50±0.9 p
Sorbitol.$1/2H_2O$[1]	1	27.7	24	115.4±5.1 p	55±1.8 p	22	87.0±3.3 q	53±2.0 q
Arabinose[1]	1	30.2	25	79.8±4.9 q	65±1.0 q	29	59.4±2.1 r	64±1.6 r
Xylose[1]	1	23.2	55	74.4±2.8 q	64±1.4 q	62	60.6±1.5 r	55±1.1 q
Basic[1]	2	23.5	66	69.5±2.0 q	74±2.0 r	67	49.6±1.6 s	67±1.3 r

[1]These sugars were tested in separate experiments by addition of 1.75% to the basic diet (Table I); they should be compared with sucrose + basic and with basic (Table II). Total sugar in all other diets was 2.24% (except ribose, 1.37%).

NOTE: Where applicable, mean values are followed by ±$s_{\bar{x}}$. Values followed by different letters (a, b . . .) differ significantly at 5% probability (Duncan's New Multiple Range Test).

greater than that which could be readily used by the insect and suggests that smaller responses are to be expected from further increases in dietary sugar concentration above this level even though the response curve (Fig. 1) shows no signs of levelling appreciably.

Utilizability of Sugars

Carbohydrate utilizability by the developing insect was studied by substituting other sugars for the sucrose present in the artificial diet. Various sugars were added at 1.75% which, with the approximately 0.5% of sucrose and raffinose present in the wheat germ, gave a total sugar more than adequate for good development. Budworm developing on diets containing readily utilizable sugars had generally better survival and reached greater average pupal weights in shorter times than those on diets without sugar or containing sugars that were poorly utilized.

The results demonstrate that spruce budworm readily develop on diets containing several mono-, di-, and trisaccharides: glucose, fructose, sorbitol, maltose, and raffinose appear equivalent to sucrose as a carbohydrate source (Table III). Galactose and trehalose in the diet permitted good survival and produced female pupae only slightly smaller than those on the sucrose diet. The development rate on the trehalose diet was equal to that on glucose; the rate on galactose was appreciably lower. This group of sugars, including galactose and trehalose, all appear to be readily utilizable by both females and males; however, as expected, the response of males was always less than that of females (Fig. 1).

Budworm growth on diets containing lactose, ribose, melibiose, mannose, melezitose, L-arabinose, and xylose was not significantly different from that on the diet without added sugar; development was generally somewhat slower but average pupal weights were slightly greater. Survival also was generally lower on these sugars than on those that were readily used, with the possible exception of melibiose and L-arabinose. L-sorbose was definitely inhibitory; although survival was almost equal to that on the control, pupal weights and development rates were substantially below those on the control diet. These eight sugars are probably not utilized to any appreciable extent by spruce budworm larvae of either sex; some of them may be deleterious.

The principal sugars of developing conifer foliage are glucose, fructose and sucrose (Little 1970; Chalupa and Fraser 1968), all three of which are readily utilized by the developing spruce budworm larvae. This conclusion was tested further with a separate series of diets containing these sugars individually and in combination (Table IV). Compared with the diets used in Table III the casein

Table IV. Carbohydrate composition[1] of diets used to study comparative nutritive value of sugars and cornstarch alone and in combination

Diet	Glucose	Fructose	Sucrose[2]	Starch	Total
1	—	—	2.07	—	2.07
2	1.75	—	0.32	—	2.07
3	—	1.75	0.32	—	2.07
4	0.87	—	1.19	—	2.06
5	0.87	0.87	0.32	—	2.06
6	0.58	—	0.90	0.58	2.06
7	—	—	0.32	1.75	2.07

[1]g/100 g fresh diet; diet recipe as for control (Table I).
[2]Values include sucrose and raffinose present in 2.0 g/100 g diet of wheat germ. All diets contained casein at 3.5 g/100 g diet.

Table V. Effects of sugars and cornstarch, alone and in combination, on survival, pupal weight, and development time of spruce budworm larvae

Carbohydrate: Diet No.[1]:	Sucrose 1	Glucose 2	Fructose 3	Su/Glu 4	Glu/Fru 5	Su/Glu/St 6	Starch 7
Larvae	245	249	249	240	255	237	263
Established (%)	82.9	79.5	82.3	83.3	79.6	78.5	69.2
Pupae (% of established)	40.4	46.0	44.4	46.5	47.8	41.9	36.8
Adults: ♀	36	28	27	40	41	35	26
♂	38	48	32	44	50	32	38
♀ Pupal wt. (mg)	100.8±5.2 a	101.1±3.9 a	97.2±5.8 a	98.1±5.0 a	87.7±4.7 ab	87.5±4.5 ab	80.2±4.0 b
♀ Dev. time (half days)	47 ±1.0 ac	49 ±1.1 ad	48 ±1.5 ad	48 ±1.5 ac	52 ±1.3 abd	52 ±1.7 bd	51 ±1.7 abd
♂ Pupal wt. (mg)	73.6±3.6 a	66.9±3.1 ab	66.1±3.2 ab	68.4±2.8 a	68.6±2.8 a	65.3±3.0 ab	56.9±2.7 b
♂ Dev. time (half days)	45 ±1.0 ab	46 ±1.4 ab	48 ±1.3 b	44 ±1.0 a	46 ±1.1 ab	47 ±2.0 ab	47 ±1.1 ab
Wt. gain/day (mg): ♀	4.3	4.1	4.0	4.1	3.4	3.4	3.1
♂	3.2	2.9	2.9	3.1	3.0	2.8	2.4

[1]See Table IV.
NOTE: See Note, Table III.

level was increased and the wheat germ level reduced. Diet 7 can be considered the control diet as cornstarch appears to be used minimally, if at all (Shaw 1972; Harvey unpublished data).

It is apparent from the results of this experiment (Table V) that glucose, sucrose, the combination of these two, and fructose are of equivalent nutritional value to both sexes of the budworm, whether pupal weight and development time are considered separately, or expressed as mean daily weight gain. Diets 5 and 6, containing glucose and fructose, and sucrose, glucose and starch, respectively, produced somewhat lower pupal weights and longer development times in females but not in males. The poorer performance on the diet with one-third of the sugar replaced by starch was expected from the reduction in soluble sugar. The poorer performance on the mixture of glucose and fructose is anomalous.

In summary, the three principal sugars of coniferous foliage are equally well utilized alone or in various combinations by the spruce budworm. Consequently, changes in the relative proportions of these sugars during bud and shoot development (Little 1970) would appear unimportant to the development of this insect. Therefore, in studies of the effects of sugar levels in foliage on budworm growth it should be sufficient to measure the sum of these three sugars.

Transfer Experiments

Measurements were made of soluble sugars, total nitrogen (Kjeldahl), and budworm development in mid-crown samples of current foliage from several trees of both balsam fir and white spruce. They showed that sugar levels are low during the early-larval feeding period and increase to higher values during the later instars while nitrogen levels are highest in flushing buds and decrease throughout the season (Table VI). The results are in agreement with published reports (Edel'man 1963; Little 1970; Neish 1958; Durzan and Lopushanski 1968) and initiated two experiments to compare the effects of high versus low nutrient levels on early- versus late-instar larvae.

In the first of these experiments two sucrose levels, 2.07% and 0.77%, were used in the standard diet. The low sugar level was below the threshold found for both males and females and also below that found in early buds (Table VI). At the time of transfer the larvae were in the third and fourth instar, those starting on the low sugar diet being slightly behind in development (Table VII). Larvae receiving the high sugar level throughout their development were significantly heavier at maturity than those on any other diet combination; however, larvae started on the low sugar level and transferred to a high sugar diet, mimicking natural

Table VI.   Total nitrogen and soluble sugars in current foliage of white spruce and balsam fir and in artificial diets used in transfer experiment

	Nitrogen (mg/g fresh)	Sugars[1] (mg/g fresh)	Larval instar (mean)
White spruce buds, May 26	8.8	13.6 ⎫	
Balsam fir buds, May 26	11.6	17.3 ⎬	2.8
Early diet[2]	7.1	8.5	
White spruce needles, June 23	4.0	23.4 ⎫	
Balsam fir needles, June 23	4.9	21.3 ⎬	6.6
Late diet[2]	3.4	21.6	

[1]Sum of glucose, fructose, sucrose, and raffinose.
[2]Calculated values based on diet recipe. (Early diet: casein 3.5 g/100 g, sucrose 0.442 g/100 g fresh. Late diet: casein 1.2 g/100 g, sucrose 1.75 g/100 g fresh; diet recipe as in control (Table I) with wheat germ 2.5%. Results in Table VIII.)

Table VII. Effects of two levels[1] and of transfers at mid-development on survival, pupal weight, and development time of spruce budworm larvae

	Initial diet: Final diet:	High High	High Low	Low Low	Low High
Larvae		85	85	85	85
Established (%)		98.0	84.7	82.4	83.5
Instar at transfer, $\bar{x}$		3.23	3.27	3.12	3.19
Pupae (% of established)		25.6	25.0	27.1	32.4
Adults: ♀		7	8	9	9
♂		10	10	5	10
♀ Pupal wt. (mg)		103.8±7.9 a	72.6±6.3 b	84.1±3.4 b	84.3±3.9 b
♀ Dev. time (half days)		49 ±1.9 a	47 ±2.6 a	49 ±1.1 a	49 ±1.3 a
♂ Pupal wt. (mg)		71.5±4.3 a	56.5±5.3 a	66.1±3.4 a	64.6±5.5 a
♂ Dev. time (half days)		47 ±1.9 a	45 ±2.3 a	40 ±1.9 b	49 ±2.0 a
Wt. gain per day (mg): ♀		4.2	3.1	3.4	3.4
♂		3.0	2.5	3.3	2.6

[1]Sucrose levels, including wheat-germ sugars: High, 2.07 g/100 g; Low, 0.77 g/100 g fresh wt. Diet recipe as in standard (Table I) with wheat germ 2.0%.
NOTE: See Note, Table III.

conditions, did not show a significant increase in survival or female pupal weight over those remaining at the low sugar level. Because of small numbers of insects in this experiment other possible effects of the diets and transfers were not large enough to be significant, or meaningful.

In a second transfer experiment two sugar levels were combined with two protein levels to mimic even more closely the composition of early and late foliage (Table VIII). In the early diet, the sugar concentration of 8.5% was only about half that measured in buds on 26 May while the nitrogen level of 7.1% was above the average available during the early larval feeding stages. Establishment was more successful on the early diet, as was survival during post-transfer development, although the differences were small (Table VIII). Differences in pupal weights among the four treatments were not significant in either sex, but when weights were grouped according to the starting or finishing diet, females completing their development on the late diet were significantly heavier than those maturing on the early diet. Female larvae starting on the early diet developed significantly faster than those starting on the late diet but all such females averaged about the same weight.

Table VIII. Effects of early versus late diets[1] and of transfers at mid-development on survival pupal weight, and development time of spruce budworm larvae

	Initial diet: Final diet:	Early Early	Early Late	Late Late	Late Early
Larvae		500		500	
Established (%)		83.6		80.2	
Larvae transferred		205	213	202	199
Instar at transfer, $\bar{x}$		3.80	3.67	3.54	3.60
Pupae (% of established)		86.3	83.6	81.7	86.4
Adults: ♀		89	81	81	77
♂		81	91	77	84
♀ Pupal wt. (mg)		86.1±2.0 a	90.6±2.3 a	91.6±2.4 a	86.0±2.3 a
♀ Dev. time (half days)		50.8±0.6 a	50.2±0.8 a	53.9±0.8 b	52.2±0.5 ab
♂ Pupal wt. (mg)		69.6±2.6 a	68.2±1.8 a	65.1±1.8 a	66.8±1.6 a
♂ Dev. time (half days)		44.9±1.5 a	45.4±0.6 ab	48.9±1.0 c	47.1±0.4 bc
Wt. gain per day (mg): ♀		3.39	3.60	3.40	3.30
♂		3.10	3.00	2.66	2.84

[1]See Table VI.
NOTE: See Note, Table III.

Thus the best performance, i.e. maximum weight gained in the least time, was accomplished by those females starting on the early diet and completing their development on the late diet. Weights of male pupae showed no significant differences, but, again, those starting on the early diet had significantly faster development than those starting on the late diet.

These results confirm the importance of sugar particularly during late larval development. They also suggest that the high protein diet during early instars had a significant effect on development rate.

Discussion

Spruce budworm confined inside a plastic creamer or other container with a potential food source usually feed readily on a fairly wide variety of diets. In the present studies diet acceptance was good in all cases, and there was no evidence of rejection of particulate remnants of the wheat germ. Nor was there any evidence of feeding or developmental inhibition caused by the antimicrobial substances incorporated into, or sprayed upon, the diets. No attempt was made to determine dietary intake or frass production, or to quantify food utilization according to current methods (Waldbauer 1968). It is therefore possible that some of the differences in insect development reported herein were due to differences in the amount of food consumed. Further studies would be required to separate such behavioural effects from nutritional ones. The incomplete definition of the artificial diet and the fact that it contained some of the dietary substances being tested are further weaknesses of the technique. However, significant increases in insect size and development rate were produced by addition to the basic diet of some sugars and not others. Although all of this effect cannot be attributed to utilization of the additional ingredient, most of it probably was.

The feeding responses of penultimate-instar spruce budworm to various sugars were explored by Heron (1965) using a pith-disc technique. He found that fructose, maltose, raffinose, and sucrose were "the most acceptable" sugars; the present results are in agreement with his findings. However, glucose, which in the present tests was equal to these sugars, elicited only a "slight feeding response" in Heron's experiment. Other sugars similarly classified were galactose and trehalose, which perhaps could explain their apparent lower utilizability in the present studies. The low utilizability of melibiose and melezitose may result from their "slight feeding response." However, although for most sugars the utilizability was consistent with or explained by the palatability results, the marked exception of the good growth on the glucose diet demonstrates that the present results reflect more than palatability and are, in fact, evidence of utilization. The general agreement with Heron's results suggests also that second-instar larvae, which initiate feeding and perhaps influence feeding preferences of later instars, resemble closely the fifth-instar larvae in their feeding preferences.

The principal sugars of needle tissues of both host species are glucose, fructose, and sucrose, with raffinose reaching appreciable levels in the cold season (Little 1970; Neish 1958); stachyose is reported in some parts of white spruce (Chalupa and Fraser 1968). Present results indicate that all of the sugars common in the insect's natural diet are readily used. Although at times sucrose may be the only sugar present at any appreciable level, as in pollen, glucose is always accompanied by one or usually both of the other sugars; hence, the low feeding stimulus it provides would appear unimportant for budworm feeding under natural conditions.

Galactose is probably not present as a free hexose in current tissues of either host but it is present as a constituent of raffinose. During the period of insect feeding raffinose levels are very low (Little 1970) except prior to budbreak in the spring when newly emerged second-instar larvae are forced to mine previous years' needles for about 2–3 weeks. Although sucrose is still the major sugar in these needles, ability to utilize raffinose and all its component hexoses may contribute to survival during this period.

The ability of insects to utilize di- and trisaccharides has often been interpreted as evidence of digestive enzymes which split them into their component mono-saccharides. From evidence presented above some inferences can be made about the digestive enzymes present in the budworm. The ready utilization of raffinose and galactose, coupled with the inability of this insect to utilize melibiose, strongly suggests that raffinose may be split enzymatically into sucrose and galactose, rather than into melibiose and fructose. This implies the presence of an α-galactosidase, that does not split melibiose, along with an invertase. The ready use of maltose suggests the presence also of an α-D-glucosidase. However, the larger molecules may be absorbed directly (Dadd 1970) so that the presence of the enzymes cannot be considered proven.

Little has been published on dietary requirements of coniferophagous insects; however, the general pattern of utilization of dietary sugars by eastern spruce budworm larvae resembles that of many other insects (Altman and Dittmer 1968; House 1965), particularly those feeding on fresh leaf tissue. Sugars used by this insect show a somewhat broader spectrum than those used by insects feeding on corn or rice; they show the closest resemblance to those used by *Bombyx mori* L. which feeds on the broad-leaved mulberry. However, lactose, mannose, melezitose, and melibiose would appear less readily used by spruce budworm than by *B. mori* (Ito 1960). L-sorbose was found deleterious to the silkworm also (Ito 1960).

The transfer experiments indicated that there are probably no important differences in requirements or utilizability of sugars alone in different stages of larval development. Nutrient levels much below the threshold level must inevitably result in smaller, more slowly developing insects regardless of the stage at which they are encountered. The attempt to explore the effects of interacting levels of protein and sugars was more revealing, linking rapid development to early high protein levels and large mature weight to high sugar levels in later larval stages. This picture is obviously far from complete as levels of other important nutrients also change in the natural diet. Relative proportions of nutrients in diets have been found important for other insects (House 1969). However, these results do furnish a basis for suspicion that departure from the normal synchrony of development of spruce budworm and its host can affect both rate of development and mature size of the insect, and thereby influence survival and fecundity.

Acknowledgments

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