ニカメイガ幼虫の生育にたいする各種炭水化物の栄養価

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Nutritive Values of Carbohydrates for the Growth of Larvae of the Rice Stem Borer, *Chilo suppressalis* WALKER[1)]

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Due to its great rice plant damage in Japan, it is of importance to control the rice stem borer, *Chilo suppressalis* WALKER. As previously stated, it seems necessary to investigate the nutritional requirements of this insect, in controlling the borer larvae and decreasing the damage by a useful culture method of resistant rice plant varieties to this insect. From the point of view of comparative physiology, it would be of interest to know the nutrition of the rice stem borer larva as compared with that of other animals. The requirements of the borer larva for vitamins, the fat soluble growth factor, and the amino acids have already been studied with a synthetic diet constituted from chemically defined materials under aseptic conditions (16, 17).

Many workers have reported the nutritive values of several carbohydrates to insects. In many of these studies, however, experiments were carried out to examine the utilization of carbohydrates which was indicated by duration of longevity of adult insects which were fed on several carbohydrates. Little is known of the nutritive value of carbohydrates for the growth of larval insects. Leclercq (19) and Bernard and Lemonde (3, 20) are the only workers who have studied systematically on the carbohydrate nutrition of the larvae, using stored product beetles. Insects which feed on green plants have not yet been studied qualitatively on their carbohydrate nutrition (11).

The present paper deals with the results of experiments under aseptic conditions, on the nutritive values of various carbohydrates for the growth of the rice stem borer larva on synthetic diets containing different carbohydrates.

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I Materials and Methods

A. The eggs of the rice stem borer. The eggs used for the experiment

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1) Formerly *Chilo simplex* BUTLER.

were obtained from moths which originated from hibernating larvae collected in Yamagata pref. (Y1), and from moths of the first and the second generations collected in Aichi pref. using a light trap (A1 and A2, respectively). The eggs were laid in a mass on paraffin paper.

B. Preparation of diet. The synthetic diet used in this experiment was derived from diets which had been used in the previous experiments with the borer. The composition of the basal diet per flask was as follows:

Total water	10 ml
Agar	0.1 g
Cellulose	0.3
Casein	0.7
Inorganic salt mixture (Wesson's)	0.06
Cholesterol	0.006
Vitamins	
Thiamine hydrochloride	100 μg
Riboflavin	50
Nicotinic acid	100
Pyridoxine hydrochloride	50
Calcium pantothenate	100
Folic acid	10
Choline chloride	2000
Inositol	1000
p-Aminobenzoic acid	100
Biotin	10

Vitamins were added in an aqueous 1 ml solution which contained the above mentioned amounts. By adding one carbohydrate at a time to the basal diet, the nutritive value of the carbohydrates was determined. The amount of carbohydrates added is 0.7 g per flask. The constituents of the diet were put in a 100 ml Erlenmeyer flask. The flasks were plugged with absorbent cotton, and then sterilized three time in a Koch's steam sterilizer during three days, that is, for thirty minutes at the first day, twenty minutes at the second and the last days, respectively. They were then ready for inoculation of the egg mass.

C. Inoculation of an egg mass into a flask. When the eggs almost attained embryonic development, the egg mass laid on a piece of paraffin paper was sterilized for about four minutes in 0.1 per cent solution of mercuric chloride and then washed with 70 per cent ethyl alcohol. The sterilized egg mass was inoculated into each flask under aseptic conditions.

D. Breeding. The feeding experiment was carried out in an incubator regulated at 25°C, excluding all light. After breeding for thirty-five days, the larvae taken out from flasks were counted and weighed.

The results obtained from flasks in which contaminated with microorganisms were discarded.

II Results

The results of the thirty-five days feeding experiment with diets containing different carbohydrates are given in Tables 1 to 3. Number of larvae inoculated is shown by differences in numbers between eggs inoculated and eggs unhatched.

A. Monosaccharides. All the pentoses tested are not utilized for the larval growth. It was observed that the growth of the larva receiving D-xylose or L-rhamnose is somewhat better than that of the larvae receiving other pentoses. Working with larvae of *Tenebrio* and honeybee[2], Leclercq (19) and Vogel (26) showed that D-xylose was the relative good source of the carbohydrates. Tsutsui *et al.* (24), however, observed that larva of *Chilo suppressalis* was unable to grow and died before long with sterilized rice plant stem diet adding 1 per cent of xylose. D-Ribose is the most inferior to the larval growth of the rice stem borer as same as to that of *Tenebrio* (19) and *Stegobium* (20).

As shown in Table 1, fructose is superior to all other monosaccharides tested for the larval growth of *Chilo.* Glucose also shows excellent nutritive value. Monosaccharides which are considered to support superior growth of this insect are only the sugars, fructose and glucose. Mannose is very inferior in nutritive value when compared with glucose and fructose. These three sugars are related to epimer each other, and are capable of conversion to 1,2-dienol which is common to these sugars. For adult longevity of *Calliphora* (10, 13), *Drosophila* (14) and *Phormia* (15), and larval growth of *Tribolium* (3) and *Oryzaephilus* (20), mannose showed excellent effects as well as did glucose. It is difficult to give a reason why the rice stem borer larva is unable to utilize mannose contrary to the other insects refered to above.

Galactose, a non-fermentable sugar, showed inferior nutritive value to larval growth of *Chilo,* the same as to larvae of *Tribolium* (3), *Tenebrio* (19) and *Stegobium* (20).

B. Oligosaccharides. In the case of the monosaccharides, the question is whether the borer larva is capable of absorption and utilization, whereas in the more complex sugars the further question may occur whether the larva can supply the enzymes necessary for the breaking down of the sugars into monosaccharides. Already mentioned above, monosaccharides which support superior growth of the borer larva are glucose and fructose only. It is expected that complex sugars, which do not contain glucose or fructose as a component, have not any value.

2) In *Apis,* however, Phillips (21) reported that xylose can hardly be utilized as energy source.

The experiment was carried out with the sugars containing glucose or fructose. Cellulose was excluded from the present experiment, because it is evident that its digestion to more simple sugars never occurred in the digestive tract of the borer larva (27), and it was used in our previous experiments only as an inert carrier.

Larval growth of *Chilo suppressalis* on the diet containing sucrose or maltose as carbon source, was most excellent among all oligosaccharides. Fukaya and Kaneko (12)[3] and Yushima and Ishii (27) have reported the existence of powerful activities of invertase and maltase in the larval digestive tract of this insect. Nutritive value of these sugars was less than those of their component mono-

Table 1. Growth of the larva of *Chilo suppressalis* on diets containing different monosaccharides.

Monosaccharide	Habitat and generation of test insects	Number of flasks	Total Number of larvae inoculated	Total number of larvae survived	Average body weight (mg.)	Remarks
Pentose						
D-Ribose	Y 1	3	107	0	—	All larvae died rapidly at lst instar.
D-Arabinose	Y 1	3	83	0	—	All larvae died at lst instar.
L-Arabinose	Y 1	3	67	0	—	All larvae died at lst instar.
L-Arabinose	A 2	3	90	0	—	
D-Xylose	Y 1	3	92	0	—	The most larvae died at lst instar, and a few of them at 2nd instar.
D-Xylose	A 2	3	138	0	—	
L-Rhamnose	Y 1	3	61	0	—	The most larvae died at lst instar, and a few of them at 2nd instar.
L-Rhamnose	A 2	3	104	0	—	
Hexose						
D-Fructose	A 1	3	77	76	47.66	Some larvae reached maturity at about 30 days after hatching.
L-Sorbose	Y 1	3	81	5	0.86	The most larvae died at lst instar, survivals slowly grew to 2nd instar.
L-Sorbose	A 1	3	103	36	1.54	
D-Glucose	A 1	4	87	84	31.22	Some larvae reached maturity within 30 days.
D-Mannose	Y 1	3	86	7	1.63	The larvae mostly died at lst instar, survivals grew to 2nd or 3rd instar.
D-Mannose	A 2	2	64	42	1.14	
D-Galactose	A 1	5	149	109	2.91	The larvae mostly died at lst instar, survivals grew to 2nd or 3rd instar.
D-Galactose	A 2	3	99	85	1.63	

3) Fukaya and Kaneko (12) reported that invertase activity in the gut of the borer larva was powerful, but that maltase activity was not so. However, in personal commun ication from Dr. M. Fukaya, they revised their conclusions, accepting the existence of strong maltase activity in the gut of this insect.

Table 2. Growth of the larva of *Chilo suppressalis* on diets containing different oligo- and polysaccharides.

Oligo- and polysaccharide	Habitat and generation of test insects	Number of flasks	Total number of larvae inoculated	Total number of larvae survived	Average body weight (mg.)	Remarks
Oligosaccharide						
Sucrose	A 2	3	79	74	14.90	
Trehalose	A 2	2	49	43	7.10	
Maltose	Y 1	3	87	74	18.21	
Maltose	A 1	3	98	97	15.48	
Cellobiose	A 1	3	88	0	---	All larvae died rapidly at 1st instar.
Melibiose	A 1	3	104	7	1.53	Most larvae died at 1st or 2nd instar.
Melibiose	A 2	3	91	3	0.83	
Lactose	Y 1	3	78	0	—	Most larvae died at 1st instar.
Lactose	A 1	4	144	0	—	
Melezitose	A 2	3	79	48	2.98	
Reffinose	A 2	1	29	17	3.19	
Polysaccharide						
Starch	A 2	3	125	95	4.68	
Glycogen	A 2	3	105	103	14.98	
Inulin	A 2	3	107	0	---	Most larvae died at 1st instar.

Table 3. Growth of the larva of *Chilo suppressalis* on diets containing two kinds of monosaccharides.*

Carbohydrate	Total number of larvae inoculated	Total number of larvae survived	Average body weight (mg.)
1/2 D-Glucose plus 1/2 D-Fructose	102	98	30.64
1/2 D-Glucose plus 1/2 D-Galactose	78	63	19.02
1/2 D-Fructose plus 1/2 D-Galactose	79	76	16.41

* The tests were performed with the insects of the first generation from Aichi Prefecture, using three flasks to each diet.

saccharides, that is, ½ glucose plus ½ fructose to sucrose (cf. Table 3) and glucose to maltose (cf. Table 1). It may be suggested that the larval enzyme activities to hydrolyze these oligosaccharides are not necessarily so strong *in vivo*.

Trehalose has relatively low nutritive value as compared with maltose or sucrose in *Chilo suppressalis*. This sugar has been shown as having the same excellent value as sucrose or maltose in many other insects. In either case, however, their ability to utilize trehalose may be remarkable in view of the fact that this sugar probably does not occur in their natural foods. There is no evidence concerning its physiological roles. Some workers followed Weidenhagen's view when they studied digestion and utilization of several carbohydrates in insects. However, his theory has not been generally accepted in its broadest form. Undoubtedly trehalase is a distinct enzyme.

The larva was barely able to grow on a diet containing either melibiose or lactose. As mentioned in Table 3, the larva showed a relatively good growth on ½ glucose plus ½ galactose. It seems, therefore, that both melibiose and lactose are not split into their component monosaccharides in the larval intestinal tract, and that the larva may be lacking both α- and β-galactosidases. Yushima and Ishii (27) reported the absence of β-galactosidase in gut of this insect from their experimental results *in vitro.*

Raffinose has a greater nutritive value than melibiose. Because of the absence of α-galactosidase in the larval gut, fructose must be split from raffinose molecule by the action of β-fructosidase. The data show clearly the presence of the latter enzyme in the gut.

Larval utilization to melezitose is as same as that to raffinose. In *Apis,* Phillips (21) observed that melezitose was split into glucose and turanose. Then glucose was utilized, but turanose was not utilized and was accumulated in gut as faeces. The same digestion as in *Apis* may occur in the rice stem borer larva and α-1, 3-glucosidic linkage may hardly be split.

C. Polysaccharides. On a diet containing starch the larval survival is relatively good but growth is bad. Considered from the nutritive value of glucose or maltose, amylase activity of the larva may be deficient. It is thoroughly in agreement with results of enzymatic experiments carried out *in vitro* by Fukaya and Kaneko (12) and also Yushima and Ishii (27). Glycogen, on the contrary, shows a superior value as same as maltose or sucrose. In *Melanoplus,* Brown (5) also reported that there was a difference between starch and glycogen regarding these nutritive value, and that the latter was readily assimilable.

From their experimental results *in vitro,* Yushima and Ishii (27) reported the existence of the inulin digestable enzyme from the gut of the rice stem borer larva, and Koike (18) showed the same enzyme in some larvae and pupae among Lepidoptera. The present experiment, however, shows it to be hardly possible to hydrolyze inulin *in vivo.*

III Discussion

As stated above, studies have been made of the utilization of various carbohydrates by many species of insects, by comparing the longevity of adults fed on different carbohydrates, e.g., *Anastrepha* (1), *Apis* (4, 21, 26), *Calliphora* (10, 13), *Drosophila* (14), *Macrocentrus* (22), *Phormia* (15) and others. There are, however, a few investigations on their nutritive values for larval growth of insects; that is with *Oryzaephilus* (20), *Stegobium* (20), *Tenebrio* (19) and *Tribolium* (3). It appears that there is a great difference between adults and larvae in their nutrition. The adult insects, which have already attained growth, generally require only carbohydrates as the energy source for maintaining their life, except that certain adult females which require protein for their reproduction. In *Apis* and *Calliphora,* it is shown that application of proteins to the adult insects is not of use for prolongation of life, and, occasionally, reduces their life period (10, 25). On the contrary, larvae, being in the active developmental stage, require an adequate amount of nutrients containing a considerable quantity of proteins. For example, in *Chilo suppressalis,* a 15 per cent amount of digestable carbohydrates to the dry diet bring the larva to suitable growth, whereas one third amount of protein to the dry diet is necessary to satisfy good larval growth[4]. It is considered that similar differences between larvae and adults may, as a matter of course, exist in qualitative aspects.

The results obtained systematically by some workers on the nutritive values of several carbohydrates for the growth of insect larvae are summarized in Table 4. The nutritive value of several carbohydrates did not always agree among the test insects. In experiments to examine the utilization of starch for the growth with synthetic diets, the present result does not in agreement with that of the others, in which it was shown that starch was a best source of carbohydrates. This disagreement may be due to the differences in the native foods of test insects. It was generally reported that the leaf feeding insects were able to utilize glucose and sucrose but not starch (2, 5, 6, 7, 8, 9). In *Chilo suppressalis,* the present data similarly show that the larva may utilize mainly mono- and disaccharides in rice plant tissues as Fukaya and Kaneko (12), Yushima and Ishii (27), and Tsutsui *et al.* (23, 24) suggested. As already mentioned, there is a great difference in nutritive value between starch and glycogen in the present data. It is difficult to explain the cause of the difference from to-days enzymological knowledge on amylases. The similar fact also reported in *Melanoplus* (5). On the other hand, *Oryzaephilus* does not utilize glycogen to the same extent as starch (20).

When we consider the nutritive value of complex sugars, it is of interest to compare them with their component monosaccharides; i.e., maltose, trehalose, glycogen or starch with glucose; sucrose with ½ glucose plus ½ fructose; melibiose

4) Ishii and Hirano (1957) (in press).

Table 4. Nutritive values of carbohydrates for the growth of larvae of several species of insects.

Carbohydrate	*Chilo suppressalis* (Hirano and Ishii)	*Tenebrio molitor* (Leclercq, 1948)	*Tribolium confusum* (Bernard and Lemonde, 1949)	*Stegobium paniceum* (Lemonde and Bernard, 1953)	*Oryzaephilus surinamensis* (Lemonde and Bernard, 1953)
Monosaccharide					
Pentose					
D-Ribose	−	−	※	−	−
D-Arabinose	−	−	※	※	※
L-Arabinose	−	※	−	±	−
D-Xylose	−	+	−	+	−
Methyl pentose					
L-Rhamnose	−	※	+	+	−
Hexose					
D-Fructose	+	※	−	※	※
L-Sorbose	−	−	※	+	−
D-Glucose	+	+	+	+	+
D-Mannose	−	※	−	−	+
D-Galactose	± or −	−	−	−	+
Oligosaccharide					
Maltose	+	+	+	+	+
Cellobiose	−	※	+	−	±
Trehalose	+ or ±	※	※	+	+
Sucrose	+	※	+	+	+
Melibiose	−	※	+	±	+
Lactose	−	+	+	+	+
Raffinose	± or −	+	+	+	+
Melezitose	± or −	※	※	+	+
Polysaccharide					
Starch	±	+	+	+	+
Glycogen	+	+	※	+	±
Inulin	−	−	+	+	−

(Carbohydrates marked with ※ were not tested.)

or lactose with ½ glucose plus ½ galactose; inulin with fructose. Several enzyme activities hydrolyzing complex sugars, *in vivo,* may be reasoned from such comparisons.

From the present results, it is concluded that the rice stem borer larva is able to utilize glucose, fructose, maltose, sucrose and glycogen in their food, and that they may utilize practically glucose, fructose and sucrose in rice plant stems. The conclusion obtained here is in agreement thoroughly with experimental data concerning other leaf feeding insects.

IV Summary

1. The nutritive value of several carbohydrates for the growth of the rice stem borer larva is estimated by rearing with the synthetic diet under aseptic conditions.

2. The data show that larva is able to utilize glucose, fructose, maltose, sucrose and glycogen. Fructose and glucose have the greatest nutritive value. The order of the nutritive value of several carbohydrates for the larval growth is as follows: monosaccharides—fructose > glucose > galactose ≧ mannose = sorbose > rhamnose = xylose > arabinose > ribose; oligosaccharides and polysaccharides—maltose = sucrose = glycogen > trehalose > starch = raffinose = melezitose > melibiose = lactose ≧ inulin ≧ cellobiose.

3. In the larval intestinal tract, maltase (hydrolyzing α-1, 4-glucosidic linkage), trehalase, β-fructofranosidase, and amylase are present clearly. But β-glucosidase, α- and β-galactosidases, and inulin hydrolyzing enzyme are probably not present.

4. In paddy fields, it seems evident that the rice stem borer larva gets nourishment in the carbohydrate from glucose, fructose and sucrose in rice plant tissues. Starch is practically not utilized.

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ニカメイガ幼虫の生育にたいする各種炭水化物の栄養価

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摘　要

ニカメイガの栄養生理学的研究の一環として，人工飼料を用い無菌条件下に幼虫を飼育し，その生育にたいする 21 種類の炭水化物の栄養価をしらべた。得られた結果を要約すると次の通りである。

1. 単糖類では fructose, glucose が栄養価高く，galactose, mannose も多少は炭素源として利用されるが，前2者にくらべ遥かに劣る。sorbose 及び pentose の全部は全く栄養価なく，或種の pentose は幼虫の生育にたいし毒的に作用するとさえ考えられる。

2. 寡糖類及び多糖類では sucrose, maltose 及び glycogen に高い栄養価が認められるが，それぞれの成分である fructose, glucose には劣る。栄養価の順に列記すれば次の通りである：sucrose = maltose = glycogen > trehalose > starch = raffinose = melezitose > melibiose > lactose ≧ inulin ≧ cellobiose。

3. 単糖類及び2種の単糖類を混合した場合の栄養価と，寡糖類及び多糖類の栄養価とを比較した結果，幼虫の消化管内の炭水化物分解酵素としては β-fructofuranosidase, 及び α-glucosidase の1種が強力であり，trehalase, amylase の存在も明かである。これに対し β-glucosidase, α-galactosidase, β-galactosidase 及び inulin 分解酵素の活性は殆んど又は全く認められない。

4. 以上の結果及び稲茎内に存在する炭水化物の種類よりみて，野外において稲茎を食害しているニカメイガ幼虫は，炭水化物として fructose, glucose 及び sucrose を利用していると考えられる。