

FACTORS AFFECTING DEVELOPMENT OF *Oryctes rhinoceros* IN SOME SUBSTRATES COMMONLY FOUND IN THE OIL PALM ENVIRONMENT

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A laboratory study was conducted to evaluate the factors which affected larval development in four different substrates commonly found in the oil palm replanting environment. The percent survivorship of *Oryctes rhinoceros* was lowest in raw empty fruit bunches (EFB), followed by coconut trunk (CT) and oil palm trunk (OPT). Processed EFB and oil palm fronds (OPF) were found to be less suitable substrates, as indicated by the incomplete development of the larval stages. There were lower percentage of nitrogen in the OPF (0.45%) and EFB (0.35%), compared to CT (1.98%) and OPT (0.56%) substrates, which could have affected the duration for each developing stage. The higher starch content in OPT compared to raw EFB may also have influenced the development of the larvae. The weights of almost all the developing stages were higher in CT substrate. The second and third larval instars had consumption rates of 2.2 g day⁻¹ and 4.1 g day⁻¹ of CT and OPT substrates respectively. Although the consumption rates were higher in OPT, the weight of larvae remained significantly lower ($p < 0.05$) than in CT. There was a significant linear relationship ($p < 0.001$) between the percent moisture content and weight of the third instar larvae, showing water to be an important factor in ensuring weight increase in the larval and subsequently, pupal stages. Moisture content of 77% and above was essential for the complete development of *O. rhinoceros*. It is hoped that this information will lead to a modification of the zero burn replanting practice, so as to create less suitable environments for the beetle to breed in, thus avoiding the risk of *O. rhinoceros* attack.

Keywords:

Oryctes rhinoceros, habitats, oil palm trunk, empty fruit bunches, consumption rates, moisture content, nutrients.

INTRODUCTION

There are several potential breeding sites for *O. rhinoceros* (L.) (Coleoptera: Scarabaeidae) within or surrounding a zero burned oil palm replanting area. Apart from rotting OPT heaps, the others include EFB, compost heaps, coconut and rubber tree stumps (Norman and Basri, 1997).

The developmental duration of *O. rhinoceros* depends on its response towards the microclimatic and nutritional conditions of certain types of habitat. Bedford (1980) found a varied duration for the third instar larval stage, between 60 to 165 days, in several different kinds of habitats (CT, sawdust mixture and cowdung). Wood (1968) also found a longer developmental period in decomposing oil palm tissue (around five to six months) compared to in a mixture of sawdust and cowdung (between four to five months). This suggests that the differences in the moisture content and nutritional conditions of different habitats play a role in determining the life cycle duration and optimal development of this pest.

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The objective of this study was to evaluate the effects of different substrates on the development of the larval stages of *O. rhinoceros*.

MATERIALS AND METHODS

The experiments were conducted in an insectary at MPOB Bangi, Selangor (temperature: 21°C minimum, 28°C maximum; relative humidity: 53% minimum, 81% maximum). Four substrates commonly found in the vicinity of oil palm replanting areas were tested on the larval stages of *O. rhinoceros*. These substrates were OPT, CT, OPF and EFB. The EFB was provided both as raw and fibre forms. The raw materials for OPT, CT and EFB were collected from an estate at Sepang, Selangor and were shredded manually. The OPF and EFB substrates were provided in the processed form of shredded chips and fibre respectively.

The substrates were half filled into 250 ml plastic containers (diameter, 7.5 cm; height, 7 cm). These substrates were moistened with distilled water (approximately 20 ml) and given to the first, second and third larval instars. All the larval stages were collected from OPT heaps in an estate at Sepang, Selangor. The head capsule of each larvae was measured and recorded to confirm the stages prior to the tests.

Development of the larval stages was monitored every 10 days, by weighing every individual larva. The consumption of each larva in different substrates was relatively measured. This was done by weighing the substrate before and after provision of the larva into each substrate. The faecal pellets excreted by the larvae during the course of the study were collected and analysed for nutritional elements. The nutritional elements analysed for were nitrogen, phosphorus, potassium, calcium and magnesium, according to the standard soil analysis method (Schinner *et al.*, 1996).

The development of the larvae was also monitored against several levels of moisture content within OPT. This was measured by using a Shigometer (Osmose Wood Preserving Company of America, 1980). The equipment measures the value of electrical resistance (kOhm), which reduces with the increase of moisture content.

Three levels of moisture content of OPT were tested on the third instar larval stage to deter-

mine the optimal level for complete development of *O. rhinoceros*. The first level was low, 85-187 kOhm; medium, 30-48 kOhm and high, 0.4-0.8 kOhm. These values corresponded to moisture contents of 10% - 40%, 57% - 65% and 77% - 78%, respectively.

In addition to the laboratory experiments, samples of *O. rhinoceros* were collected from OPT and EFB in the field. The substrates were applied during replanting at two different estates, one at Sepang, Selangor and the other, at Telok Intan, Perak. The OPT was stacked, while the EFB were applied as a single mulch, along the interrows. Samples of *O. rhinoceros* larvae were collected at three different intervals and brought back to the laboratory for rearing, as described above. Percent emergence of adults from each substrates were recorded.

RESULTS

Head Capsule Measurements for *O. rhinoceros* Larvae

It was observed that the range for head capsule widths of larvae used in this study was between 2 - 10 mm (*Table 1*). The maximum width of the head capsule of *O. rhinoceros* recorded by Bedford (1974) was between 10.6-11.4 mm.

Larval Weight and Developmental Period of *O. rhinoceros* in Different Substrates

The mean weight for the larval stages of *O. rhinoceros* is as listed in *Table 2*. The mean weight for third instar larvae in CT substrate was between 10.08 g, while for the prepupal and pupal stages, their weights were about half the weight of the third larval instars. This is because feeding had ceased at the prepupal stage and the body appearance seems to be a bit shrivelled compared to the third larval instar. At this time, the prepupal is preparing to pupate inside its pupal cell. Mean weights of female and male adults were 2.76 and 3.31 g respectively. There was no significant difference ($p > 0.1$) in weight between them (*Table 2*).

For OPT substrate, the mean weight of the third instar larval stages was 7.02 g, while the weights for both prepupal and pupal stages were also about half the third larval instar weight. The mean weight of male and female adults was 2.13 and 3.89 g respectively. There was also no sig-

nificant difference in weight between them ($p>0.1$) (Table 2).

The mean weight for third instar larvae was 3.70 g and 4.90 g when reared on OPF and EFB fibre substrates, respectively. No succession to the prepupal stage was recorded on these two substrates (Table 2).

Overall, there was a significantly higher ($p<0.05$) weight for larvae reared on CT substrate. This was prevalent in almost all stages of development (Table 2). The males which were reared on CT were also significantly heavier ($p<0.05$) compared to those reared on OPT substrate (Table 2).

The developmental periods from the first to the third instar stage were about 28, 39, 43, 50 and 59 days for OPF, OPT, raw EFB, EFB fibre and CT substrates respectively (Table 3). The different substrates did not seem to affect the

larval developmental period from the first to the second instar (Table 3). The duration from the third instar to the prepupal stage and later, from prepupal to the pupal stage, was significantly longer on OPT and raw EFB substrates compared to CT substrate ($p<0.05$) (Table 3). However, the development from the pupal stage to adult was longer in raw EFB substrate ($p<0.05$) compared to both CT and OPT substrates (Table 3). The duration from the first larval instar to adult took about 154, 180 and 230 days for CT, OPT and raw EFB substrates, respectively (Table 3).

The larval stages that were reared in both OPF and EFB fibre substrates did not manage to succeed into the pupal stages (Tables 2 and 3). During processing of EFB into fibres, the starch content was removed during the separation of parenchymatous tissues (Anis, pers. comm.). This may have therefore affected the development of the larvae. The importance of

TABLE 1. HEAD CAPSULE WIDTHS OF THE LARVAL STAGES OF *O. rhinoceros*

Larval stage	Head capsule width (mm)	Range	n
Instar 1	2.2 ± 0.1	2.0-2.6	10
Instar 2	4.4 ± 0.1	3.8-5.0	12
Instar 3	9.1 ± 0.1	8.5-10.0	34

Note: n = number of individuals.

TABLE 2. WEIGHT OF DEVELOPMENTAL STAGES OF *O. rhinoceros* REARED IN FOUR DIFFERENT SUBSTRATES

Type of substrate	Mean individual weight (g)						
	I1	I2	I3	Prepupal	Pupal	Male	Female
CT	0.93±0.07a	2.08±0.09a	10.08±0.19a	5.95±0.33a	5.01±0.29a	3.31±0.42a	2.76±0.27a
OPT	0.17±0.04b	2.03±0.11a	7.02±0.14b	4.39±0.24b	3.89±0.23b	2.13±0.21b	2.49±0.27ab
OPF	0.25±0.11b	1.33±0.06b	3.70±0.13c	n.a.	n.a.	n.a.	n.a.
EFB a	0.24±0.08b	1.77±0.09a	4.90±0.11d	n.a.	n.a.	n.a.	n.a.
EFB b	0.18±0.01b	1.40±0.09b	7.05±0.17b	3.90±0.24b	3.35 ±0.21b	1.98±0.12b	2.05 ±0.13b

Notes: n.a. = stage not developed.

I1-I3: larval stages 1-3.

EFB a: processed empty fruit bunch (fibre).

EFB b: raw empty fruit bunch.

Values in a column with the same letters are not significantly different with one-way ANOVA, DMRT and student-t test ($p>0.05$).

TABLE 3. DURATION OF DEVELOPMENT FOR EACH STAGE TO THE NEXT IN FOUR DIFFERENT SUBSTRATES

Type of substrate	Mean duration of development (days)				
	I1-I2	I2-I3	I3-PP	PP-P	P-A
CT	15.7±1.4a	42.9± 4.4a	73.2±18.1a	8.7± 0.33a	12.6± 2.0a
OPT	14.8± 2.4a	24.1± 1.5ac	116.1± 8.3b	10.5± 0.3b	13.9± 1.4a
OPF	11.0a	16.9± 3.9bc	n.a.	n.a.	n.a.
EFB a	11.0a	44.1± 5.7a	n.a.	n.a.	n.a.
EFB b	12.5± 4.5a	30.7± 2.6ac	151.4± 15.4b	12.0b	22.5 ± 1.3b

Notes:

n.a. = stage not developed.

I=instar, PP=prepupal, P=pupal, A=adult.

EFB a: processed empty fruit bunch (fibre).

EFB b: raw empty fruit bunch.

Values in a column with the same letters are not significantly different with one-way ANOVA, DMRT and student-t test ($p>0.05$).

starch in the development of larvae may be indicated by the complete development of larvae reared on raw EFB (Tables 2 and 3).

A life table for *O. rhinoceros* based from their development in different substrates was constructed, following the method of Deevy (1947). The expectation of life, (e_x) for the first instar larvae reared in OPT (Table 4b) and CT (Table 4c) was exceeding between four to five life stages. This means that the first instar larvae would be able to develop to pupal and adult. In contrast, the e_x for first instar larvae in raw EFB (Table 4a) was only two life stages, meaning development is only up to the third instar stage. This seems to indicate the EFB as a less suitable substrate for development compared to OPT and CT substrates.

The percentage of emergence from raw EFB was significantly low (11%) (Table 4a) compared to OPT (73%) (Chi-square = 34.391, df=1, $p<0.001$) (Table 4b) and CT (64%) (Chi-square = 20.062, df=1, $p<0.001$) substrates (Table 4c). This could be due to the lower nitrogen content in EFB. There was no significant difference in the percent survivorship of *O. rhinoceros* larvae on both OPT and CT substrates (Chi-square = 0.212, df =1, $p = 0.645$) (Tables 4a to 4c).

In the field observations, the mean percent

survivorship of *O. rhinoceros* in OPT (52%) was significantly higher ($z= 5.372$; $p<0.001$) than in EFB (26%) (Table 5). This further supports the findings of the laboratory experiments.

Analysis of Elements in Faecal Pellets

There were higher contents of elements in the faecal pellets from larvae on CT substrate compared to OPT (Table 6). Elements such as nitrogen, phosphorus, potassium and calcium were richer in CT compared to OPT substrate. The CT substrate however lacked magnesium compared to OPT (Table 6).

The differences in element contents between the various substrates in the field are given in Table 7. The elements of both OPT and fronds are basically similar. EFB had higher potassium content compared to the fronds and trunks (Table 7). CT had higher contents of nitrogen and phosphorus compared to OPT, OPF or EFB. On the other hand, potassium content was lower on CT (Table 7).

In general, the nutrient contents found in the faecal pellets were relatively higher than from the substrates itself (Tables 6 and 7). These indicate the ability of the larvae to increase the concentration of the nutrients, therefore enriching the soil organic matter in the field.

TABLE 4. LIFE TABLE FOR *O.rhinoceros* REARED IN THREE DIFFERENT TYPES OF SUBSTRATES

a. Raw EFB

x	l_x	L_x	d_x	100_{qx}	S_x	T_x	e_x
Egg*	55	55	0	0.0	100	180	3.26
Instar 1	55	54	2	3.6	96.4	125	2.26
Instar 2	53	37	32	60.4	39.6	71	1.33
Instar 3	21	16	10	47.6	52.4	34	1.60
Prepupal	11	10	2	18.2	81.8	18	1.59
Pupal	9	8	3	33.3	66.7	8	0.83
Adult	6	3	-	-	-	-	-

Percent survivorship: 10.9.

b. OPT

x	l_x	L_x	d_x	100_{qx}	S_x	T_x	e_x
Egg*	37	37	0	0.00	100.00	204	5.51
Instar 1	37	37	0	0.00	100.00	167	4.51
Instar 2	37	37	0	0.00	100.00	130	3.51
Instar 3	37	34	6	16.22	83.78	93	2.51
Prepupal	31	31	1	3.23	96.77	59	1.90
Pupal	30	29	3	10.00	90.00	29	0.95
Adult	27	-	-	-	-	-	-

Percent survivorship: 72.9.

c. CT

x	l_x	L_x	d_x	100_{qx}	S_x	T_x	e_x
Egg*	22	22	0	0.00	100.00	112	5.09
Instar 1	22	22	0	0.00	100.00	90	4.09
Instar 2	22	21	3	13.64	86.36	68	3.09
Instar 3	19	18	2	10.53	89.47	48	2.50
Prepupal	17	16	3	17.65	82.35	30	1.74
Pupal	14	14	0	0.00	100.00	14	1.00
Adult	14	-	-	-	-	-	-

Percent survivorship: 63.6.

Notes:

* eggs were assumed to have 100% hatchability.

x = the pivotal stage of development.

l_x = the number surviving at beginning of stage.

L_x = the number alive between stage x and x+1.

d_x = the number dying in stage.

100_{qx} = the mortality rate (per hundred alive) at beginning of stage, or d_x as a percentage of l_x .

S_x = the survivorship rate ($100 - 100_{qx}$).

T_x = the total number of stage units beyond the stage x.

e_x = the expectation of life remaining for individuals of stage x ($e_x = T_x/l_x$).

TABLE 5. PERCENT SURVIVORSHIP OF *O. rhinoceros* WITHIN OPT AND EFB IN FIELD CONDITIONS

Type of substrate	MAA	Total larvae collected	Number emerged as adults	% Survivorship
OPT	4	94	50	53.2
	7	106	40	37.7
	9	72	47	65.3
			Mean	52.1
EFB	5	56	25	44.6
	7	114	11	9.6
	9	8	2	25.0
			Mean	26.4

Notes: MAA=months after application of substrates.
OPT and EFB were placed along the interrows.

TABLE 6. PERCENT NUTRIENT CONTENT IN THE FAECAL PELLETS OF *O. rhinoceros* REARED IN TWO DIFFERENT SUBSTRATES

Type of substrate	Mean nutrient content (%)					
	N	P	K	Ca	Mg	n
CT	1.95a	0.43a	2.62a	0.53a	0.28a	9
OPT	1.57b	0.17b	2.09b	0.47b	0.42b	13

Notes: values in a column with the same letters are not significantly different with the student-t test ($p>0.05$).
n = number of observations.

TABLE 7. PERCENT NUTRIENT CONTENT IN THE VARIOUS SUBSTRATES IN THE FIELD

Type of substrate	Mean dry weight (%)						References
	Starch	N	P	K	Ca	Mg	
CT	n.a.	1.98	0.40	0.67	n.a.	n.a.	Abad <i>et al.</i> (1987)
OPT	57.9	0.56	0.05	1.62	0.31	0.15	Khalid <i>et al.</i> 1999), Tomimura (1992)
EFB	2	0.35	0.03	2.29	0.15	0.18	Suwandi <i>et al.</i> (1991), Anis, pers.comm.
OPF	n.a.	0.45	0.05	1.52	0.43	0.11	Khalid <i>et al.</i> (1999)

Note: n.a. = data not available.

Consumption of Substrates by the Larvae

During the development of the second to the third larval instars, they consumed 151 g and 95 g of CT and OPT substrates, respectively. These CT and OPT substrates were consumed within 45 and 20 days, respectively (Table 8). These corresponded to the consumption of 3.4 g and 4.8 g of CT and OPT substrates per day, respectively. The amount consumed by the second instar larvae was significantly higher ($p < 0.05$) on CT substrate compared to OPT. In comparison, the second instar larvae consumed the CT substrate at about three-quarter (71%) the rate of the OPT substrate. The consumption of the larvae was also longer ($p < 0.05$) on CT substrate compared to OPT.

Subsequently, during the development of the third larval instars to the prepupal stage, they consumed 211 g of CT substrate and 320 g of OPT substrate in 99 and 70 days, respectively (Table 8). These corresponded to a daily consumption of 2.1 g and 4.6 g of CT and OPT

substrates, respectively. This shows that the second instar larvae consumed the CT substrate at about half the rate (46%) of the OPT substrate. The amount consumed by the third instar larvae was significantly lower ($p < 0.05$) on CT substrate compared to OPT. However, there was no significant difference ($p > 0.05$) between the consumption period of CT substrate compared to OPT.

Development of *O. rhinoceros* under Different Moisture Conditions

The larval stages of *O. rhinoceros* developed successfully into adults under high moisture content (Table 9). Under medium moisture content, the larval stages only managed to develop into male adults. Finally, under low moisture content, the larval stages were unable to complete their development to enter the pupal stage. All of them died before entering the prepupal stage (Table 9). There were also significant differences in larval weights under different moisture conditions: the highest larval weight was

TABLE 8. CONSUMPTION BY *O. rhinoceros* OF TWO SUBSTRATES

Type of substrate	Mean weight of substrate consumed (g)		Mean duration of development (days) (n)	
	I2-I3	I3-pp	I2-I3	I3-pp
CT	151.40 ± 10.96a	211.04 ± 12.15a	45.3 ± 2.0a (7)	98.65 ± 21.29a (15)
OPT	94.63 ± 12.54b	319.76 ± 15.32b	20.38 ± 3.82b (8)	70.47 ± 5.54a (16)

Notes: the larval stages were reared until the prepupal stage.

n = number of observations.

Values in a column with the same letters are not significantly different with the student-t test ($p > 0.05$).

I = Instar, pp = prepupal.

TABLE 9. WEIGHTS OF *O. rhinoceros* STAGES REARED IN OPT SUBSTRATE WITH THREE LEVELS OF MOISTURE CONTENT

Moisture content of substrate	Mean individual weight (g) (n)				
	Instar 3	Prepupal	Pupal	Male	Female
Low	5.44a (77)	n.a.	n.a.	n.a	n.a
Medium	7.24b (118)	5.05a (2)	4.74a (9)	2.70a (2)	n.a
High	11.62c (102)	6.56a (6)	5.75b (13)	3.21a (3)	3.09 (3)

Notes: n.a., stage not developed.

Values in a column with the same letters are not significantly different with one-way ANOVA, DMRT and student-t test ($p > 0.05$).

n = number of observations.

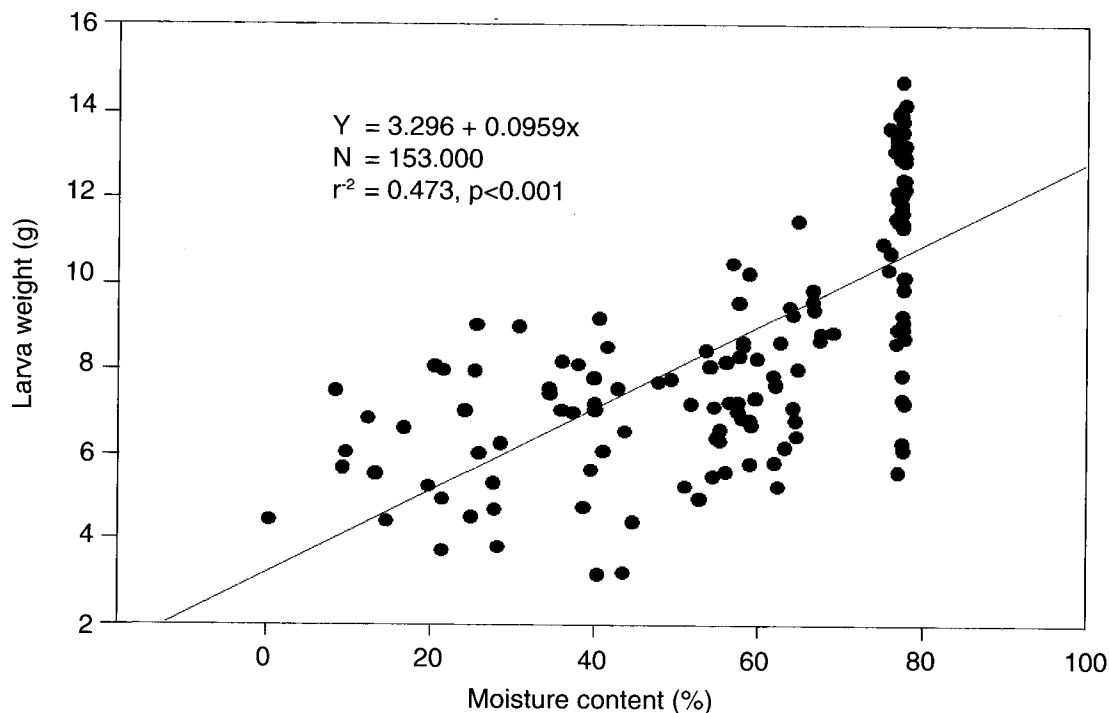


Figure 1. Relationship between moisture content in oil palm substrate and instar larval weight.

achieved under high moisture content, followed by the medium and low moisture contents. Although the prepupal weight was not significantly different between the medium and high moisture contents ($p > 0.05$), the weight of the pupal was higher in the latter than in the former ($p < 0.05$). The weight of the adult males that emerged was also not significantly different ($p > 0.05$) between those two groups (Table 9). There was also a significant linear relationship ($p < 0.001$) between percent moisture and the weight of the third larval instars (Figure 1).

DISCUSSION

In this study, CT and OPT were the preferred substrates as habitat for *O. rhinoceros*. The larvae successfully developed into adults. On the other hand, processed EFB and OPF were found to be poor substrates, as indicated by the incomplete development of the larval stages. This is suggested to be caused by the lower nitrogen content in the OPF and EFB, compared to the CT and OPT substrates. In processed materials (in this case the OPF and EFB fibres), the parenchymatous tissues which contains starch and sugars has been separated to avoid spoilage by microorganism (Gurmit Singh, 1994). Therefore, all the larvae reared in those substrates could not surpass the third instar

stage. In raw EFB, where there are some starch present, some of the larvae managed to develop into adults. However, its emergence of adults was lower compared to the CT and OPT substrates. In the field, larvae that were collected from the EFB mulch had a lower percentage of emergence compared to those collected from OPT (Table 5; Ramle, pers. comm.). This indicates that a higher nitrogen content in the substrates favours the complete development of *O. rhinoceros*. The levels of plant nitrogen (an index of protein) are indicative of the insect performance (Lindroth, 1993). Besides nitrogen, higher starch content in OPT compared to EFB (Table 7) may have also influenced their development.

The weights of almost all the developing stages were higher in the CT substrate. This shows that CT was suitable as habitat for *O. rhinoceros*, as has been earlier indicated by its importance as a pest for coconut in Malaysia and the Pacific Islands (Catley, 1969; Hinckley, 1973; Bedford, 1976a, b).

Generally, the rates of consumption and growth of the larval stages increased exponentially with age (Lindroth, 1993). In the current study, the weight of the third instar larvae increased to 17 g in the CT substrate. However, the weight decreased when it entered the prepupal and subsequently the pupal stage.

This was likely due to the cessation of feeding at the prepupal stage. On average, the weights of the prepupal and pupal stages were approximately half the weight of the third larval instar stage.

The durations for each developing stages were longer on OPT compared to the CT substrate. In the current study, the developmental period from the first larval instar to adult on CT was about five months, compared to about six months on OPT. This also suggests an indication of lower nitrogen content in the former compared to the latter. Generally, insects consuming food with high nitrogen content have effective consumption and absorption rates, which equate to faster development (Lindroth, 1993). These same phenomena apply to the Colorado potato beetle (Cloutier *et al.*, 1999). Potato leaves with 1% oryzacystatin hastened the development of the third larval stage by 14% with 20% increase in weight (Cloutier *et al.*, 1999).

The faecal pellets from larvae consuming CT substrate had higher contents of nitrogen, phosphorus, potassium, calcium and magnesium compared to those consuming OPT. These higher percentages of elements, especially nitrogen, in the faecal pellets therefore corresponded to the higher percentages of elements in the substrate itself. In monocots, such as oil palm and coconut, they have higher nitrogen and sugar contents but lower tannin and lignin contents, compared to dicots (Lindroth, 1993; Tomimura, 1992).

The duration of development from the first to the third instars was shorter in the processed OPF substrate compared to process EFB substrate, suggesting a higher nitrogen content in the OPF compared to EFB. However; the larval stages were still unable to complete their life cycle. This could be due to the lack of moisture in the processed substrates. High moisture content is a critical factor for the successful development of *O. rhinoceros* (Catley, 1969). Low moisture conditions will disrupt the absorption of nitrogen and other developmental processes (Scriber, 1977). There was a significant linear relationship ($p < 0.001$) between percent water content and the weight of the third instar larvae, showing water as an important factor in ensuring weight increase in the larval and subsequently, pupal stages.

In this study, the moisture content at the highest level favoured development of the third lar-

val instar into adult. This shows that a moisture content of 77% and above is essential for the complete development of *O. rhinoceros*. The weights of larvae and pupae were also highest at this level of moisture content compared to the other two levels. This finding supports the earlier study of Scriber and Feeny (1979), who reported the highest survival of insect larvae on leaves having a moisture content between 75% and 95%. On the other hand, a moisture content at the medium level (between 57% to 65%) seemed to have caused physiological stress to the larvae, as indicated by the non-emergence of female beetles. The lowest level of moisture content (between 10% to 40%) seemed to be an adverse condition which caused death to all the larvae before the prepupal stage.

There were higher larval mortalities in EFB compared to OPT or CT. Apart from the nitrogen content which could have affected the development, this could also be due to some physiological factors of the larvae. Hinckley (1973) mentioned that higher larval mortality mainly occurred in the first and third larval instars. The former occurred when it tried to feed on harder wood while the latter occurred when it was unable to accumulate enough fat reserve for pupation.

The second and third larval instars had a total consumption rate of 2.5 g day⁻¹ and 4.6 g day⁻¹ of CT and OPT substrates, respectively. These seemed to indicate that the lower nitrogen content in OPT had induced the larvae to consume at a higher rate daily (in this case, about twice the rate of CT). Lindroth (1993) explained that most insects increased their consumption rates as a feedback towards low nitrogen content.

The efficiency of conversion of digested food (ECD) is the proportion of digested food that is transformed into insect biomass. The efficiency of conversion of ingested food (ECI) is a product of assimilation efficiency (AD) and ECD (Scriber and Slansky, 1981). Although the consumption rates were increased, the weight of larvae in OPT remained significantly lower than in CT. This showed that the higher consumption rates only accelerated the passage of food through the gut, thereby reducing its AD (Lindroth, 1993). This was also quite evident in the development of the third instar larval stage into prepupal. Although the amount consumed was significantly higher in OPT substrate, the duration for

development may not significantly different ($p>0.05$) from CT substrate. This indicated that the assimilation efficiency was better in the latter compared to the former.

Based on this study, the beetle population in the field can be reduced by creating unsuitable breeding sites. In the current zero burn replanting practice, the trunk chips are often heaped between the interrows. This creates a microclimate which is moist and highly suitable for the development of *O. rhinoceros* larvae. An example to alleviate the situation is to spread the trunk chips throughout the area prior to replanting. Khalid *et al.* (1999) evaluated several replanting techniques which involved spreading evenly the trunk chips (about 10 cm thick) and avoiding a thick pile formation. In this way, the trunk chips dried out faster, preventing the beetle from breeding in it. In addition to this, the trunk chips were decomposed quicker, releasing nutrients to the soil more rapidly (Khalid *et al.*, 1999). As expected, no high population of *O. rhinoceros* was experienced in the replanting area (Khalid *et al.*, 1999).

CONCLUSION

This study has shown that a higher nitrogen content in substrates favours the development of *O. rhinoceros* as indicated by the increase in larval weights and shorter developmental periods.

Moisture conditions of more than 77% were an important factor in ensuring optimal growth in the larval and pupal stages for the development of adults. Lower moisture conditions caused physiological stress to the larvae, and induced the development of male beetles or death before pupation.

This information can be exploited to modify the zero burn replanting environment so as to create less suitable breeding environments for *O. rhinoceros*.

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