

Effect of the Larger Grain Borer, Prostephanus truncatus (Horn)  
(Coleoptera: Bostrichidae), on Stored Corn as Assessed by Abiotic,  
Biotic, and Bioenergetic Variables

by

Colin John Demianyk

A thesis  
presented to the University of Manitoba  
in partial fulfillment of the  
requirements for the degree of  
Master of Science  
in  
Department of Entomology

Winnipeg, Manitoba

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ISBN 0-315-37274-5

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## ACKNOWLEDGMENTS

I wish to thank the chairman of my M.Sc. advisory committee, and supervisor, Dr. R.N. Sinha, Agriculture Canada, for his guidance and support throughout the course of this program. I also wish to thank the other committee members, Dr. R.A. Brust, Department of Entomology, and Dr. W.E. Muir, Department of Agricultural Engineering, University of Manitoba, for reviewing this thesis.

I wish to express my appreciation to present and past directors, Drs. T.G. Atkinson and D.G. Dorrell, Agriculture Canada Research Station, Winnipeg, who allowed this research to proceed while I remained a full-time employee of the station, P.S. Barker and N.D.G. White for critically reviewing, D. Sabourin for recommending statistical procedures for the first manuscript, S.R. Loschiavo and F.J. Madrid for critically reviewing the second manuscript, and other scientists and staff for their assistance.

I am also grateful to Ms. C. Letain for typing the manuscript.

I am especially grateful to my wife, Carole, to whom this thesis is dedicated, for her much appreciated support and patience during my graduate studies, to my children Alexandra and Bryan, and to my parents who encouraged me to succeed with whatever I chose.

## TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGMENTS.....	i
TABLE OF CONTENTS.....	ii
LIST OF TABLES.....	v
LIST OF FIGURES.....	vi
LIST OF APPENDICES.....	viii
ABSTRACT.....	1
FOREWARD.....	3
INTRODUCTION.....	4
LITERATURE REVIEW.....	6
Physical Description.....	6
World Distribution.....	6
Pest Status and Biology.....	9
Bioenergetics.....	13
 MANUSCRIPTS:	
I. Effect of infestation by the larger grain borer, <u>Prostephanus truncatus</u> (Horn), and the lesser grain borer, <u>Rhyzopertha dominica</u> (F.) (Coleoptera: Bostrichidae), on stored corn.....	18
Introduction.....	19
Materials and Methods.....	20

	<u>Page</u>
Results.....	23
Insect Numbers.....	23
Dust Production.....	24
Fat Acidity Values.....	24
Moisture Content.....	25
Germination.....	25
Microflora.....	26
Discussion.....	26
Insect Numbers and Dust Production.....	26
Fat Acidity Values.....	28
Moisture Content.....	28
Germination.....	29
Microflora.....	30
II. Bioenergetics of the larger grain borer, <u>Prostephanus truncatus</u> (Horn) (Coleoptera: <u>Bostrichidae</u> ), feeding on corn.....	35
Introduction.....	36
Materials and Methods.....	38
Rearing Procedures and Sample Preparation.....	38
Gravimetry.....	40
Calorimetry.....	40
Respirometry.....	41
Energy Budget Calculations.....	41

	<u>Page</u>
Results.....	43
Distribution of Life Stages and Biomass.....	43
Consumption and Energy Determination.....	44
Respiration.....	44
Energy Budget and Efficiencies of Energy Transfer.....	45
Discussion.....	46
Life Stages and Biomass.....	46
Consumption and Energy Determination.....	48
Respiration.....	51
Efficiencies of Energy Transfer.....	53
GENERAL DISCUSSION.....	67
SUMMARY.....	71
LITERATURE CITED.....	73
APPENDICES.....	87

## LIST OF TABLES

	<u>Page</u>
MANUSCRIPT II. Bioenergetics of the larger grain borer, <u>Prostephanus truncatus</u> (Horn) (Coleoptera: Bostrichidae), feeding on corn.	
Table 1. Distribution of life stages, in percentages, of <u>P. truncatus</u> , reared at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH on stored corn.....	57
Table 2. Dry weight, energy values, ash percentage of various components of insect biomass, rejecta, food, and cumulative consumption for <u>P. trunca-</u> <u>tus</u> reared at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH on stored corn.....	58
Table 3. Comparative energy budget data and efficiencies for developmental stages (to last instar or prepupa) of nine stored-product insects and <u>P.</u> <u>truncatus</u> , reared under optimal conditions.....	60

## LIST OF FIGURES

	<u>Page</u>
<b>LITERATURE REVIEW</b>	
Fig. 1. Global distribution of <u>Prostephanus truncatus</u> occurring and intercepted in grain and other materials.....	8
 <b>MANUSCRIPT I. Effect of infestation by the larger grain borer, <u>Prostephanus truncatus</u> (Horn), and the lesser grain borer, <u>Rhyzopertha dominica</u> (F.) (Coleoptera: Bostrichidae), on stored corn.</b>	
Fig. 1. (A) Mean number of <u>P. truncatus</u> and <u>R. dominica</u> adults (live and dead) in 120 g corn, (B) mean weight of dust produced in insect-infested corn, (C) mean percentage increase for FAV, and (D) mean moisture content for insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	33
Fig. 2. (A) Mean percentage of germination, (B) mean percentage of fungal infection by <u>Aspergillus glaucus</u> group, (C) mean percentage of fungal infection by <u>Penicillium</u> spp., and (D) mean percentage of bacterial infection for insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	34
 <b>MANUSCRIPT II. Bioenergetics of the larger grain borer, <u>Prostephanus truncatus</u> (Horn) (Coleoptera: Bostrichidae), feeding on corn.</b>	
Fig. 1. Cumulative daily energy budget, in J/individual, for <u>P. truncatus</u> reared at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH on corn. Complete histogram, total material removed from kernel or consumed plus chewed but uneaten kernel; clear histogram, frass composed of chewed but uneaten kernel plus a portion of feces. The line defined as consumption is total material removed minus frass. Respiration values were determined using Warburg respirometry data. Lifestages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult.....	62

- Fig. 2. Mean hourly oxygen consumption and standard error per milligram dry weight for P. truncatus reared at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH on corn. Life-stages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult..... 63
- Fig. 3. Mean daily respiration and standard error, in J/individual, and respiratory quotient (RQ) values for P. truncatus reared at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH on corn. Lifestages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult..... 64
- Fig. 4. Cumulative respiration and standard error, in joules, used by individual P. truncatus during development at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH. Life-stages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult..... 65
- Fig. 5. Energy flow schema showing energy used, in joules, by various stages of P. truncatus reared at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH on corn..... 66

## LIST OF APPENDICES

	<u>Page</u>
MANUSCRIPT I. Effect of infestation by the larger grain borer, <u>Prostephanus truncatus</u> (Horn), and the lesser grain borer, <u>Rhyzopertha dominica</u> (F.) (Coleoptera: Bostrichidae), on stored corn.	
Appendix 1. Mean number and standard error of <u>P. truncatus</u> and <u>R. dominica</u> adults (live and dead) in 120 g corn stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	88
Appendix 2. Mean dust production and standard error (in grams dry weight) by <u>P. truncatus</u> and <u>R. dominica</u> in 120 g corn stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	89
Appendix 3. Mean fat acidity value (FAV) and standard error (mg KOH/100 g dry seed) of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	90
Appendix 4. Mean moisture content and standard error in percentages of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	91
Appendix 5. Mean germination and standard error in percentages of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	92
Appendix 6. Mean percentage and standard error of infection by <u>Aspergillus glaucus</u> group of insect-infested corn, uninfested corn and dockage and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	93
Appendix 7. Mean percentage and standard error of infection by <u>Penicillium</u> spp. of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	94
Appendix 8. Mean percentage and standard error of infection by bacteria of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH for 20 wk.....	95

	<u>Page</u>
MANUSCRIPT II. Bioenergetics of the larger grain borer, <u>Prostephanus truncatus</u> (Horn) (Coleoptera: Bostrichidae), feeding on corn.	
Appendix 9. Mean energy content and standard error of individual <u>P. truncatus</u> dissected from implanted kernels at $30\pm 0.5^{\circ}\text{C}$ and $70\pm 2\%$ RH.....	97
Appendix 10. Mean hourly oxygen consumption and carbon dioxide production with standard errors, and calculated respiratory quotient (RQ) values for <u>P. truncatus</u> as determined by a Warburg respirometer at $30\pm 1^{\circ}\text{C}$ .....	98
Appendix 11. Energy equivalents of oxygen and carbon dioxide for various respiratory quotient (RQ) values, due to utilization of different proportions of carbohydrates and fats.....	99
Appendix 12. Energy equivalents of oxygen, in joules, for various respiratory quotient (RQ) values calculated for <u>P. truncatus</u> as determined by a Warburg respirometer at $30\pm 1^{\circ}\text{C}$ .....	100
Appendix 13. Mean energy and standard error, in joules, used for respiration, per milligram and per individual <u>P. truncatus</u> at $30\pm 1^{\circ}\text{C}$ .....	101

## ABSTRACT

The impact of infestation by Prostephanus truncatus (Horn) on the quality of stored corn was determined both quantitatively and qualitatively in two parts: first, by assessing several abiotic, entomological, and microbial variables; and second, by developing a complete energy budget.

In the first part, quantitative and qualitative losses in stored corn infested by P. truncatus, and stored for 20 wk at 30°C and 70% RH, were compared with those of Rhyzopertha dominica (F.). Treatments included insect-infested whole corn, uninfested whole corn plus ground corn (dockage), and uninfested whole corn. The quality-assessment criteria included adult insect number, dust weight production, seed moisture content, changes in seed fat acidity value, germination, and microfloral infection of seeds. Both insect species multiplied quickly, with P. truncatus peaking at 880 adults per 120 g corn by week 14, then declining slightly because of an exhausted food supply. R. dominica numbers increased to 550 adults per 120 g corn by week 14 and 1300 adults per 120 g corn by week 20. P. truncatus dust production was significantly different from that of R. dominica ( $P < 0.005$ ). Infested treatments had significantly different seed moisture content, fat acidity values, and bacterial infection of seeds compared with controls ( $P < 0.005$ ). Seed germination was significantly reduced for both species compared with controls ( $P < 0.005$ ). There was no difference in Penicillium spp. infection levels among treatments ( $P > 0.05$ ); only the P. truncatus treatment

showed a difference in infection by Aspergillus glaucus group with a decrease after week 11 ( $P < 0.005$ ).

In the second part, an energy budget was developed for all life stages of P. truncatus reared singly on whole corn kernels at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH. Materials removed from kernels, estimated consumption, respiration, insect biomass, and rejecta were determined. Mean energy in joules (J) accumulated in biomass per individual in each developmental stage was as follows: egg, 0.6; first instar ( $L_1$ ), 1.2;  $L_2$ , 7.8;  $L_3$ , 37.9; prepupae, 40.4 J. The mean energy content of one corn kernel was 4537 J. A mean of 547 J was removed by larval feeding, of which 252 J was estimated to be consumed. Adults consumed an estimate of 1128 to 4210 J over a lifespan of 45-168 d, and could remove between 5728 to 21,383 J. During development, 295 J was lost to frass and feces. The highest rate of  $\text{O}_2$  consumption ( $16.4 \mu\text{L O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ ) occurred in  $L_1$  at 6 d development, but most oxygen was consumed by  $L_3$  at 16 d ( $28.2 \mu\text{L O}_2$  per individual per h) equivalent to an energy loss of  $13.6 \text{ J} \cdot \text{d}^{-1}$ . Cumulative respiration was 78 J for larval development and 85 J for new adults at 26 d. Cumulative assimilation efficiency was 47.2%, gross production efficiency 16.0%, and net production efficiency 34.0%. The energy budgets of P. truncatus and nine stored-product pests were compared.

## FOREWORD

This thesis is written in a manuscript style intended to yield two papers in a refereed journal. The first manuscript entitled "Effect of infestation by the larger grain borer, Prostephanus truncatus (Horn), and the lesser grain borer, Rhyzopertha dominica (F.) (Coleoptera: Bostrichidae), on stored corn" has been published in Environmental Entomology 16: 618-624 (1987). The second manuscript entitled "Bioenergetics of the larger grain borer, Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae), feeding on corn" has been submitted for publication in the Annals of the Entomological Society of America. These manuscripts are Contribution No. 1226 and 1289, respectively, from the Agriculture Canada Research Station, Winnipeg, Manitoba.

## INTRODUCTION

The larger grain borer, Prostephanus truncatus (Horn), has long been known as an important primary pest of farm-stored corn (Giles 1975). Adults and larvae penetrate corn kernels generating large quantities of corn dust and causing serious economic losses. P. truncatus was once restricted to Central America, but now ranges from the southern United States (Chittenden 1911) to northern South America (Cotton & Good 1937). P. truncatus was introduced into Africa from infested, imported corn, subsequently becoming established; it now presents a serious threat to the critically-short food supplies of subsistence farmers (Cross 1985). Since 1981, P. truncatus has become widespread within Tanzania, and has now reached southern Kenya (Kega & Warui 1983), Burundi (Hodges 1986), and Togo (Harnish & Krall 1984).

Long-range protection of stored grain from this pest requires accurate estimates of potential food and energy losses from the crop. Qualitative and quantitative losses and the interrelations between abiotic and biotic variables of stored corn must also be understood before a rational strategy of stored-grain management can be developed. Presently no data are available describing the transfer of food energy from a stored crop to this species, although several studies exist for other serious stored-product insects (Campbell & Sinha 1978, Klekowski et al. 1967, Imura & Sinha 1986, Campbell et al. 1976). In recent reviews on P. truncatus (Wright & Spilman 1983, Hodges 1986), most publications dealt with its distribution, control, and general biology; papers

investigating interrelations between abiotic and biotic variables of stored corn infested with P. truncatus are scarce.

The objective of this study was to measure the impact of infestation by P. truncatus by measuring changes in established physical, biological, and chemical quality-loss criteria, and by determining the energy flow from stored corn. Identifying the causes of damage, the flow of energy from consumed corn through the developmental stages of P. truncatus, and various efficiencies of energy use, may give a more accurate assessment of the ecological and economic impact of this species. This may aid in development of mathematical models for predicting damage or for controlling infestations of this pest.

## LITERATURE REVIEW

### Physical description

Prostephanus truncatus (Horn) is a beetle belonging to the Coleopteran family Bostrichidae, and is similar, but slightly larger than the lesser grain borer, Rhyzopertha dominica (F.). Adult Prostephanus are 3-5 mm long, brown, and cylindrical. The elytra are flattened and steeply inclined posteriorly, having two pronounced lateral ridges; these two features distinguish Prostephanus from other similar Bostrichids, Dinoderus spp. and R. dominica (Hodges 1982). Adults may be identified using keys by Fisher (1950) and Kingsolver (1971). Other keys are provided for sexing adults (Shires & McCarthy 1976) and pupae (Bell & Watters 1982), identifying larvae and pupae (Spilman 1984), and larval instars (Subramanyam et al. 1985).

### World distribution

Prostephanus is believed to be indigenous to Central America, where it was first reported in Guatemala in 1884 and Mexico in 1895 (Chittenden 1911). Figure 1 shows occurrences of this beetle including records from Guatemala (Zacher 1926), Costa Rica, Nicaragua (Fisher 1950, Giles & Leon 1974), Panama, Honduras, El Salvador (McGuire & Crandall 1967), Columbia (Posada et al. 1976), and Peru (Wright 1984). A Brazilian report exists (Cotton & Good 1937), however, recent publications of beetle fauna did not include P. truncatus (Hodges 1986).

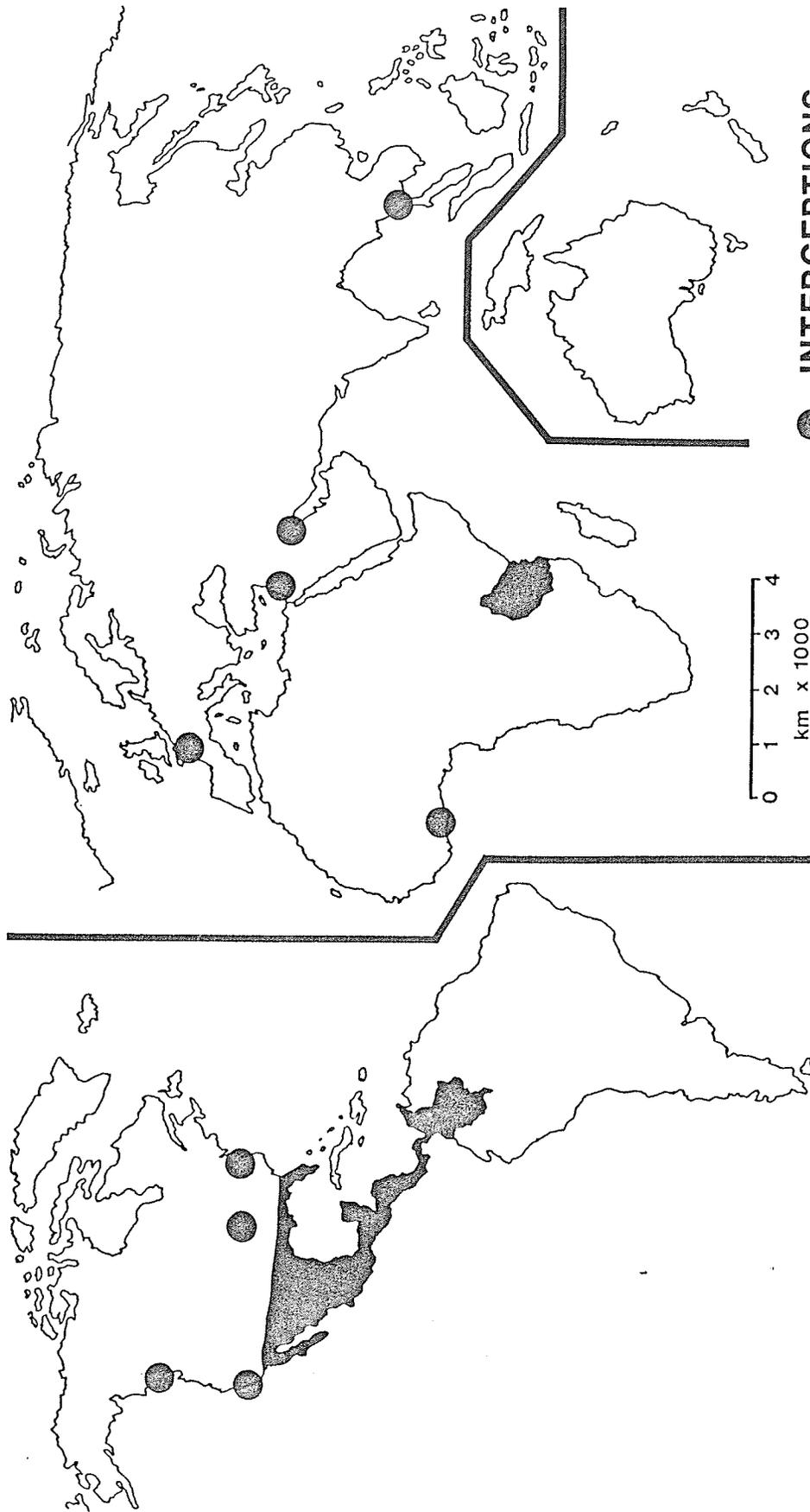
Its range now includes the southern United States (Back & Cotton 1940), including California and Texas (Cotton & Good 1937). Isolated cases of infested, imported corn and wooden ornaments have been reported in Arizona, Missouri, and New York State (Fisher 1950).

P. truncatus was imported on corn into Israel (Calderon & Donahaye 1962) and Iraq (Al-Sousi et al. 1970), however, it did not become established. Two specimens were found in an enamelled Mexican box in Vancouver, Canada (Hatch 1962), and in France, on a plant imported from Central America (Wright 1984). P. truncatus appeared on a 1976 list of stored-product insects of Thailand, however, Hodges (1986) believed this record may need confirmation because Dinoderus spp. have often been confused with P. truncatus.

In 1979, P. truncatus became established in the hot, dry Tabora region of Tanzania (Cross 1985), where it caused serious damage for several years before being identified (Dunstan & Magazini 1981). Since 1981, P. truncatus has spread throughout Tanzania, now reaching southern Kenya (Kega & Warui 1983) and Burundi (Hodges 1986). A recent outbreak in Togo, West Africa, is believed to have originated several years earlier when the state storage company began storing imported grain (Krall 1984).

P. truncatus now poses a serious threat by extending its distribution southward to Zambia and Malawi from Tanzania (Cross 1985), and into Ghana and Benin, whose borders are 3 and 15 km, respectively, from infestation sites in Togo (Krall 1984).

Fig. 1. Global distribution of Prostephanus truncatus occurring and intercepted in grain and other materials.



● INTERCEPTIONS

0 1 2 3 4  
km x 1000

### Pest status and biology

P. truncatus has been described as a typical granary pest of farm-stored corn attacking both whole grains and cobs before and after harvest (Giles 1975, Golob & Hodges 1982). Corn stored on the cob suffered considerably more damage than shelled grain; similar results were found using simulated cobs, blocks or stabilized kernels in the laboratory (Cowley et al. 1980, Bell & Watters 1982, Howard 1984). Susceptibility also varied with varietal differences; harder, flintier grains suffering less damage than softer, floury varieties (Bell & Walters 1982, Howard 1984).

Attempts to rear the species in economically-important stored commodities showed success only with corn and a soft variety of wheat (Shires 1977). In Tanzania, P. truncatus did not infest sorghum, but bred and produced heavy infestations in dried cassava causing weight losses up to 73.6% (Hodges et al. 1983, 1985). This selective feeding behavior conforms to the view of Chittenden (1911) that edible roots and tubers may form natural breeding sites for this species, and that P. truncatus only recently acquired its grain feeding habit (Cotton 1963). In addition, P. truncatus is a wood-borer capable of damaging wooden storage structures and utensils.

Weight losses in corn of 40% after 6 mo storage have been reported in Nicaragua (Giles & Leon 1974), and losses of 34% after 3-6 mo in Tanzania (Golob & Hodges 1982). By comparison, damage caused over a longer entire storage season by common stored-product pests such as the rice weevil, Sitophilus oryzae (L.) in Zambia, the maize weevil, Sitophilus

zeamais Motschulsky in Kenya, and the Angoumois grain moth, Sitotroga cerealella (Olivier) in Malawi was only 2-6% (Adams 1977), 3-5% (De Lima 1979), and 2-5% (Golob 1981), respectively. Most corn losses to P. truncatus result from conversion of whole grains into powder by adult boring; feeding activity may be somewhat secondary until a large larval population is established (Hodges et al. 1983). Potential corn losses in Tanzania have been estimated at 534,000 t annually, having a value of US \$83.7 million (Autry & Cutkomp 1982).

P. truncatus is also considered a pest at altitudes of 2249 m in Mexico, where it ranks ahead of S. oryzae, S. cerealella, and the saw-toothed grain beetle, Oryzaephilus surinamensis (L.) (Quintana et al. 1960) in terms of storage losses. An almost temperate climate exists at this elevation with a maximum recorded temperature of 24.6°C, and the occurrence of seasonal frost, therefore, this species may be quite cold tolerant. At a higher altitude of 2675 m, where mean annual temperature was 15.0°C, P. truncatus fared less well than S. oryzae or R. dominica cultured on wheat under the same conditions (Wilbur et al. 1962).

Optimum conditions for development of P. truncatus on corn are 32°C and 70-80% RH (Shires 1979, 1980, Bell & Watters 1982), and development can occur over a wide range of temperatures (12-40°C) and humidities (30-90% RH). Under optimum conditions, Bell & Watters (1982) observed that the life cycle was completed in 24-25 d on whole kernels or firmly packed corn flour, whereas Shires (1979, 1980) observed a development period of 35.4 d on loosely-packed flour. Dobie (1978) has developed a simple curve describing P. truncatus development; Sinha & Watters

(1985), from various sources, have given an egg-to-adult development range of 24-267 d and adult longevity of 45-168 d. Fecundity varied from a mean of 50.5 eggs per female on loose kernels (Shires 1980) to 430 eggs per female on simulated cobs (Bell & Watters 1982); two females that produced 600 eggs were also noted. Fecundity increased proportionally to the weight of dust produced by boring and with infestation of softer corn varieties (Howard 1984).

P. truncatus is tolerant to dry conditions, this being confirmed during laboratory studies (Young et al. 1962, Hodges & Meik 1984), and in field studies in Nicaragua (Giles & Leon 1974) and Tanzania (Hodges et al. 1983). P. truncatus' ability to develop on grain of low moisture content may be one reason for its success. It probably benefits from the absence of any significant competition from other stored-product pests (Hodges 1986).

In Tanzania, P. truncatus usually dominated mixed populations with Sitophilus spp. on cobs, however, Sitophilus spp. dominated P. truncatus on loose grain (Golob et al. 1985). Numbers of the red flour beetle, Tribolium castaneum (Herbst) showed a positive correlation with those of P. truncatus (Hodges et al. 1983). I. castaneum had little or no survival on crushed and whole corn, but it multiplied successfully on corn flour. I. castaneum will feed on corn flour produced by P. truncatus and perhaps also on the eggs and immature stages; it suppressed numbers of P. truncatus infesting cobs by up to 50% (Hodges 1986). The predatory histeoid, Teretriosa nigrescens Lewis has been associated with P. truncatus infesting traditional storages of corn in Mexico and Hon-

duras (Rees 1985). P. truncatus populations increased ten-fold, whereas populations in the presence of I. nigrescens were reduced to below their initial numbers. Immature P. truncatus fell prey to larvae and adults of I. nigrescens; its ability to survive and remain an effective predator under dry conditions may be of considerable practical value for control of P. truncatus. Large numbers of the hymenopteran parasite, Anisopteromalus calandrae (Howard) have been associated with dehusked cobs heavily infested with P. truncatus; the relationship between these two species, however, has not been investigated (Hodges et al. 1983).

The processes involved with stored-grain deterioration have been extensively investigated (Zeleny 1954, Christensen & Kaufmann 1969, Sinha & Muir 1973). Many recent studies have investigated the abiotic and biotic relationships of grain infested with storage mites (White et al. 1979, Sinha 1979, Sinha & White 1982), moths (Demianyk & Sinha 1981, Madrid & Sinha 1983, Imura & Sinha 1984), and beetles (Sinha 1975, 1983, 1984, Campbell & Sinha 1976, Lustig et al. 1977, Sinha et al. 1979, White & Sinha 1980).

Data on qualitative changes of corn infested with P. truncatus are minimal. Adem and Bourges (1981) showed an apparent decline in the concentration of two amino acids, lysine and tryptophan, in corn infested with P. truncatus. Infested corn stored for up to 90 d also had decreased energy content, ash content, ether extract, and increased nitrogen concentration (Torreblanca et al. 1983). Changes in quality-assessment criteria including seed moisture content, seed fat acidity value (FAV), germination, microfloral infection, and dust production for infested corn are provided by Demianyk & Sinha (1987).

### Bioenergetics

No data presently exist describing the flow of energy from infested stored corn through the developmental stages of P. truncatus. I present an overview giving a general understanding of bioenergetic concepts.

The acquisition of energy is a primary objective in the search for nutrition. Energy is defined as the ability to do work, and the performance of internal work is a necessity for maintenance of the living state. Thus, to an organism, energy is the means of continuing and expanding life; the means of maintenance, growth, and reproduction (Wiegert 1968). All organisms must acquire energy for metabolic work, and this energy in turn is taken by consumers as organic food. This flow of food or energy among individuals and populations is one factor binding them together in a community, and is an important ecological process in defining interactions in an ecosystem (Duke & Crossley 1975).

Heterotrophs are limited either by the amount of energy they assimilate or by the amount their predators take. Therefore, knowledge of energy flow through a species or population is important in determining their role in an ecosystem (Edgar 1971). If ecologists can draw from previously-collected data on energetics of the components from various ecosystems to determine their relationships, it would then be possible to estimate all the energy parameters for a species or a population by measuring only one or two. Such an exercise may enable manipulation of ecosystems without damaging or destroying them, a necessity for solving management problems requiring knowledge of how the components of ecosystems interact (Duke & Crossley 1975).

The most important loss of plant production is loss of usable food energy intended for human and livestock consumption. This loss occurs when insect pests infest field crops, stored grain, and their byproducts. Field crops occurring in a manmade ecosystem are affected by herbivorous insects in ways similar to that in natural systems. Stored grain although alive, is unlike photosynthesizing plants, existing in a nonproducing dormant state as a nonrenewable energy source (Campbell & Sinha 1978).

Estimates of loss can range from 1-50% of total production (Sinha & Campbell 1975), depending on the conditions existing within various climatic zones of the world (Campbell et al. 1976). Estimates of potential or actual energy losses are required to develop long-range protection of food from the ravages of major pest insects. The development of energy budgets is intended to help construct energy flow models for food-storage ecosystems, enabling us to predict the magnitude of losses involving a particular species (Campbell et al. 1976).

Terminology used in energetics may vary amongst studies and authors; several commonly-used equations for energy budget expression given by Klekowski et al. (1967) are as follows:

$$C = P + R + FU \quad (1)$$

$$A = P + R \text{ or } R = A - P \quad (2)$$

$$C = A + FU \text{ or } A = C - FU \quad (3)$$

where

C = consumption = total ingested food,

P = production = body growth + exuviae + eggs,

R = respiration = heat loss + energy of maintenance,

FU = rejecta = feces + urinary or other excreted products,

A = assimilation = sum of production and respiration (food utilized);

Petrusewicz (1967) provided an additional equation:

$$MR = NU + C \quad (4)$$

where

MR = material removed,

NU = material not used, or wasted,

C = consumption.

These values are usually expressed as the energy equivalent of the dried mass of each separated material, calculated by completely incinerating a known mass of the material in a calorimeter and measuring the heat energy liberated. Respiration values are usually calculated from equations when the other components are known, or from energy equivalents for oxygen consumption measured using respirometers. The unit of energy is a joule (J), where 4.186 J is equivalent to 1 calorie, the energy required to raise the temperature of 1 g water at 15°C by 1 degree Celsius.

Klekowski et al. (1967) has also expressed energy utilization as ratios, the most common being:

A/C = net assimilation efficiency, or the efficiency of digestion;

P/C = gross production efficiency, the proportion of consumed energy available to be passed to the next trophic level;

P/A = net production efficiency, the efficiency of turning assimilated energy or food into production or living tissue.

Other ratios include R/C or R/A (Randolph et al. 1975) which deal with the ratio of respiration versus consumption or assimilation, and P/R which Wiegert (1968) referred to as a secondary production/respiration ratio. These ratios deal with the amount of energy lost to maintenance which an animal uses before any growth may occur.

Wiegert and Evans (1967) estimated net production efficiencies of 37-47% for insect populations, and Odum et al. (1962) estimated 1.5-3.0% for populations of herbivorous mammals. The higher production efficiencies of insects compared with mammals are due to the low mass-specific metabolic rate, and rapid reproduction and growth characteristics of insects (Bailey & Mukerji 1977). Wiegert & Petersen (1983) listed production efficiencies for stored-product insects slightly lower than those of the majority of species reviewed. These lower efficiencies indicate a higher energy requirement for respiration that may be required to metabolize moisture when feeding on relatively dry grains and products (Fraenkel & Blewett 1944).

Assimilation efficiencies, however, are at most 30% efficient in digesting food for poikilotherms whereas most homeotherms are around 70% efficient (Engelmann 1966). Thus, poikilotherms must consume more energy to gain sufficient nutrition for maintenance and reproductive tasks. Within terrestrial herbivorous insects, a range of assimilation efficiencies exists, with granivorous pests having the highest efficiencies of up to 90%. This high efficiency results partly because lower amounts of rejecta (FU) are produced when feeding on a highly-nutritious food source, namely grain (Campbell et al. 1976), and that by living

within their food, stored-product pests may maximize production whereas foraging herbivorous insects use energy for locomotion and maintenance (respiration) with little being directed into production until a suitable food source is located.

Studies of stored-product insect energetics include those of tenebrionid beetles, I. castaneum (Klekowski et al. 1967, Bowker 1979), Tribolium confusum Jacquelin duVal (Bowker 1979), Cynaesus angustus (Le Conte) (White & Sinha 1987); curculionid weevils, Sitophilus granarius (L.) (Campbell & Sinha 1974, Campbell et al. 1976), S. oryzae (Singh et al. 1976); a bostrichid beetle, R. dominica (Campbell & Sinha 1978); cucujid beetles, Cryptolestes ferrugineus (Stephens) (Campbell & Sinha 1978), Oryzaephilus surinamensis (L.) (White & Sinha 1981); and the moths, Ephestia cautella (Walker) (Sinha et al. 1986) and Plodia interpunctella (Hubner) (Imura & Sinha 1986).

MANUSCRIPT I. Effect of infestation by the larger grain borer, Prostephanus truncatus (Horn), and the lesser grain borer, Rhyzopertha dominica (F.) (Coleoptera: Bostrichidae), on stored corn

## Introduction

Infestation of stored cereals and their byproducts by granivorous insects results in a loss of food energy intended for human and animal consumption. Quantitative data on quality-loss criteria for insect-infested grains permit development of mathematical models for stored-grain ecosystems. Such models may aid in prediction of potential losses caused to grain by these pests (Sinha 1973). Several earlier studies have determined the extent of losses in biochemical and biological quality of infested cereals and oilseeds caused by some stored-product insect species: Hayward (1955) on Trogoderma granarium Everts; Agrawal et al. (1957) on Sitophilus granarius (L.); Sinha (1984) on S. granarius; Imura & Sinha (1984) on S. oryzae (L.) and Sitotroga cerealella (Olivier); and White & Sinha (1980) on Rhyzopertha dominica (F.), Tribolium castaneum (Herbst), and S. oryzae.

The larger grain borer, Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae), is a typical granary pest of farm-stored corn (maize), attacking both whole grains and cobs, before and after harvest (Giles 1975, Golob & Hodges 1982). It is similar to, but slightly larger than another bostrichid beetle, the lesser grain borer, Rhyzopertha dominica, a cosmopolitan pest of stored grains. P. truncatus was once thought to be restricted to Central America (Hodges et al. 1983), but its range now includes the southern United States (Back & Cotton 1940) and northern South America (Cotton & Good 1937). More recently, P. truncatus has been imported into Israel (Calderon & Donahaye 1962), Iraq (Al-Sousi et al. 1970) and the hot, dry Tabora region of Tanzania, where it has

become established (Golob & Hodges 1982). Potential corn losses have been estimated at 534,000 t annually, having a value of US \$83.7 million (Autry & Cutkomp 1982). At present, this species is one of the most serious new stored-product pests (Hodges et al. 1983), extending its distribution into Togo, and most recently, Benin (Krall 1984). All areas of Africa where corn or cassava are grown are now potential breeding grounds.

The interrelations among abiotic and biotic variables of stored corn infested with P. truncatus have not been seriously investigated. In two recent reviews (Wright & Spilman 1983, Hodges 1986), 137 publications on Prostephanus were cited, with only 25 being devoted to control and 30 to biology. Life history and optimum conditions for development have been established (Bell & Watters 1982), as were the effect of grain stability on damage caused by P. truncatus (Cowley et al. 1980), and its ability to damage and breed on several stored-food commodities (Shires 1977).

The purpose of this study was to show how free fatty acids (fat acidity values), dust production, seed moisture content, seed germination, and microfloral levels of stored corn were affected by an infestation of P. truncatus, and to compare these results with those for R. dominica.

### Materials and Methods

The effects of insect infestation and of dockage on stored corn were determined in two identical 20-wk experiments. Data from the two experiments were pooled for reporting and statistical analysis. A

farmer near Winnipeg, Man. supplied the insecticide- and fungicide-free shelled corn, Zea mays L. ('Pioneer 3995', 1983 crop year, graded no. 1 Canada Western) which was harvested at 22-27% moisture content (MC), dried in a batch drier at 66°C to ca. 14% MC, stored for 3 mo in a metal bin, and then at -15°C in the laboratory until required.

In each experiment, 124 bottles of 236-mL capacity were each partially filled with 120 g (170 mL) of corn, at  $13.7 \pm 0.2\%$  MC. The five treatments were: P. truncatus in whole corn, R. dominica in whole corn, whole corn plus dockage, whole corn control, and whole corn cold room (-15°C) control. Five grams (10 mL) of ground corn was added to the corn-plus-dockage treatment to simulate debris from insect feeding without insects. Dockage consisted of grinding whole corn in a Stein mill (model L, Fred Stein Laboratories, Atchison, Kans.) until all particles passed through a no. 10 mesh sieve (aperture, 2 mm). All treatments were stored in a controlled environment chamber at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH for 2 wk to allow moisture equilibration.

For both species, 20 adults (sex ratio ca. 1:1) were placed in each bottle of the appropriate treatment. P. truncatus and R. dominica were obtained from laboratory stock cultures maintained on whole corn and whole wheat, respectively, both at  $27.5 \pm 0.5^\circ\text{C}$  and  $65 \pm 2\%$  RH. Prior to release, all adult beetles were surface-sterilized by immersion in a 0.6% sodium hypochlorite solution for 3 min and rinsed with sterile water three times to remove external fungal contaminants. The adults were then placed on filter paper and allowed to dry; only active adults that had recovered from the treatment were used.

All bottles were sealed with filter paper under a screw-on metal lid with four ventilation holes (1 cm diameter) covered with wire mesh. Tops were wrapped with masking tape to help seal the lids to the jars. All bottles of four treatments were incubated at  $30 \pm 0.5^{\circ}\text{C}$  and  $70 \pm 2\%$  RH; the cold room control was placed at  $-15^{\circ}\text{C}$ . At 2, 5, 8, 11, 14, 17, and 20 wk of storage, four bottles (replicates) from each treatment (excluding cold room control) were examined for adult insect numbers (live plus dead), dust production, moisture content, fat acidity values (FAV), seed germination, and microfloral infection. Cold room controls were analyzed at 2, 11, and 20 wk.

Live and dead adult insects were counted by sifting the contents of each bottle on a no. 10 mesh sieve. The remaining grain was placed on a Berlese funnel for extraction of adults within the corn kernels (Smith 1977), after subsamples were taken for assessing other variables. Any adults found in subsamples removed for other analyses were subsequently added to counts recorded for the extractions. Extracted larvae were not recorded because of unreliable recovery for immatures of these internal seed feeders. Dust weight for each bottle in the infested treatments was measured by drying ( $103^{\circ}\text{C}$  for 4 h) and weighing all debris that passed through a no. 40 mesh sieve (aperture, 0.425 mm). Moisture contents were determined on a wet-weight basis (ASAE method no. S352) after one 6-g sample of corn per bottle was oven dried at  $103^{\circ}\text{C}$  for 72 h (American Society of Agricultural Engineers 1975). Fat acidity values were determined on dried grain retained after moisture determination, following general method AACC 02-01 (American Association of Cereal

Chemists 1962), measured as milligrams of KOH required to neutralize the free fatty acids in 100 g of dry seed, and expressed as a percentage of increase from their initial value (Zeleny 1954).

Microfloral infection and percentage of seeds germinating were determined for each bottle by surface-sterilizing 10 seeds for 3 min in 0.6% sodium hypochlorite solution, rinsing three times in sterile distilled water, thoroughly drying in a laminar flow cabinet, then plating on sterile filter paper soaked with 5.5 mL of sterile distilled water (Wallace & Sinha 1962). An additional microfloral determination on 10 sterilized seeds per bottle was made with filter paper and an aqueous solution of 7.5% (wt/vol) NaCl; this method preferentially estimates infection by fungi of the Aspergillus glaucus group (Mills et al. 1978). Petri dishes containing the seeds were stacked, bagged, and incubated at  $22 \pm 1^\circ\text{C}$  for 1 wk, then microfloral infection on each seed was determined under a stereomicroscope.

Two-way analyses of variance (ANOVA) were performed to compare the data from various treatments. Data were analyzed after the following transformations were made:  $\log_{10} (\underline{x} + 1)$  for adult insect number and seed germination,  $\sqrt{\underline{x}}$  for moisture content and fat acidity value, and  $\sqrt{\underline{x} + 0.5}$  for dust production and microfloral infection.

## Results

**Insect Numbers.** Fig. 1A shows the mean number of live and dead adult beetles observed over 20 wk. P. truncatus and R. dominica populations were significantly different ( $\underline{P} < 0.005$ ), as was the interaction between

each treatment ( $P < 0.01$ ). P. truncatus reached a mean maximum of 880 adults per 120 g corn by week 14, followed by a decline to 800 adults per 120 g corn by week 20. The populations of R. dominica continued to increase throughout the entire 20 wk, reaching 1300 adults per 120 g corn.

**Dust Production.** Both species produced significantly different amounts of dust ( $P < 0.005$ ), with interaction being significant between the treatments ( $P < 0.01$ ) (Fig. 1B). Maximum dust production was  $>30$  g for P. truncatus by week 11, with a subsequent decrease by week 20. Dust production for R. dominica showed a steady increase to  $>14$  g by week 20. P. truncatus produced the most dust, accompanied by a ca. 80% decrease in kernel volume. The majority of kernels were reduced to flinty fragments of hull and endosperm by week 20, though some totally undamaged kernels at the top of the grain mass remained. The R. dominica treatment had progressive dust production, with all kernels having fairly uniform damage after week 11.

**Fat Acidity Values.** The percentage of increase in fat acidity for all treatments was significantly different from that for the cold room control ( $P < 0.005$ ) (Fig. 1C), which had an initial value of 20.23 mg KOH/100 g dry seed. Insect-infested treatments had the highest increases, with up to 410% for R. dominica, and up to 300% for P. truncatus. Initially, FAV increased fastest for P. truncatus until week 11, after which a sharp reduction to a  $<100\%$  increase occurred by week 20. The FAV of the R. dominica treatment peaked at week 14 and then decreased to a 300% increase by week 20. The corn-plus-dockage treatment also

differed significantly from the corn-only control, reaching a 200% increase by week 11 ( $P < 0.005$ ). Interaction was significant between the insect-infested treatments, and between the R. dominica and control treatments ( $P < 0.01$ ).

**Moisture Content.** Both insect species caused a significant difference in seed moisture content over time ( $P < 0.05$ ), with insect-infested treatments also having different moisture contents from those of the uninfested controls ( $P < 0.005$ ) (Fig. 1D). Moisture content of the P. truncatus treatment reached a maximum of 16.5% by week 8, then fell to ca. 15% for the remainder of the experiment. The R. dominica treatment had a steady increase in moisture content over 20 wk. There was no significant difference between the insect-infested treatments, or between the corn-plus-dockage and control treatments, in which moisture content remained near 13% ( $P > 0.05$ ). Interaction was significant between insect-infested treatments ( $P < 0.05$ ), and between the R. dominica and the corn-plus-dockage treatment ( $P < 0.01$ ).

**Germination.** Initial seed germination for all treatments was low for sound corn; the cold-room control treatment maintained germination between 44 and 51% during 20 wk; all other treatments showed a difference in germination over time ( $P < 0.005$ ) (Fig. 2A). Germination of insect-infested corn was significantly different from uninfested corn ( $P < 0.005$ ), R. dominica-infested corn dropping to 0% germination by week 11, and P. truncatus-infested corn reaching ca. 2% by week 20. Germination was different between infested treatments, and between the corn-plus-dockage and corn-only treatments, corn plus dockage having lower germination than clean corn alone ( $P < 0.05$ ).

**Microflora.** Initial infection by Aspergillus glaucus group was ca. 40% for all treatments, and ranged from 41 to 60% over 20 wk for the cold-room control (Fig. 2B). All treatments showed an increase in A. glaucus infection to between 55 and 79% throughout the study, except the P. truncatus treatment, which differed significantly ( $P < 0.05$ ), having a decrease from 60% in week 11 to 25% by week 20. Penicillium infection (Fig. 2C) was similar among treatments ( $P > 0.05$ ). All treatments, excluding cold-room control, however, had significantly different infection levels over time ( $P < 0.005$ ). After week 5, Penicillium infection was minimal, varying between 0 and 12%. Bacterial infection differed significantly from 4 to 23 and 36% for R. dominica and P. truncatus treatments, respectively ( $P < 0.005$ ) (Fig. 2D). P. truncatus-infested corn also showed different bacterial infection levels ( $P < 0.005$ ) from the corn-plus-dockage and corn-only controls; the R. dominica treatment was different from only the corn-plus-dockage treatment ( $P < 0.05$ ).

### Discussion

**Insect Numbers and Dust Production.** The rapid population increase and large quantities of dust produced by P. truncatus indicate extensive feeding and reproduction on the corn. The plateau in insect numbers reached at week 14 was caused by exhaustion of the food supply within the bottles. The decrease in dust production after week 11 indicated that P. truncatus consumed some of the dust that was produced from feeding on kernels. By week 20, most kernels were reduced to small flinty fragments of hull and endosperm. Field studies have documented the

voracity of P. truncatus through its ability to cause weight losses in corn of up to 40% after 6 mo storage in Nicaragua (Giles & Leon 1974), and up to 34% after 3-6 mo storage in Tanzania (Golob & Hodges 1982). By comparison, damage caused over an entire storage season by more common storage pests such as Sitophilus oryzae in Zambia, Sitophilus zeamais in Kenya, and Sitotroga cerealella in Malawi was only 2-6% (Adams 1977), 3-5% (De Lima 1979), and 2-5% (Golob 1981), respectively.

Howard (1984) has shown that P. truncatus prefers softer flour corn cultivars, where it causes more damage and weight loss, and produces more offspring than on the harder flint grain types. This pest also develops more successfully in corn on the cob, which is the traditional storage method of East African farmers (Golob 1984). The recommendation for storing shelled grain as a preliminary step to controlling Prostephanus (Golob 1984) may be less advantageous than originally thought, considering the extent of damage observed in this study.

Some undamaged kernels were found near the surface of the dust, however, suggesting that P. truncatus was incapable of grasping these loose kernels for feeding (Cowley et al. 1980). These seeds contributed to the remaining germination levels observed throughout the 20 wk. The decrease in population at week 20 may have been caused by food depletion, overcrowding, accumulation of toxic nitrogenous byproducts, fungal toxins, or by a combination of two or more of these factors (Demianyk & Sinha 1981). Populations of R. dominica steadily increased throughout the study, surpassing P. truncatus by week 17. Dust production by R. dominica, however, was less than one-half of that for P. truncatus. The

R. dominica population increase could presumably have continued, because an adequate food supply was still available at week 20. The differences in linearity of the two curves in both Fig. 1 A and B were responsible for the significance in interaction between these species for adult populations and dust production.

**Fat Acidity Values.** Fat acidity values, often used as a measure of deterioration in stored grain (Zeleny 1954), were highest for the insect-infested treatments. Insects cause seed damage by feeding, elevate moisture content through accelerated respiration associated with reproductive activity and growth, and produce frass. These changes are likely to create a favorable substrate and environment for the growth of postharvest fungi (Agrawal et al. 1957). Enzymatic activity by fungal metabolism breaks down the fat within the seed to produce free fatty acids (Zeleny 1954). Decreases in FAV of infested treatments after week 11 may result from consumption of the germ and soft portions of the kernel, which have higher fat concentrations (Matz 1969) than the remaining flinty portions. The fast rise and subsequent fall in FAV to near control treatment levels in the P. truncatus treatment was responsible for the significant interaction between the two infested treatments. The rise in FAV of the corn-plus-dockage treatment, above that of the control, may be caused by enzymes released from the ground corn dockage, or by accelerated fungal growth on the dockage causing additional liberation of free fatty acids.

**Moisture Content.** Moisture content of corn kernels increased from an initial level of ca. 13.3% to >16% in the presence of each insect

species. This increase resulted mainly from metabolic moisture produced by the thriving insect populations. Under similar conditions, moisture content of wheat infested with a large S. oryzae population increased to >35% (Sinha 1984). This did not occur when seed was artificially infested with other stored-product beetles and moths (Sinha 1973, Lustig et al. 1977, Demianyk & Sinha 1981), reflecting smaller population sizes and the type of seed damage caused by these species; physiological differences in the metabolic rates of different insect species, and type of microfloral development could also have contributed to moisture fluctuations in seeds. The moisture decrease in the P. truncatus treatment after week 8 is probably related to the presence of hard, flinty fragments, which would not absorb as much moisture as the softer portions of the kernel. Interaction was significant between insect-infested treatments because of this decrease. The steady rise in moisture content of the R. dominica treatment compared with the flat curves of the controls was responsible for the significant interaction between these treatments.

The highly-localized insect populations and elevated moisture contents represented within each bottle may mimic natural pockets of infested grain stored with heterogeneous moisture content. Under natural storage conditions, increased moisture content of the grain and surrounding dust could reduce the safe storage period, after which time serious spoilage can occur (Mills & Sinha 1980).

**Germination.** R. dominica reduced seed germination to 0% by week 11 because it caused some damage to both the germ and endosperm of all kernels. P. truncatus, however, left some kernels untouched, while most

were reduced to fragments. Under heavy natural infestations, therefore, it may be possible to salvage undamaged grain that will germinate for seed use.

Although populations of R. dominica exceeded those of P. truncatus by ca. 50% at 20 wk, the smaller size of R. dominica, and its possible initial difficulty in infiltrating the corn kernels successfully, resulted in less overall damage as measured by dust production. Once R. dominica became established, it increased at about the same rate as P. truncatus, indicating that corn is a suitable diet for both species. A survey of insects in wheat and corn exported from the United States (Storey et al. 1982) revealed the presence of R. dominica in 0.3% of export corn samples, although wheat was the preferred substrate with a 5.6% infestation incidence and higher insect densities per sample.

**Microflora.** The high incidence of fungi of the A. glaucus group in all treatments reflects the initial poor quality of the corn used. This assumption was reinforced by the low initial germination rate of ca. 44%. Although the corn received a high grade when sold, some scorched, shriveled, and cracked kernels, characteristic of overheating during the drying process, were observed. Reduction in initial quality could have caused the low germination, allowing subsequent invasion of microflora. The high incidence of microflora may have also decreased viability of the kernels (Wallace 1973), thereby explaining the germination losses in the dockage and control treatments.

The decrease in A. glaucus infection after week 11 could be caused by fungal feeding by P. truncatus, as has been observed with other storage

beetles (Sinha 1971). This, however, could also be an artifact of the seed sterilizing procedure. After week 11, most plated kernels were highly fragmented. The sterilizing solution could have permeated into the endosperm and hull from the exposed interior, killing most of the microflora present.

It is noteworthy that high populations of P. truncatus did not increase A. glaucus infection above control levels even with increased moisture content during the first 8 wk. Mycotoxin formation has been associated with the presence of A. glaucus and Penicillium spp. in moist corn (Abramson et al. 1985), and has serious health consequences if contaminated grain is used for human or animal consumption (Christensen & Kaufmann 1969). The absence of accelerated fungal growth in infested treatments indicates that corn salvaged from infested stores does not pose an increased risk to possible mycotoxin contamination.

The increase of bacterial infection seemed to have resulted primarily from elevated moisture levels in the insect-infested treatments (Sinha 1984). In the present study, a slight increase in bacterial infection was observed for the corn-plus-dockage and control treatments with moisture contents of no more than 13.7%. The higher oil content of the corn kernels may account for this. All treatments showed some degree of bacterial increase over time, possibly causing a reduction in Penicillium spp. infection by the normal ecological succession occurring in this system (Sinha & Wallace 1965).

This study reveals that P. truncatus and R. dominica are both capable of contributing to increased moisture content and bacterial infections,

and losses in germination and grain mass within stored corn. P. truncatus produced more dust, led to accelerated initial FAV increases, and multiplied faster than R. dominica. These findings are important in understanding the biological interactions that occur within infested grains, and their subsequent deterioration. Aside from the obvious quantitative loss by direct insect feeding, qualitative losses caused by increased free fatty acids, moisture content, and microflora will reduce the number of end uses for the remaining corn. Further studies on the biology of P. truncatus and its effects on quality losses are needed to determine whether infested corn is suitable for human or animal consumption, seeding for production of viable plants, or is a total loss. This will allow us to understand and estimate better the total economical and biological impact of this important pest species.

Fig. 1. (A) Mean number of P. truncatus and R. dominica adults (live and dead) in 120 g corn, (B) mean weight of dust produced in insect-infested corn, (C) mean percentage increase for FAV, and (D) mean moisture content for insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH for 20 wk.

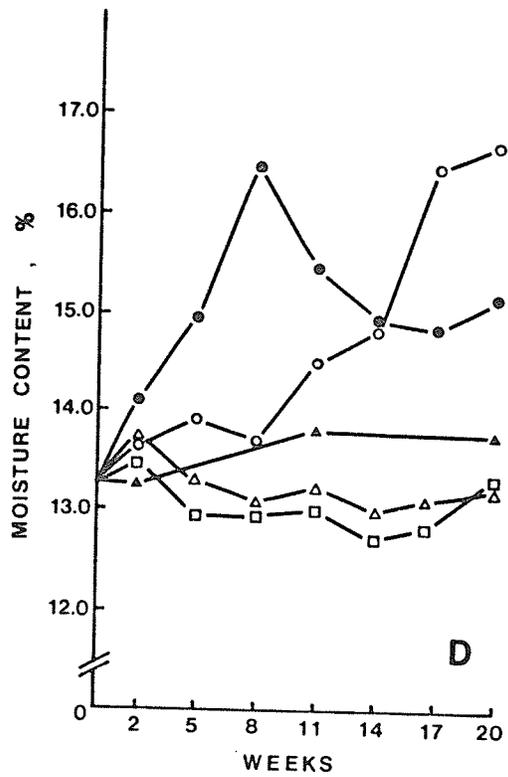
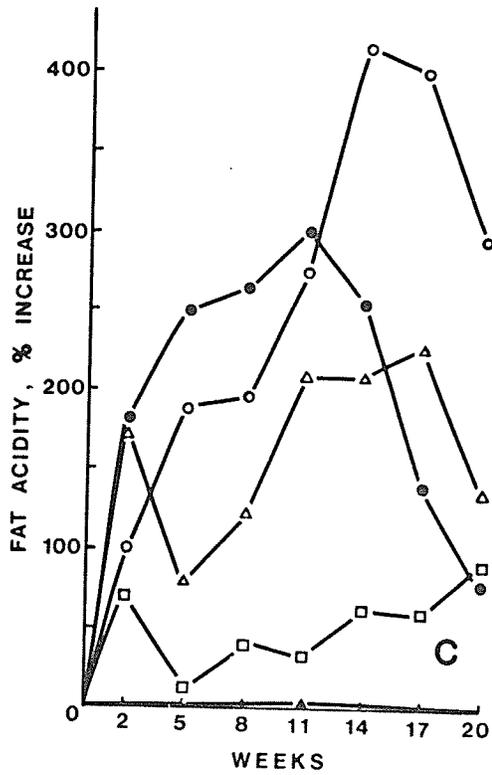
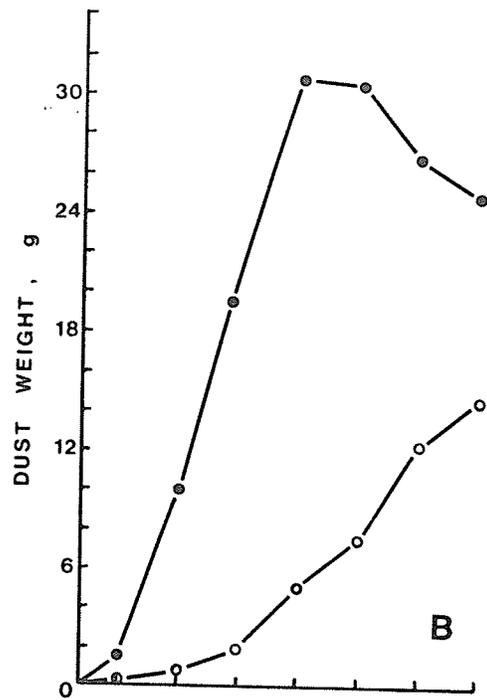
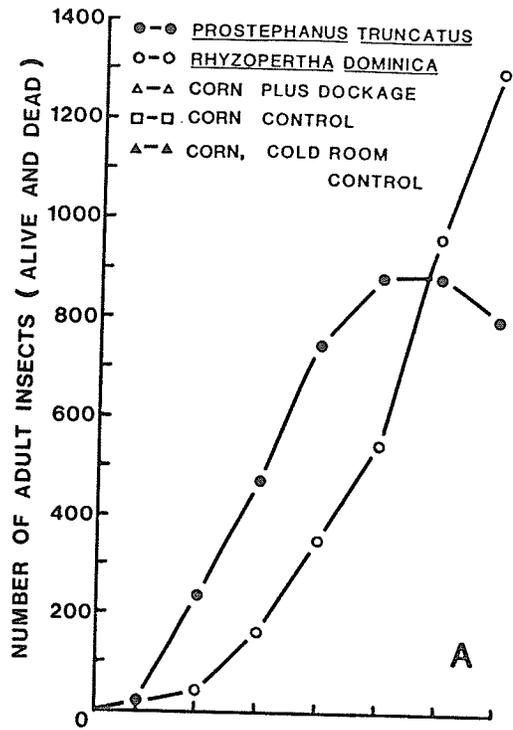
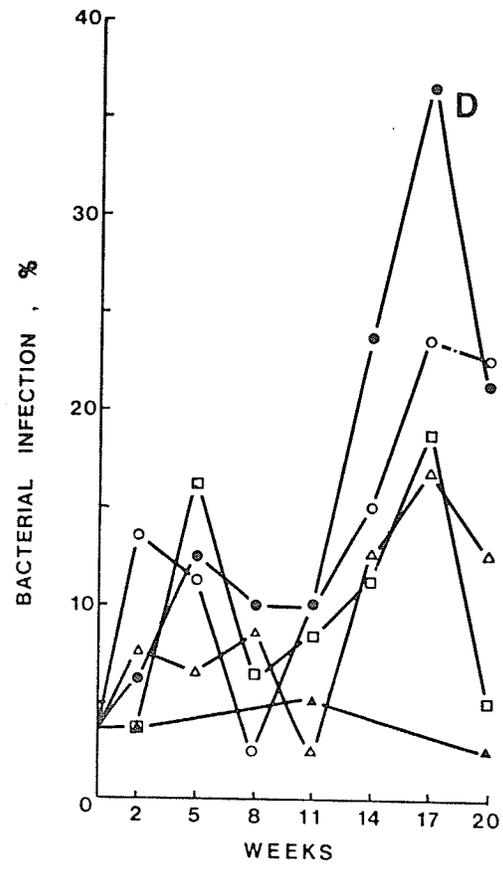
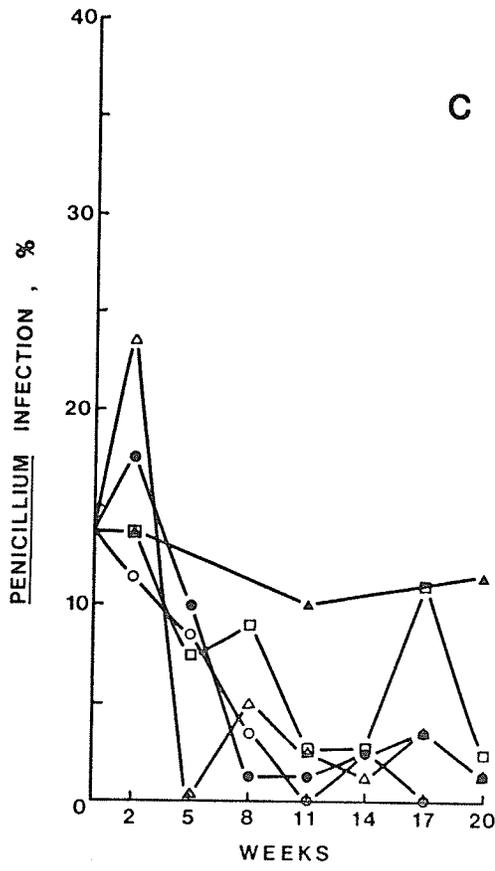
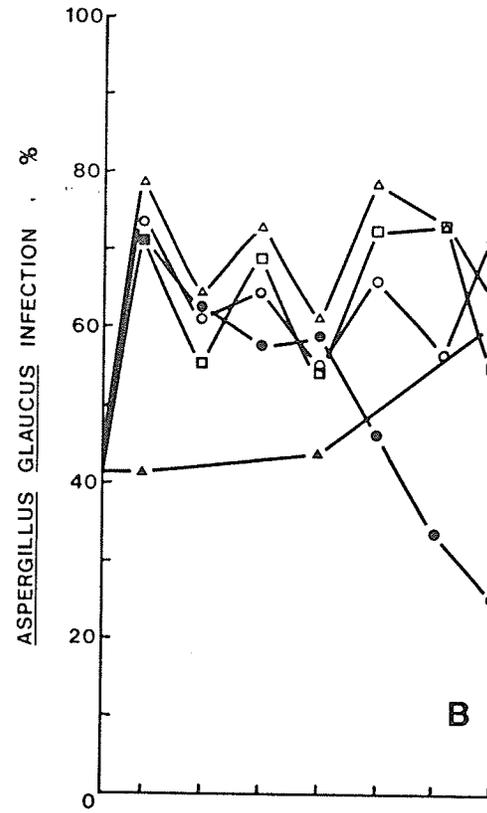
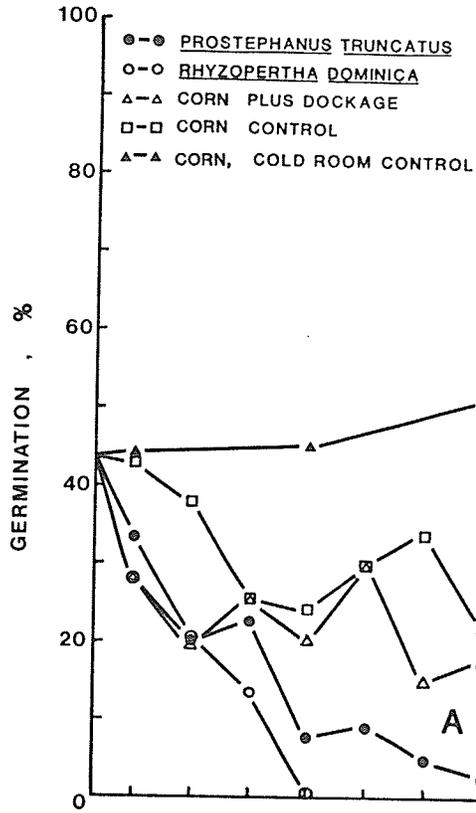


Fig. 2. (A) Mean percentage of germination, (B) mean percentage of fungal infection by Aspergillus glaucus group, (C) mean percentage of fungal infection by Penicillium spp., and (D) mean percentage of bacterial infection for insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH for 20 wk.



MANUSCRIPT II. Bioenergetics of the larger grain borer, Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae), feeding on corn

### Introduction

The larger grain borer, Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae) is a serious granary pest of farm-stored corn (maize), attacking both whole grains and cobs, before and after harvest (Giles 1975, Golob & Hodges 1982). Originating in Central America (Hodges et al. 1983), P. truncatus has now extended its range to northern South America (Cotton & Good 1937) and the southern United States (Back & Cotton 1940). In Africa, it is now established as the most destructive stored-corn pest in the hot, dry Tabora region of Tanzania (Golob & Hodges 1982), and more recently, Togo (Krall 1984). This species is causing corn losses in Tanzania estimated at 534,000 t annually and having a value of US \$83.7 million (Autry & Cutkomp 1982).

A rational strategy of stored-grain management is to minimize the flow rate of energy from grain to pest, or from producer to the higher trophic level of a primary consumer (Imura & Sinha 1986). Thus, long-range protection of stored grain from P. truncatus requires accurate estimates of potential food and energy loss from the crop. Knowing the energy flow from grain through the developmental stages of the insect may help us understand the energy flow within an infested stored-grain ecosystem, and to develop optimal preventive measures (Singh et al. 1976). Moreover, energy budget values of each insect pest species would be useful in comparing the relative amount of damage caused by various species; such values are useful indicators of the maximum amount of energy that can be removed from the food by individual pests. Species bioenergetic data can then be extrapolated to populations of known size and age structure.

Energy budgets have been constructed for several stored-product pests including Tribolium castaneum (Herbst) (Klekowski et al. 1967), Sitophilus granarius (L.) (Campbell et al. 1976), Sitophilus oryzae (L.) (Singh et al. 1976), Rhyzopertha dominica (F.) and Cryptolestes ferrugineus (Stephens) (Campbell & Sinha 1978), Oryzaephilus surinamensis (L.) (White & Sinha 1981), Plodia interpunctella (Hubner) (Imura & Sinha 1986), Ephestia cautella (Walker) (Sinha et al. 1986), and Cynaesus angustus (LeConte) (White & Sinha 1987). Wiegert & Peterson (1983) have provided an excellent review covering earlier bioenergetic data, often collected with different methodologies by many workers, on various insects including some stored-product pests.

Minimal data are available on the quantitative and qualitative losses from stored corn infested by P. truncatus (Adem & Bourges 1981, Torreblanca et al. 1983, Demianyk & Sinha 1987), and to our knowledge, no assessment of energy loss or energy budget has been developed for P. truncatus.

The aim of this study was to quantify the flow of energy from consumed corn through developmental stages of P. truncatus reared under optimal conditions so that its potential for damaging stored corn could be assessed, and to determine the various efficiencies of energy use. Such data used together with life tables and climatic information can be helpful in developing computer simulation models to predict the insect-loss potential for this pest.

## Materials and Methods

**Rearing Procedures and Sample Preparation.** Stock cultures of P. truncatus were maintained at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH in 3.6-liter glass jars containing ca. 1 liter (700 g) of corn, Zea mays L. ('Pioneer 3995').

Undamaged corn kernels of relatively uniform size and shape were selected by hand, surface-sterilized in 0.6% sodium hypochlorite solution for 1 min, washed twice with sterile distilled water, and then dried at room temperature (ca.  $22^{\circ}\text{C}$ ) on filter paper. These kernels were then kept at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH for  $>14$  d to allow the grain to reach moisture equilibrium at these conditions.

Eggs were collected from adult insects placed in a covered plastic dish (155 mm x 40 mm) containing enriched, white wheat flour which had previously been passed through a no. 60 mesh sieve (aperture 0.25 mm). The flour was sieved on a no. 50 mesh sieve (aperture 0.30 mm) every 24 h to yield eggs aged 1 d or less.

Moisture-conditioned kernels were punctured with a no. 22 needle in the middle of the face on the germ side to a depth of one-half the kernel thickness. Kernels were weighed on an electronic microbalance (M3, Mettler Instrumente, Zurich, Switzerland) with a  $1\text{-}\mu\text{g}$  sensitivity. A single egg was carefully placed into the puncture with a soft single-haired brush. Each implanted kernel was placed into a numbered glass vial (15 mm x 45 mm), and sealed with a cotton plug. Fifteen groups of 40 vials containing 30 implanted kernels and 10 nonimplanted control kernels were placed into  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH. The controls were used

to determine the dry mass and moisture content of kernels in each group. An estimate of the initial dry mass of each partially-consumed infested kernel could be obtained using the linear relationship between the wet and dry mass of seeds (Campbell et al. 1976). One group of vials was removed every second day from 4 to 32 d post-implantation and stored at  $-15^{\circ}\text{C}$  for later examination.

To obtain sufficient numbers of insects at various stages of development for respirometric and calorimetric determinations, glass vials (30 mm x 70 mm) were filled with ground corn which had passed a no. 50 mesh sieve. Fifty eggs were added to each vial and then incubated for periods ranging from 4 to 32 d. Insects at various stages of development were removed by sieving; only apparently-undamaged and active individuals were used. Developmental times were similar for insects from eggs implanted into kernels or added to ground corn.

Processing involved removing a group of kernels from cold storage, dissecting them and separating the insect, exuviae, frass, and uneaten part of the kernel. Frass consisted of feces, urinary products, fragmented exuviae, and small particles of chewed but unconsumed kernel which were inseparable.

Head capsule widths (mean  $\pm$  standard error) calculated from original data by Bell & Watters (1982) were used to identify each larval instar. These were:  $L_1$ ,  $0.342 \pm 0.026$ ;  $L_2$ ,  $0.480 \pm 0.090$ ;  $L_3$ ,  $0.715 \pm 0.037$  mm. Larval stage was confirmed where possible by noting the numbers of whole or fragmented exuviae or mandibles. Prepupae, distinguished from third instar larvae by their more elongated, cylindrical shape, were

relatively immobile and nonfeeding. Although the prepupa is a transitional stage, we have considered it as a distinct stage for respiratory and energy budget calculations.

**Gravimetry.** All biological materials, namely, insects, exuviae, food, and byproducts of feeding were placed in numbered, preweighed foil dishes (3 mm x 13 mm), dried at 60°C for 48 h in a vacuum oven (model 281, Fisher Scientific Company, Pittsburgh, Penn.), and weighed. Control and uneaten portions of kernels, other than specimens for calorific determination, were dried at 103°C for 72 h in a circulating air oven (Am. Assoc. Cereal Chem. 1962). All dry, weighed material was placed in glass vials covered with airtight plastic lids and stored in a desiccator containing anhydrous calcium sulfate to eliminate moisture.

**Calorimetry.** Each of the materials, namely, eggs, exuviae, frass, insect bodies, and corn was formed into pellets weighing between 7.878 and 20.570 mg. Energy values for these pellets were determined using a modified Phillipson (1964) nonadiabatic microbomb calorimeter (Gentry-Wiegert Instruments, Aiken, S.C.). The calorimeter was kept at 15±1°C for all determinations and calibrated by igniting benzoic acid (26.468 J·mg<sup>-1</sup>) pellets weighing from 4.107 to 13.066 mg (Phillipson 1964). When biological material was limited to pellets <7 mg, a known weight of benzoic acid was added as a carrier so that combustion would yield sufficient energy to heat the microbomb (Paine 1971). One to eight samples of various materials were placed in small ceramic crucibles, ashed at 600°C for 2 h in a muffle furnace (Blue M Electric Company, Blue Island, Ill.), and then weighed to determine ash content of the incinerated material.

**Respirometry.** Respiration rates were determined for groups of 8-200 individuals of known age in a constant-volume Warburg respirometer (Umbreit et al. 1959) with 25-mL reaction vessels at  $30 \pm 1^\circ\text{C}$ . Oxygen consumption was determined by placing groups of insects in the center well of the reaction vessel, with the side-arm containing 0.2 mL of KOH solution to absorb  $\text{CO}_2$  and provide a  $70 \pm 2\%$  RH (Solomon 1951); 0.2 mL of distilled water instead of KOH was used for determination of  $\text{CO}_2$  production. Consecutive hourly measurements were taken for up to 8 h; metabolic energy consumption was calculated from the amount of  $\text{O}_2$  uptake, using energy equivalents of oxygen for various respiratory quotients ( $\text{RQ} = \text{CO}_2 \text{ produced} / \text{O}_2 \text{ consumed}$ ) (Southwood 1966) (Appendix 11, 12). Insect biomass was vacuum-dried and weighed for determining respiration by weight per individual.

**Energy Budget Calculations.** The cumulative energy budget for P. truncatus was constructed adopting the terminology of Klekowski et al. (1967) and Petruszewicz & Macfadyen (1970). Production (P) during insect development is defined as the change per unit time of the energy content of insect biomass, including the exuviae discarded during each molt. Mass and energy content of insects and exuviae were determined from dissected material. We assumed that the absence of exuviae in the late instars was caused by larval ingestion, therefore, the mean values for exuviae collected for that particular stage were substituted for the missing exuviae and included as part of P; consumed exuviae was also included as part of consumption. Cumulative P from reproduction was estimated because egg production was not directly measured. Lifetime

egg production of an adult female P. truncatus feeding on blocks of kernels and ground corn at 30°C and 70% RH was 430 and 205 eggs, respectively (Bell & Watters 1982). Maximum total egg production was estimated by multiplying the energy content of day-old eggs by the number of eggs produced by females feeding on blocks of kernels.

The energy consumed by P. truncatus was not directly determined because this insect produces frass consisting of finely-chewed uneaten powder (NU), feces and urinary products (FU), and sometimes fragmented exuviae, which cannot be separated. Equations (1),(2), and (3) on page 14 cannot be used to determine the energy budget of P. truncatus because both consumption (C) and rejecta (FU) are unknown. An approximation of C was made by subtracting the energy equivalent of the mass of collected frass from that of the material removed (MR) from kernels. MR is the difference between the corrected original dry mass and the unconsumed remainder of the kernel. Equation (4) on page 15 was modified and expressed as:  $C = MR - \text{Frass}$ , where NU has been replaced by frass (NU plus a portion of FU). This equation, however, underestimates actual C by a portion of FU because some liquid urinary products were absorbed by the uneaten remainder of the kernel. Lifetime adult C was estimated by multiplying adult longevity, which ranges between 45 and 168 d (Sinha & Watters 1985), by the average daily C observed on days 28 to 32, when all dissected individuals were adults with hard, darkened exoskeletons.

Respiration (R) estimates were calculated using respirometry because gravimetric methods require an accurate measure of FU to estimate assimilation (A) and calculate  $R = A - P$  (Wightman 1981). Using P and cumulative R values from Warburg respirometry data, A and P/A were

calculated for each insect life stage. From this, R was then estimated for insect P data obtained from the implanted kernels; P and R were summed to determine A and construct the energy budget.

The efficiency of P. truncatus as an energy converter was calculated using energy values in the following ratios:  $(A/C) \times 100\%$  = cumulative assimilation efficiency;  $(P/C) \times 100\%$  = cumulative gross production efficiency; and  $(P/A) \times 100\%$  = cumulative net production efficiency. All data for individual insects are shown as group performance (by age or instar) for energy transfer in terms of means and standard errors.

## Results

**Distribution of Life Stages and Biomass.** The distribution of each life stage in the same age group is shown in Table 1. The mean development periods for eggs, three larval instars (L<sub>1</sub>-L<sub>3</sub>), prepupae (L<sub>3</sub>pp), and pupae were 3.0, 3.8, 5.1, 4.3, 3.9, and 2.4 d, respectively. The total developmental period from egg to adult ranged from 24 d when 55% of insects had reached the adult stage to 30 d when 100% had done so.

The smallest stage of P. truncatus was the newly-emerged first instar (L<sub>1</sub>) larvae weighing 0.019 mg, and the largest was the prepupae weighing 1.648 mg (Table 2). Mean egg biomass was 0.027 mg; this decreased as eggs developed from 1 to 4 d. The biomass of successive larval instars increased 5-fold; pupae were slightly less than prepupae. Adult biomass was 1.207 mg at 24 d and 1.757 mg at 32 d; the mean biomass of adults 24- to 32-days old was 1.469 mg. The mean mass of exuviae for L<sub>1</sub> was 0.006, L<sub>2</sub> 0.017, and L<sub>3</sub> 0.046 mg.

**Consumption and Energy Determination.** Consumption of corn peaked at 252.01 J when larvae began pupation (Table 2). The highest C occurred during the L<sub>3</sub>-L<sub>3pp</sub> periods. Adult C reached 312.05 J by 32 d, with a mean of 270.13 J for adults of all ages.

Pre-adult stages of P. truncatus varied in energy contents; larvae ranged from 22.0 J·mg<sup>-1</sup> (L<sub>1</sub>) to 25.2 J·mg<sup>-1</sup> (L<sub>2</sub>), the highest energy content of any stage (Table 2). Eggshell, eggs, and pupae contained 16.4, 22.2, and 24.4 J·mg<sup>-1</sup>, respectively. The mean adult energy content was 23.8 J·mg<sup>-1</sup> for all adults. Frass had an energy content of up to 19.0 J·mg<sup>-1</sup>; unconsumed corn and whole corn had 18.4 and 18.9 J·mg<sup>-1</sup>, respectively. Ash contents ranged from 2.6 to 4.4% for developmental and adult stages, 5.1% for exuviae, and 4.3% for frass. The lowest ash contents of 1.4% and 1.7% were found in unconsumed corn and whole corn kernels, respectively.

Cumulative energy losses due to insect development on corn kernels, in terms of MR and frass are shown in Figure 1. MR by L<sub>3</sub> amounted to 539.41 J by 20 d, decreased to 357.22 J during pupation by 24 d, then steadily increased to ca. 970 J by 32 d. The pattern of energy lost to frass accumulation was similar, reaching 309.18 J by 18 d, fluctuating from 128.32 J by 24 d to 619.11 J by 32 d. The equivalent energy content of one corn kernel was 4537.17 J.

**Respiration.** Maximum O<sub>2</sub> used per unit biomass occurred during L<sub>1</sub>, reaching 16.40 μL O<sub>2</sub>·mg<sup>-1</sup>·h<sup>-1</sup>; such high consumption levels remained in subsequent instars (Fig. 2). Respiration rapidly decreased after L<sub>3</sub> and was at its lowest during prepupal and pupal stages, ranging from

4.98 to  $1.92 \mu\text{L O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ . A gradual increase in respiration occurred in adults from 26 to 32 d. The daily respiratory quotient (RQ) for P. truncatus ranged from 0.48 (egg) to 0.87 ( $L_2$ ) with a mean of 0.78 for development of larvae to adults (Fig. 3). The RQ values were used to calculate the energy used to consume  $1 \mu\text{L O}_2$ , and thus, the energy equivalent for  $\text{O}_2$  consumed for respiration (Fig. 3). Mean daily  $\text{O}_2$  consumption for individuals ranged from 0.24 J ( $L_1$ ) to a maximum of 12.43 and 13.63 J per individual ( $L_3$ ) on 18 and 16 d, respectively. Respiration fell to 1.37 J per individual per day during pupation and increased at a steady rate of  $1.48 \text{ J} \cdot \text{d}^{-1}$  for adults from 28-32 d. Cumulative energy lost to respiration was more than 79.13 J per individual ( $L_{3pp}$ ) by 22 d, and 85.13 J for newly-developed adults by 26 d (Fig. 4).

**Energy Budget and Efficiencies of Energy Transfer.** An energy budget for P. truncatus feeding on corn at  $30^\circ\text{C}$ , based on data from Table 2 and Figures 1-4, is presented schematically in Fig. 5. During larval development, P. truncatus removed only 12% (547.27 J) of the corn energy from a kernel containing 4537.17 J. Of this, 252.01 J was estimated for C and 295.26 J was lost through chewed but uneaten food and feces in the form of frass. A total of 118.86 J was assimilated, 78.45 J was required to maintain an individual, and 40.41 J was converted to larval biomass during growth to  $L_{3pp}$ . Exuviae accounted for a 1.25 J loss from the larval biomass. Pupae contained 35.97 J and used 4.76 J from 26-28 d for R during development to adults having biomass equivalent to 31.92 J. Data collected during 28 to 32 d for adults showed that MR accounted for  $127.28 \text{ J} \cdot \text{d}^{-1}$ , with frass and C accounting for 102.22 and  $25.06 \text{ J} \cdot \text{d}^{-1}$ , respectively; R accounted for  $9.56 \text{ J} \cdot \text{d}^{-1}$ .

The mean cumulative assimilation efficiency ( $A/C \times 100\%$ ) for  $L_1$  was 16.2,  $L_2$  26.8,  $L_3$  46.2%, all instars including  $L_{3pp}$ , 47.2%; the efficiency for pupae was 51.8% and adults 56.7%. The mean cumulative gross production efficiency ( $P/C \times 100\%$ ) for  $L_1$  was 8.9,  $L_2$  14.6, and  $L_3$  25.4%; for all instars including  $L_{3pp}$ , 16.0%. Pupae and adult gross production efficiency was 16.3 and 13.4%, respectively. The mean cumulative net production efficiency ( $P/A \times 100\%$ ) for  $L_1$  was 54.7,  $L_2$  54.5, and  $L_3$  55.0%; for all instars including  $L_{3pp}$ , 34.0%. Pupae and adult net production efficiency was 31.5 and 23.6%, respectively. The secondary production/respiration efficiency ( $P/R \times 100\%$ ) for  $L_1$ - $L_3$  ranged from 1.20-1.22.

### Discussion

**Life Stages and Biomass.** The developmental time for *P. truncatus*, between 24 and 30 d under optimum conditions, is similar to that reported by Shires (1979) and Bell & Watters (1982). Differences in developmental time between individuals could be caused partly by differential larval feeding. Upon dissection of kernels for retrieval of larvae, most larvae had burrowed towards and into the germ while a few burrowed into the endosperm. Development of larvae in the nutrient- and energy-rich germ was presumably faster than for larvae which fed on endosperm. Similar results were obtained for *Sitotroga cerealella* (Olivier) feeding on sorghum or corn (Khare & Mills 1968) and wheat (Mills 1965). Some  $L_{3pp}$  individuals dissected from hard, flinty portions of endosperm showed a 6- to 10-d lag in development when compared to those larvae feeding on softer and more-nutritious portions of the kernel.

The energy budgets of P. truncatus and nine other stored-product insects are shown in Table 3. P. truncatus has three instars, the fewest for any stored-product pest, C. angustus has nine, T. castaneum seven, and most of the other species between four and five. Because it has fewer instars, P. truncatus may need to feed more frequently than other species. Consequently, it can develop and molt faster and conserve relatively more of the energy consumed than the other species. Another bostrichid beetle, R. dominica, has one additional instar and a developmental time 2 d longer; its biomass is only about 25% that of P. truncatus. C. angustus, with the most instars, has the longest developmental period.

Mean maximum biomass of P. truncatus was 1.648 mg (L<sub>3pp</sub>), which decreased during metamorphosis to 1.207 and 1.469 mg for new adults, and for all adults, respectively. These biomass losses can be attributed to larval excretion, loss of exuviae during pupal eclosion, and respiration. Subsequent biomass gain in maturing adults resulted from feeding, whether by increased gut contents or production of new tissue; this gain corresponded with the observed increase in MR and frass production. The biomass of P. truncatus was surpassed only by that of the stored-product moths, E. cautella and P. interpunctella, and a beetle, C. angustus. P. truncatus is a relatively large, economically-important stored-product pest; but unlike the nonfeeding moth adults, P. truncatus is a ravenous feeder which causes large energy losses. A further 244.78 J could be produced as biomass from a female laying a maximum of 430 eggs during its life.

**Consumption and Energy Determination.** Energy consumed by larvae of different pest species is relatively proportional to the species biomass. P. interpunctella, E. cautella, and C. angustus have the highest, and O. surinamensis and C. ferrugineus, the lowest C. Consumption by P. truncatus is similar to that of I. castaneum. This value for the latter species is, however, calculated from a substituted efficiency value of another tenebrionid beetle, Tenebrio molitor (L.) (Klekowski et al. 1967). Consumption for P. truncatus larvae is most accurately described as MR minus NU minus a portion of FU; therefore, it underestimates actual C (MR - NU). The inability to accurately estimate FU creates an imbalance in the energy budget for P. truncatus. To produce a balanced energy budget (Fig. 5), the equation  $C = A + FU$  was used to provide an estimate of  $FU = 133.15$  J. But FU already comprises a portion of the frass, therefore, by subtraction the NU portion of frass can be estimated as 162.11 J. The problem of not directly measuring FU produced by P. truncatus results in overestimates of the cumulative assimilation and gross production efficiencies because estimated C is smaller than actual C. A similar problem exists with R. dominica, therefore, because the known value of energy consumed, as calculated by Campbell & Sinha (1978), was less than that for assimilation, MR was substituted for C in Table 3. The C for P. truncatus may actually be closer to that for the weevil, S. granarius.

Estimates of C can further be complicated when portions of frass are consumed. Larvae of a scarab beetle, Aphodes rufipes (L.), feeding in dung, may ingest a given particle of food sometimes twice or more (Holter 1975). Upon dissection of kernels, P. truncatus larvae and adults

had sometimes consumed their own cast exuviae. This observation necessitated the inclusion of the energy equivalent of this exuviae as part of C. Exuviae are often neglected when calculating energy budgets, this part of P being regarded as insignificant (Hagvar 1975). Bailey & Riegert (1973) measured exuviae of grasshopper as 6-11% of secondary production, whereas Klekowski et al. (1967) measured Tribolium larval exuviae as 8.3% of net production. Exuviae of P. truncatus accounted for 3.1% of larval energy production; its energy content was about equal to that of whole corn, therefore, ingestion of exuviae may supplement the insect nutritionally.

During an adult life span of 45-168 d, P. truncatus could consume 1128-4210 J, slightly less than the energy content of one corn kernel. C. angustus could consume 8569 J, or 2.0-, 20.7-, and 27.6-fold more than an adult P. truncatus, R. dominica, or C. ferrugineus, respectively. The shorter developmental periods, greater reproductive rates, and different feeding behaviors make these species far more serious pests, despite the greater C by C. angustus. Although the two moth species have the largest larval C, they do not feed as adults; this fact reduces their overall C relative to other species. The high adult C for I. castaneum is directly related to its longevity of 335 d (Sinha & Watters 1985), about ca. 2x that of the other stored-product pests including P. truncatus (Table 3). The voracious nature of adult P. truncatus contributed to a C of 75% that of I. castaneum.

MR for both P. truncatus and R. dominica gives a more realistic assessment of the food energy lost for human and animal use. The total

energy removed by a P. truncatus larva from a whole kernel was 539 J at 20 d; MR increased again as the adult matured and began feeding (Fig. 1). During pupation, when no feeding occurs, MR and frass production should not change. The observed decrease in MR between 20 and 28 d seems to be an artifact of the dissection procedure; some frass remained hidden in cavities behind hard, cemented secretions of urinary products and dust. These secretions were similar in appearance to surrounding flinty endosperm, consequently, a portion of MR and frass were not measured for energy consumption. The result is a decrease in MR and frass by equal amounts, however, the calculated C value for this period generally follows the trend expected during pupation and adult development. The observed rate of MR for adults during 28-32 d could result in a lifetime energy loss of 5728-21,383 J or the equivalent energy of 4.7 corn kernels; this value was greater than those observed for the other stored-product pests. Frass could account for 4600-17,173 J of this energy loss.

An examination of the energy content of frass may give some insight into its composition. Frass ( $19.0 \text{ J}\cdot\text{mg}^{-1}$ ) was slightly higher in energy than whole corn ( $18.9 \text{ J}\cdot\text{mg}^{-1}$ ) and the remaining unconsumed portions of corn ( $18.4 \text{ J}\cdot\text{mg}^{-1}$ ). This relatively high value may be caused by the apparent feeding preference of P. truncatus for the germ portion of the kernel which has high energy ( $23.4 \text{ J}\cdot\text{mg}^{-1}$ ) (Imura & Sinha 1986). Consequently, P. truncatus produced chewed but uneaten powder of high energy content. The range in energy content of feces for various stored-product pests is relatively low:  $15.9 \text{ J}\cdot\text{mg}^{-1}$  for P.

interpunctella (Imura & Sinha 1986) to  $17.8 \text{ J}\cdot\text{mg}^{-1}$  for S. oryzae (Singh et al. 1976). The high energy content observed for frass may signify that the feces component is minimal, therefore, the estimated C may approximate that of actual C.

Energy contents of last-instar larvae varied from  $22.8$  to  $31 \text{ J}\cdot\text{mg}^{-1}$  for the ten stored-product species; P. truncatus larval energy content was  $24.3 \text{ J}\cdot\text{mg}^{-1}$ , at the lower end of the range. It is possible that the range in energy content for these species is less because of experimental error; one major source being lipid losses during the preparation and pressing of pellets for calorimetry (Wightman 1981). No trend was observed relating the energy content of different species to that of their food (corn and rolled oats versus wheat).

**Respiration.** Most stored-product insects have a pattern of  $\text{O}_2$  uptake similar to that of P. truncatus. The smallest  $\text{L}_1$  larvae had the highest  $\text{O}_2$  consumption rate, and as they grew the metabolic rate per unit mass decreased. Cumulative energy lost through R is loosely related to the relative size of the insect, with large species having greater total respiratory energy losses than small species.

Larval activity and mobility also seem to affect respiratory energy losses. P. truncatus and R. dominica immatures are internal grain feeders with poorly-developed legs. Larvae are confined within their food source where the only movement is by pushing against walls of tunnels created from feeding. Cumulative R values for these species were lower than those for highly-mobile larvae, including lepidopterous caterpillars and flour beetles. Another internal seed feeder, the granary wee-

vil, S. granarius had R losses similar to those for mobile larvae. This high loss seems to be directly related to the high total consumption and low production efficiencies for this species.

Respiration rates may vary somewhat depending on the type of metabolism, as measured by the ratio of volume of CO<sub>2</sub> produced to that of O<sub>2</sub> consumed or respiration quotient (RQ) (Southwood 1966). Brody (1945) has suggested that RQ values of 0.7 and 1.0 involve metabolism of lipids, and carbohydrates, respectively. Egg metabolism for P. truncatus ranged from 0.48 to 0.67, indicating metabolism of lipids. Although these values are lower than the usual range, other metabolic processes may theoretically influence the RQ (Kleiber 1961). Larval RQ was 0.69 to 0.87 indicating metabolism ranging from lipids to carbohydrates. Pupal RQ was ca. 0.82 probably indicating metabolism of proteins during metamorphosis. Maturing pupae, showing some adult characteristics, had an RQ of 0.69, indicating metabolism of stored lipids. This is typical of what most insect pupae utilize (Brody 1945). Adult RQ values ranged from between 0.75-0.80. Studies of RQ determined for immature insects indicate that the respiratory substrate can be a metabolite synthesized inside the body, a food, or both (Wightman 1981). A precise determination of the food type being metabolized was difficult because much variation in RQ occurred on successive days.

Our most probable source of error originates from calculating O<sub>2</sub> consumption and CO<sub>2</sub> production using different individuals of similar age that may have been in slightly different metabolic states. Nevertheless, RQ never appeared to approach 1.0, a level which would have indi-

cated metabolism of pure carbohydrate. Most larvae had fed extensively on lipid-rich germ and to a lesser extent on the endosperm portions of the kernel; this may account for the observed RQ values. Also, corn kernels contain a higher oil content than wheat (Matz 1969), which may yield lower RQ values for corn feeders (P. interpunctella, Imura & Sinha 1986; C. angustus, White & Sinha 1987) than for wheat feeders. Values of RQ for several species feeding on wheat are: R. dominica, adults 0.8, larvae 1.0; C. ferrugineus, adults and larvae 0.8-0.9; S. granarius, adults 0.9, larvae 0.7; S. oryzae, adults 0.76, larvae 1.0.

**Efficiencies of Energy Transfer.** The assimilation efficiency for P. truncatus was lower than that for most stored-product pests. Possible ingestion of exuviae and frass, both containing higher proportions of ash than corn, may have provided a less-digestible food. The voracious feeding habit of P. truncatus may offset, or be required for this lower efficiency of digestion where food may pass through the gut with minimal handling or energy loss. The high energy value of grain kernels compared to that of most vegetation may account for an assimilation efficiency still greater than that calculated for most other herbivorous insects (Wiegert & Petersen 1983). The observed similarities in this efficiency for P. truncatus, R. dominica, and I. castaneum may be erroneous because C is estimated.

The gross production efficiencies of P. truncatus and other stored-product pests are lower than many herbivorous insects, with the exception of O. surinamensis feeding on rolled oats. The crushing of oats may allow efficient and preferential feeding where the insect can select

more-digestible food and ignore portions such as the husk, that yield higher amounts of feces. Cereals are stored at low moisture contents, usually in the range of 12-15%. Stored-product pests feeding on these products may use more energy to acquire water for body fluid by oxidizing digested food (Fraenkel & Blewett 1944).

Net production efficiency was similar for P. truncatus, R. dominica, and O. surinamensis, comparing closely to the overall mean P/A value of 38.8% for 49 nonsocial, herbivorous insects reported by Humphreys (1979). E. cautella had the highest efficiency, whereas the other species had low values similar to net production efficiencies (23%) for herbivorous homeotherms (Schroeder 1981). The higher net efficiencies found for P. truncatus and several other serious stored-product pests may indicate a more-efficient mechanism for producing metabolic moisture. This ability may allow P. truncatus to thrive in the relatively dry regions of Africa by escaping predation, parasitism, and feeding competition in conditions unsuitable for other insects (Hodges 1982).

Using the regression equation of Campbell & Sinha (1978) relating net production efficiency for adults to rate of population increase, we estimate a rate of increase per lunar month of 40. This rate is within the range found for serious stored-product pests (Sinha & Watters 1985) and is substantiated by the serious losses occurring to corn in Africa (Autry & Cutkomp 1982) and Central America (Giles & Leon 1974). Potentially, such a high rate of increase will make P. truncatus a serious pest anywhere corn is grown in sub-tropical and tropical countries. Its

ability to develop on a soft variety of wheat (Shires 1977) and dried cassava (Hodges et al. 1985) may further its range.

Consumption, utilization, allocation of food, and efficiencies of energy transfer often depend on varying physiological, behavioral, and genetic responses of insects, that frequently have nutritional implications (Slansky 1982). White & Sinha (1987) hypothesized that this process mainly occurs through natural selection. Most stored-product insects have genotypes that allow them to show plasticity in habitat selection and feeding behavior. Such adaptability enables them to successfully exploit a wide range of human foods in an environment that is often an unstable, immature ecosystem with high levels of disturbance (Sinha 1973). The narrow range of products infested by P. truncatus may indicate that the species has evolved to become highly selective regarding its food source, or that its gene pool lacks variation to allow expanding its range of foods. Chittenden (1911) believed that edible roots and tubers may form natural breeding sites for P. truncatus, and that its acquired grain-feeding habit is a recent adaptation (Cotton 1963).

P. truncatus is an efficient energy user like several other major stored-product insects. Its feeding preferences are evident from the burrowing of larvae towards the germ in corn kernels, thus maximizing energy intake. Total energy removal and consumption of food destined for human or animal use by this species are high when one considers that a single insect can remove the energy equivalent to five corn kernels.

Bioenergetic studies of stored-product pests to date have been at near-optimal conditions of temperature, relative humidity, and unlimited food supply. Studies under controlled conditions limit comparisons of the nutritional ecology of stored-product insects under less-than-optimum environmental conditions. Nevertheless, P. truncatus seems to have overcome low relative humidity in semi-arid regions by adapting to man-made storages where favorable conditions occur.

Management strategies for conserving stored food based on available energy will likely become more important in the future, especially for areas of chronically-short food supplies. These basic data on bioenergetics, in conjunction with other biological and ecological characteristics, may allow the development of computer simulation models for accurately determining potential losses in corn and cassava in African countries devastated by outbreaks of this highly-specialized pest. A model for S. oryzae infesting wheat has been developed by Hardman (1978) and modified by Longstaff & Cuff (1984), using in part, bioenergetic data determined by Singh et al. (1976). Models may form the basis for formulation of future control strategies by accurately assessing, and predicting quantitative energy losses caused by P. truncatus.

Table 1. Distribution of life stages, in percentages, of *P. truncatus*, reared at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH on stored corn

Age (days)	$\bar{n}$	Egg	L <sub>1</sub>	L <sub>2</sub>	L <sub>3</sub>	L <sub>3pp</sub> (prepupa)	Pupa	Adult
0	30	100						
2	30	100						
4	24		100					
6	23		100					
8	21		62	38				
10	23		13	87				
12	17			41	59			
14	25			20	80			
16	23			9	91			
18	25			4	20	48	28	
20	27				18		82	
22	24						100	
24	18					6	39	55
26	28						14	86
28	32					3	6	91
30	34							100
32	23							100

Table 2. Dry weight, energy values, ash percentage of various components of insect biomass, rejecta, food, and cumulative consumption for *P. truncatus* reared at 30±0.5°C and 70±2% RH on stored corn

Components	Dry wt (mg × 10 <sup>-3</sup> )		Energy content (J·mg <sup>-1</sup> )		J·mg <sup>-1</sup> (ash (Ash) free) %		Cumulative consump- tion (J) Mean ± SE
	<u>n</u>	Mean ± SE	<u>n</u>	Mean ± SE			
Egg (1 d)	20 <sup>a</sup>	28.62 ± 0.24	5	19.89 ± 0.90			
Egg (2 d)	20 <sup>a</sup>	27.71 ± 0.27	7	22.84 ± 0.41			
Egg (4 d)	19 <sup>a</sup>	25.02 ± 0.16	5	23.54 ± 0.35			
Egg (all)	59 <sup>a</sup>	27.15 ± 2.37	17	22.18 ± 0.49	23.01	3.62	
Eggshell	4 <sup>b</sup>	3.36 ± 0.16	1	16.42	16.79	2.18	
L <sub>1</sub> (newly emerged)	4 <sup>b</sup>	18.56 ± 0.80					
L <sub>1</sub> (all)	58	54.69 ± 4.21	8	22.04 ± 1.09	23.01	4.21	13.568± 2.044
L <sub>2</sub>	43	305.33 ± 22.76	8	25.15 ± 0.29	26.31	4.42	53.319±11.221
L <sub>3</sub>	60	1539.98 ± 76.47	8	24.52 ± 0.43	25.41	3.49	146.166±10.733
L <sub>3</sub> (prepupa)	13	1648.46 ± 30.38	8	24.26 ± 0.28	24.90	2.58	252.012±22.019
Pupa	66	1422.03 ± 18.90	9	24.43 ± 0.11	25.26	3.28	200.152± 7.301
Adult (24 d)	10 <sup>c</sup>	1207.40 ± 33.69					
Adult (26 d)	23 <sup>c</sup>	1258.74 ± 39.18	5	23.86 ± 0.29	24.57	2.87	} 231.586±55.040
Adult (28 d)	29 <sup>c</sup>	1387.66 ± 37.97	4	22.92 ± 0.17	23.60	2.88	
Adult (30 d)	34 <sup>c</sup>	1562.62 ± 29.67	4	23.69 ± 0.12	24.31	2.57	} 312.049± 9.121
Adult (32 d)	23 <sup>c</sup>	1756.91 ± 36.94	4	24.77 ± 0.08	25.49	2.83	
Adult (all)	119 <sup>c</sup>	1469.10 ± 23.57	17	23.81 ± 0.18	24.49	2.79	270.127± 6.384
Exuviae (L <sub>1</sub> )	4	6.00 ± 0.82					
Exuviae (L <sub>2</sub> )	3	17.00 ± 2.08					
Exuviae (L <sub>3</sub> )	83	46.08 ± 1.30	3	18.15 ± 0.41	19.13	5.14	

Table 2. (cont'd) Dry weight, energy values, ash percentage of various components of insect biomass, rejecta, food, and cumulative consumption for *P. truncatus* reared at 30±0.5°C and 70±2% RH on stored corn

Components	Dry wt (mg x 10 <sup>-3</sup> )		Energy value				Cumulative consumption (J) Mean ± SE
	<u>n</u>	Mean ± SE	(J·mg <sup>-1</sup> )		J·mg <sup>-1</sup>	(Ash)	
			<u>n</u>	Mean ± SE	(ash free)	(%)	
Whole corn	50	240189.14±7656.91	5	18.89 ± 0.24	19.22	1.70	
Uneaten corn (4-8 d)			5	18.35 ± 0.11	18.63	1.51	
Uneaten corn (10-14 d)			5	18.34 ± 0.08	18.61	1.43	
Uneaten corn (16-24 d)			5	18.65 ± 0.50	18.92	1.37	
Uneaten corn (26-32 d)			5	18.23 ± 0.25	18.49	1.40	
Uneaten corn (all)			20	18.40 ± 0.14	18.67	1.43	
Frass (4-8 d)			3	18.67 ± 0.06	19.28	3.15	
Frass (10-14 d)			5	19.23 ± 0.15	20.11	4.38	
Frass (16-24 d)			5	19.45 ± 0.08	20.50	5.12	
Frass (26-32 d)			5	18.64 ± 0.14	19.34	3.64	
Frass (all)			18	19.03 ± 0.10	19.88	4.27	

<sup>a</sup>Number of groups of 50 individuals weighed.

<sup>b</sup>Number of groups of 20 individuals weighed.

<sup>c</sup>Data for males and females combined.

Table 3. Comparative energy budget data and efficiencies for developmental stages (to last instar or prepupa) of nine stored-product insects and *P. truncatus*, reared under optimal conditions

Species	Diet	No. of instars	Developmental period (d)	Maximum larval dry wt. (mg)	Adult dry wt. (mg)	Cumulative energy lost by respiration during development (J)	Total consumption (J)	Energy content of last instar (J·mg <sup>-1</sup> )	Efficiencies (%)		
									larvae	adults	Net
<i>P. truncatus</i>	corn	3	28	1.648	1.469	78	252a	24.3	47.2	16.0	34.0
<i>R. dominica</i> <sup>b</sup>	wheat	4	30	0.455	0.345	19	62a	25.2	48.7	18.5	38.0
<i>C. angustus</i> <sup>c</sup>	corn	9	64	2.803	2.982	247	598	31.0	55.5	14.7	26.5
<i>I. castaneum</i> <sup>d</sup>	flour, yeast	7	32	1.157	0.955	78	237a	27.2	46.0	13.6	29.4
<i>O. surinamensis</i> <sup>e</sup>	rolled oats	4	22	0.244 <sup>+</sup>	0.296	23	42	22.8	89.9	31.3	34.8
<i>C. ferrugineus</i> <sup>b</sup>	wheat	4	28	0.125	0.107	14	25	25.4	59.2	12.4	21.0
<i>S. granarius</i> <sup>f</sup>	wheat	4	30	1.695	1.226	208	330	27.1	75.9	10.5	18.4

Table 3. (cont'd) Comparative energy budget data and efficiencies for developmental stages (to last instar or prepupa) of nine stored-product insects and *P. truncatus*, reared under optimal conditions

Species	Diet	No. of instars	Developmental period (d)	Maximum larval dry wt. (mg)	Adult dry wt. (mg)	Cumulative energy lost by respiration during development (J)	Total consumption (J)	Energy content of last instar (J·mg <sup>-1</sup> )	Efficiencies (%)		
									larvae	adults	Net
									A/C	P/C	P/A
<i>S. oryzae</i> <sup>g</sup>	wheat	4	28	0.632	0.609	115	130	25.5	77.7	17.4	22.4
<i>E. cauttella</i> <sup>h</sup>	wheat	5	28	2.962	3.108	176	605	23.7	26.1	11.9	48.0
<i>P. interpunctella</i> <sup>i</sup>	corn	5	31	2.758	1.916	280	639	26.2	51.7	12.0	23.4

<sup>a</sup>Consumption not measured directly. <sup>f</sup>Campbell et al. (1976).  
<sup>b</sup>Campbell & Sinha (1978). <sup>g</sup>Singh et al. (1976).  
<sup>c</sup>White & Sinha (1987). <sup>h</sup>Sinha et al. (1986).  
<sup>d</sup>Klekowski et al. (1967). <sup>i</sup>Imura & Sinha (1986).  
<sup>e</sup>White & Sinha (1981).

Fig. 1. Cumulative daily energy budget, in J/individual, for P. truncatus reared at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH on corn. Complete histogram, total material removed from kernel or consumed plus chewed but uneaten kernel; clear histogram, frass composed of chewed but uneaten kernel plus a portion of feces. The line defined as consumption is total material removed minus frass. Respiration values were determined using Warburg respirometry data. Lifestages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult.

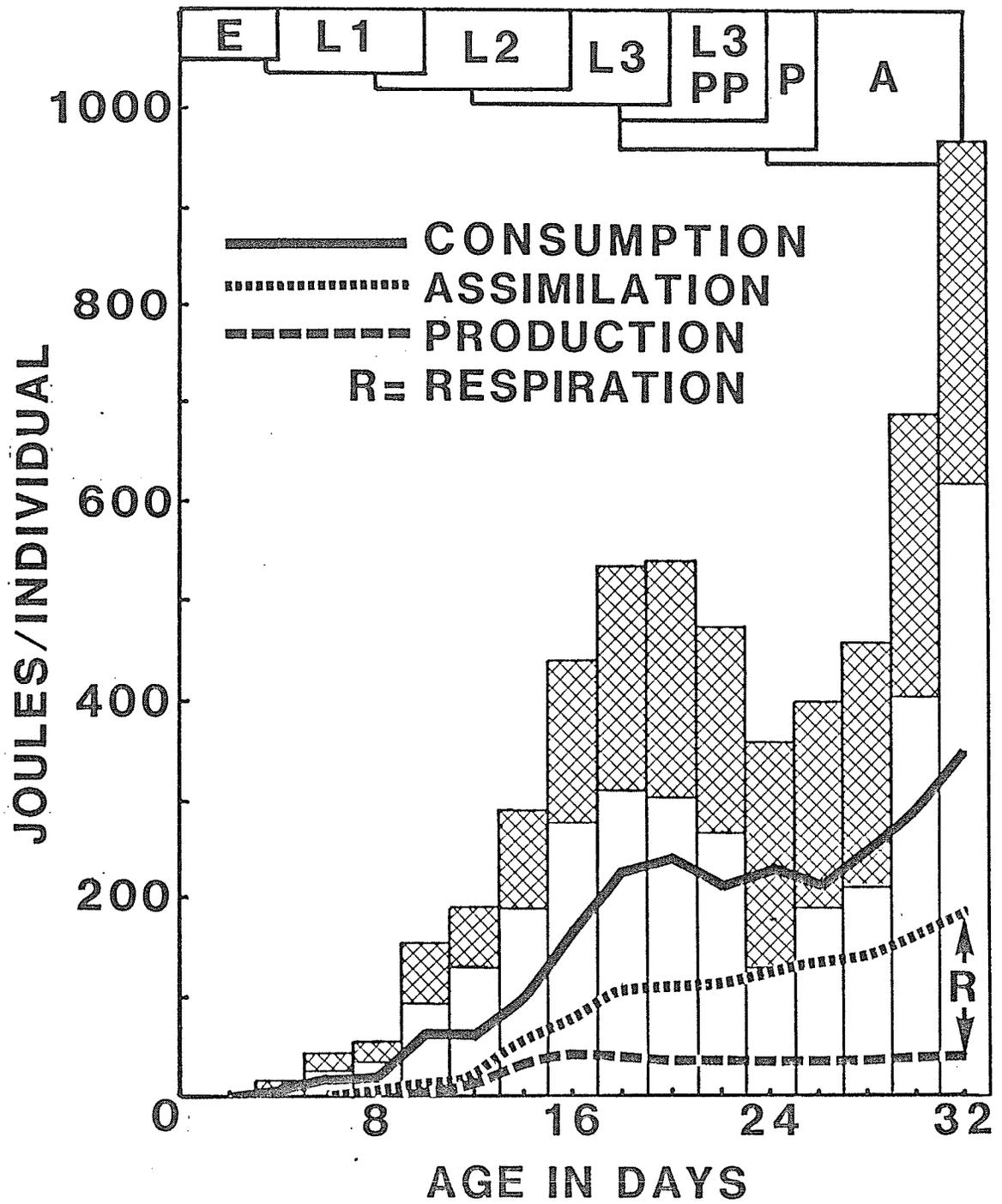


Fig. 2. Mean hourly oxygen consumption and standard error per milligram dry weight for P. truncatus reared at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH on corn. Lifestages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult.

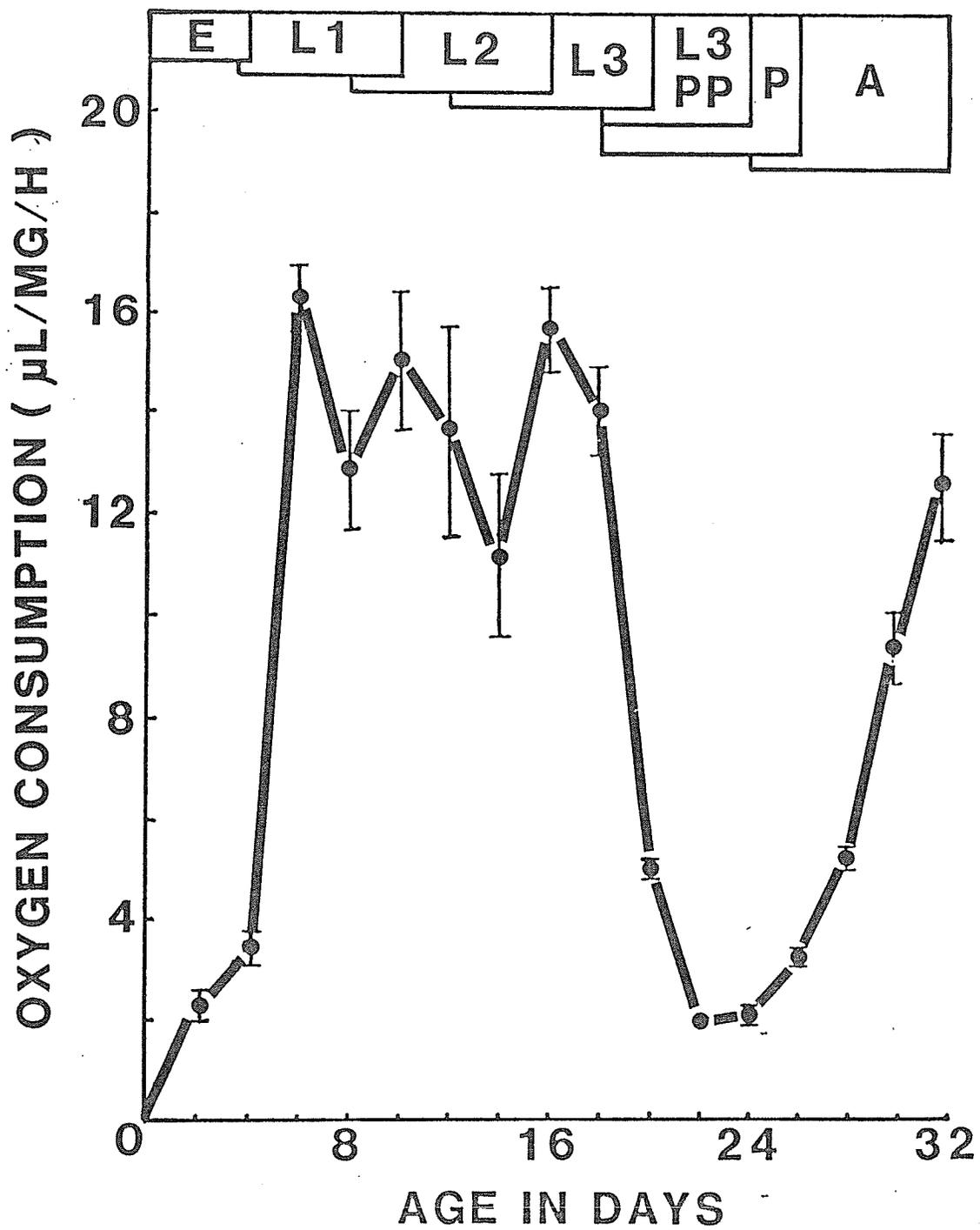


Fig. 3. Mean daily respiration and standard error, in J/individual, and respiratory quotient (RQ) values for P. truncatus reared at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH on corn. Lifestages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult.

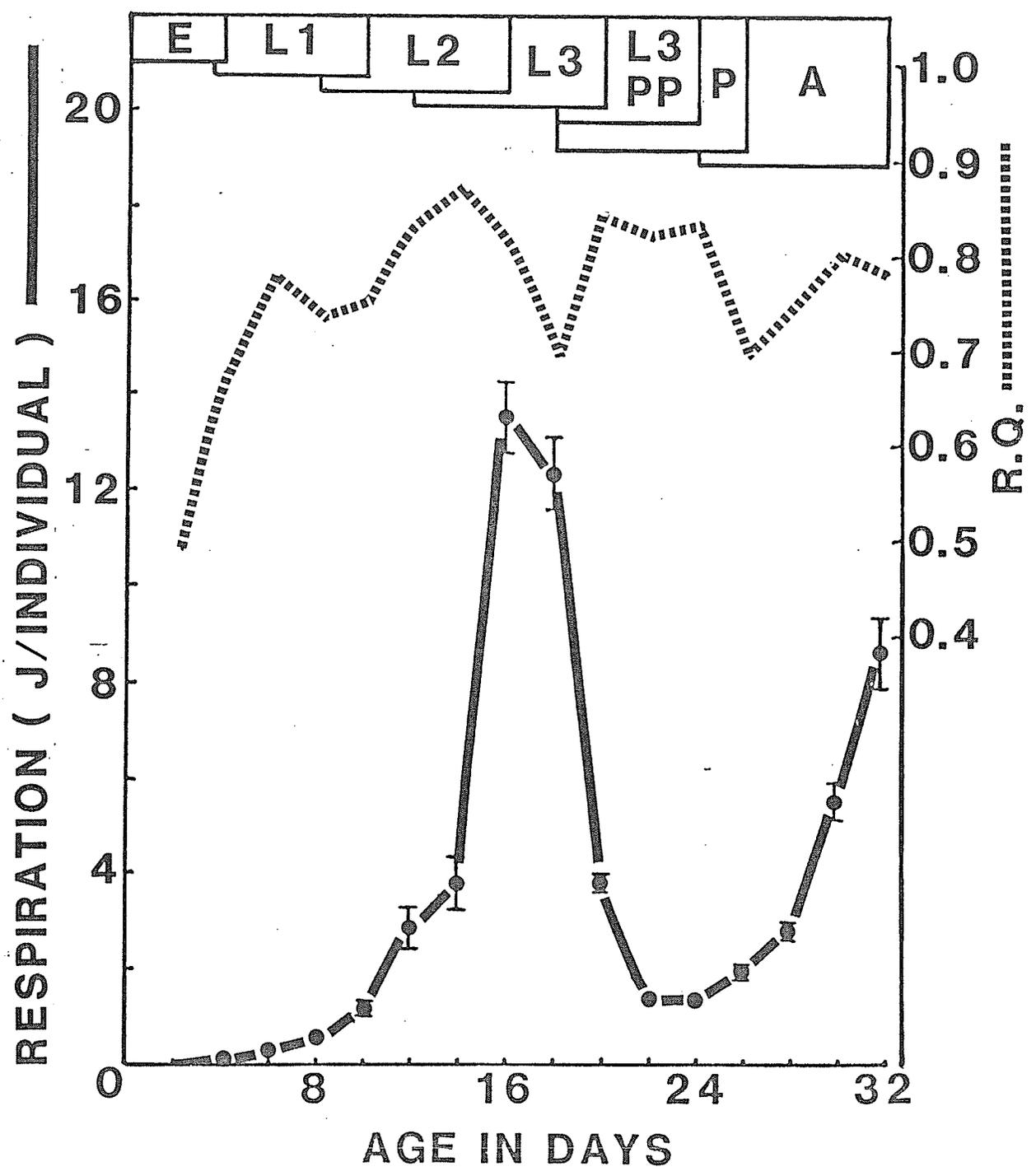


Fig. 4. Cumulative respiration and standard error, in  $\bar{m}$  joules, used by individual P. truncatus during development at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH. Lifestages shown were: E = egg, L1-L3 = 3 larval instars, L3pp = prepupa, P = pupa, A = adult.

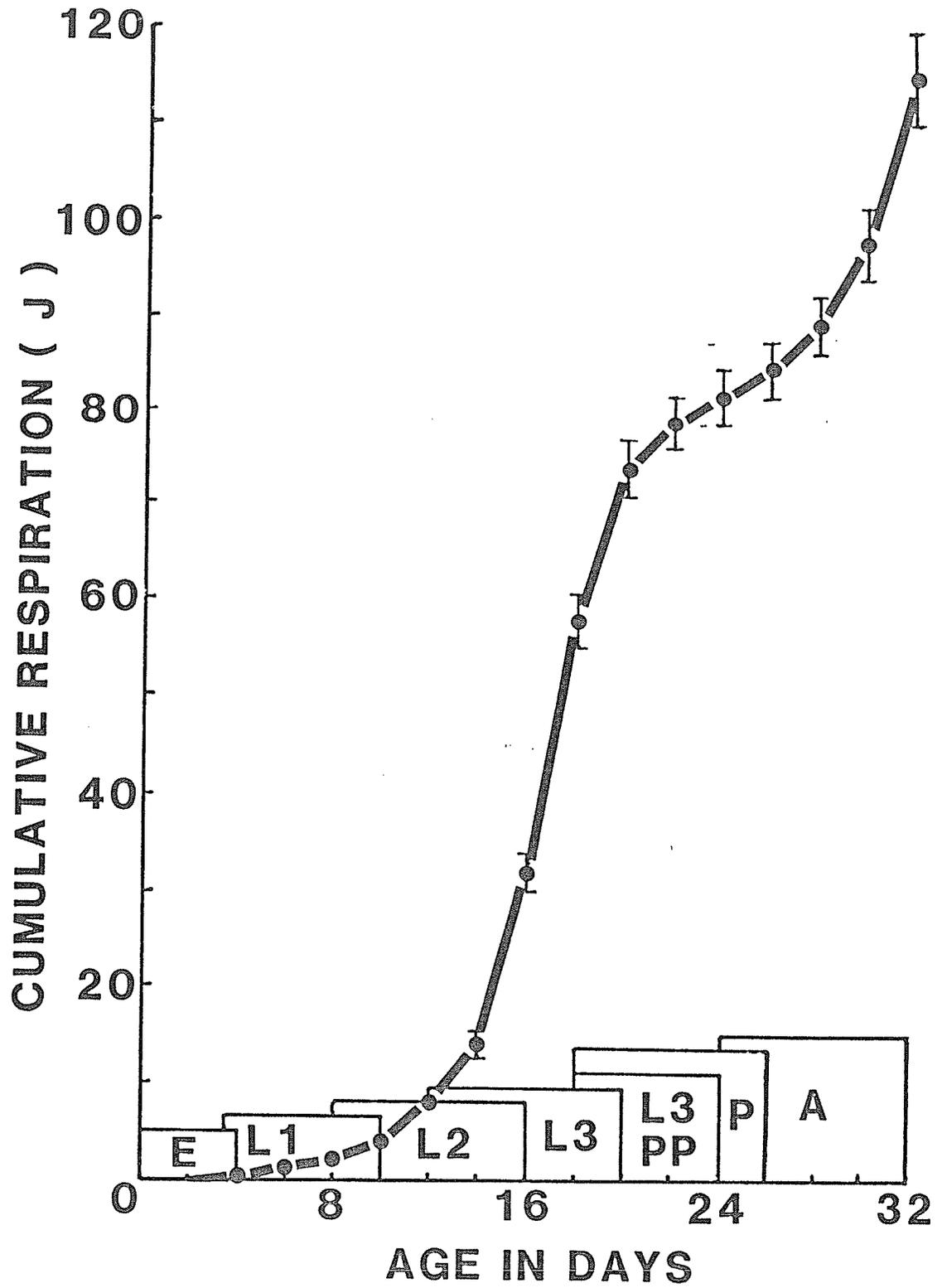
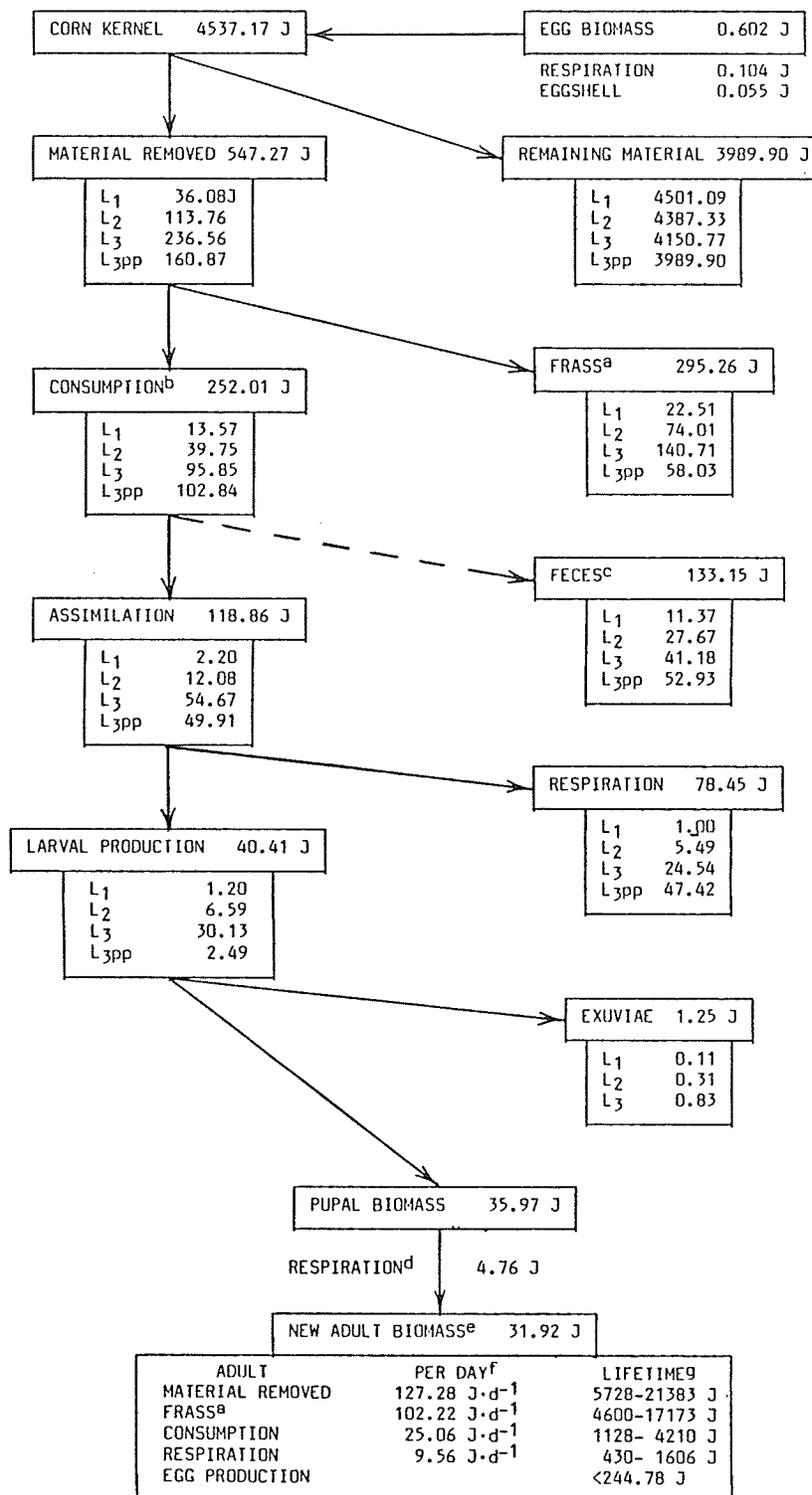


Fig. 5. Energy flow schema showing energy used, in joules, by various stages of P. truncatus reared at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH on corn.

Fig. 5. Energy flow schema showing energy used, in joules, by various stages of *P. truncatus* reared at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH on corn.



<sup>a</sup>Frass = material not used + a portion of feces, therefore, energy representing material not used is less than that shown.

<sup>b</sup>Consumption = material removed - frass.

<sup>c</sup>Feces values are calculated for a balanced budget. Feces was not measured because it comprised an unknown portion of the frass.

<sup>d</sup>Based on cumulative respiration for day 28 minus day 26.

<sup>e</sup>Based on means for new adults from 24 to 28 d.

<sup>f</sup>Based on data for adults from 28 to 32 d.

<sup>g</sup>Extrapolated for an adult longevity of 45-168 d.

## GENERAL DISCUSSION

Previous studies have given an indication of the weight losses that occur in corn infested with P. truncatus (Giles & Leon 1974, Golob & Hodges 1982). In this study, losses have been investigated using criteria most important to human and animal needs, namely, quality and energy. After 14 wk, an initial population of 20 adult P. truncatus produced 880 adults; energy consumed from corn for their development would be ca. 221.76 KJ. Over 5.7 KJ was lost to dust production, however, some energy is unaccounted for because dust was consumed after 11 wk. Total energy content of each bottle containing 120 g of 13.7% MC was estimated at 1.956 MJ; a loss of ca. 80% of the corn over 20 wk represents a loss of 1.565 MJ attributed to both adult and larval boring and feeding.

Similar calculations for R. dominica yield 80.6 KJ lost to adult development, 0.538 MJ total energy removed from 120 g of corn, and 2.664 KJ lost to dust production over 20 wk. These values are conservative estimates of energy losses based on the mean energy content of a corn kernel. P. truncatus preferentially consumed the germ portion of the kernel which contains higher energy than does the endosperm or flinty exterior. This observation is disputed by some studies indicating no preference exists (Hodges 1986), however, under heavy infestation, only portions of flinty endosperm remained which would be of lower energy content and food value than the consumed portions. The voracious nature of P. truncatus caused higher energy losses than larger populations of the cosmopolitan R. dominica, also a dry-tolerant species.

Within this simulated stored-corn ecosystem several interrelations exist, forming a food web through which additional energy is lost besides that removed by the insect pest. Elevated levels of microflora occur when the moisture content of grain exceeds ca. 15% (Christensen & Kaufmann 1969). Infested corn exceeding 16% MC provided a favorable substrate for postharvest fungi and bacterial growth. Although P. truncatus can infest corn stored under dry conditions, its large size, respiration rate, and ability to produce metabolic moisture are sufficient to cause a moisture increase. The large amounts of frass also presented a nutrient-rich energy source for fungal growth. Enzymatic activity by fungal metabolism breaks down the fat within the seed to produce free fatty acids (Zeleny 1954), reflected in elevated fat acidity values. Apparent losses of amino acids (Adem & Bourges 1981) may also contribute to the further deterioration in food value of the corn. These losses in quality may make corn salvaged from infested bulks of limited use for feed. Microfloral infection may further decrease the viability of kernels; lower germination decreases the potential to produce food energy through new crops. The energy lost to microflora, reduced quality, and for future crop production has not been calculated, but must be for determining the full impact of this pest infesting the stored-corn ecosystem.

These interrelations vary under different climatic and storage conditions, and may be quite significant when examining the total energy flow from stored corn. Energy losses to microflora may be very important in Togo, where a tropical, humid climate exists (Trewartha 1968). Traditional storage consists of stacking a cylinder of cobs to form an outer

wall, then the remaining cobs are thrown loosely into the center (Krall 1984). Every layer is sprayed with water to stabilize cobs, and moisture content at initial storage may exceed 25%. The potential energy losses to P. truncatus, microfloral infection, and quality deterioration may be substantially more than those observed in this study. Under more-moist conditions, the additional danger of mycotoxin formation exists, having serious health consequences if contaminated grain is consumed or used as livestock feed.

The cumulative assimilation efficiency of P. truncatus is lower than most stored-product insects, and the gross production efficiency lower than that for herbivorous insects. These efficiencies may be reduced further because the value of C used for their determination is somewhat underestimated. However, these low efficiencies reflect high C and R rates compared to assimilated energy; some of this energy being required to produce metabolic water to overcome desiccation in dry climates. A net production efficiency similar to that of many herbivorous insects offsets the other low efficiencies because P. truncatus utilizes an abundant, highly-nutritious and energy-rich food, and has an efficient mechanism for producing metabolic water. The ability to survive in dry climates, which limits competition by other species, is perhaps the primary reason P. truncatus has become established in dry, corn-producing areas of Africa. New infestations in more humid areas, ie. Togo, may flourish because few predators or parasites exist for this newly-imported pest. Presently, P. truncatus is limited to areas of corn production, however, with new cultivars of soft wheat being introduced, the potential for expanding its range does exist.

Weight or volume decreases in stored grain have traditionally been used by our agro-food industry to measure monetary loss. Visual inspection and grading also play major roles in determining the cash value of a crop, however, these are superficial criteria when examining the nutritional and energetic content of grain. Previous studies of losses to stored-product pests have usually examined one or two quality-loss criteria. While various authors may examine a wide range of criteria, few have attempted to provide a complete view encompassing most major causes of grain deterioration. A thorough understanding of all losses associated with an insect infestation requires understanding and quantifying the interrelations that may exist with other factors that cause spoilage.

This study has attempted to relate several loss-causing variables together, namely, the insect pest, microfloral infection, and moisture content. Deterioration has been further qualified and quantified by examining seed germination, dust production, FAV, and energy flow. Conducting this study under optimum temperature and relative humidity, and limiting populations inside small bottles may have maximized the losses observed. In a large manmade ecosystem of stored corn, however, adult dispersal may limit overcrowding. Interrelations between loss-causing variables could develop differently under optimum insect density, where a higher reproduction rate could occur. The data from this study may aid in developing computer simulation models that would provide a basis for formulating future control strategies by accurately assessing and predicting qualitative, quantitative, and energy losses caused by P. truncatus.

## SUMMARY

1. Interrelations were identified between abiotic and biotic quality-loss variables within a stored-grain ecosystem infested with Prostephanus truncatus. These included usable-energy loss, moisture content, insect population size, FAV, germination, and microfloral infection.
2. P. truncatus produced more dust, led to accelerated FAV increases, and multiplied faster than Rhyzopertha dominica, a cosmopolitan pest of stored grain.
3. Infestations of P. truncatus and R. dominica were both capable of increasing moisture content and bacterial infections, and causing losses in germination and grain mass from corn initially stored at 13.7% MC in small bottles.
4. Energy budget determinations revealed that individual P. truncatus consumed 252 J and required 78 J for respiration during larval development. A further 4.210 KJ could be consumed during a maximum adult life of 168 d.
5. Total energy removed by individual P. truncatus, that energy made unavailable for human or animal consumption, was 547 J during larval development and up to 21.383 KJ or the equivalent energy of 4.7 corn kernels during adult life.
6. Estimated energy loss from 120 g of corn initially infested with 20 Prostephanus adults and stored for 20 wk was 1.565 MJ or ca. 80% of the entire energy content of the corn.

7. The cumulative assimilation efficiency of energy transfer for the developing stages of P. truncatus was 47.2%, lower than for most stored-product pests, but higher than for most herbivorous insects. This efficiency for P. truncatus is similar to that for another bostrichid, R. dominica, and a tenebrionid, Tribolium castaneum.
8. The gross production efficiency for P. truncatus was 16.0%, similar to most stored-product pests. This efficiency for stored-product pests is generally low with respect to those for most herbivorous insects.
9. The net production efficiency for P. truncatus was 34.0%, higher than for most stored-product pests and similar to those for R. dominica, a cucujid, Oryzaephilus surinamensis, and many nonsocial herbivorous insects.
10. Energy losses to microflora and by decreased future crop production must still be quantified before the total impact of P. truncatus infesting corn can be determined.
11. This information has been suggested to form a basis for developing simulation models for accurately assessing and predicting losses caused by P. truncatus.

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APPENDICES

MANUSCRIPT I. Effect of infestation by the larger grain borer, Prostephanus truncatus (Horn), and the lesser grain borer, Rhyzopertha dominica (F.) (Coleoptera: Bostrichidae), on stored corn.

Appendix 1. Mean number and standard error of P. truncatus and R. dominica adults (live and dead) in 120 g corn stored at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>	
	<u>P. truncatus</u>	<u>R. dominica</u>
2	20.0± 0.0	20.0± 0.0
5	241.9±23.9	41.0± 4.2
8	482.4±65.6	176.7±21.8
11	745.9±49.9	357.4±41.3
14	880.4±77.0	557.1±31.7
17	878.5±90.6	982.6±64.7
20	797.0±99.0	1308.4±39.6

<sup>a</sup>Note: n=8

Appendix 2. Mean dust production and standard error (in grams dry weight) by P. truncatus and R. dominica in 120 g corn stored at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>	
	<u>P. truncatus</u>	<u>R. dominica</u>
2	1.92±0.24	0.22±0.02
5	12.28±0.84	0.85±0.04
8	19.90±1.38	2.11±0.22
11	30.87±1.18	4.92±0.39
14	30.83±1.58	7.51±0.39
17	27.24±2.33	12.29±0.65
20	25.49±3.66	14.22±0.63

<sup>a</sup>Note: n=8

Appendix 3. Mean fat acidity value (FAV) and standard error (mg KOH/100 g dry seed) of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at 30±0.5°C and 70±2% RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>				
	<u>P. truncatus</u>	<u>R. dominica</u>	Dockage	Control	Cold Control
2	57.48±13.99	40.09± 5.36	54.52± 8.28	34.02±4.60	20.23±1.69 <sup>b</sup>
5	71.49±19.71	58.46± 9.30	35.93± 3.38	22.08±2.86	
8	73.18± 9.74	59.84±12.81	48.28± 5.86	28.75±3.11	
11	81.03±14.23	75.96±12.10	63.03±11.68	27.60±3.08	20.63±1.18
14	71.54±13.54	104.82±17.09	63.28± 7.85	33.56±4.37	
17	48.53± 6.39	101.12±12.60	67.69± 9.87	32.59±4.28	
20	35.76± 5.76	78.70± 6.03	47.91± 2.93	29.85±3.14	19.28±4.11

<sup>a</sup>Note:  $\bar{n}=8$

<sup>b</sup>Note: initial value 20.23 mg KOH/100 g dry seed;

Appendix 4. Mean moisture content and standard error in percentages of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at  $30 \pm 0.05^\circ\text{C}$  and  $70 \pm 2\%$  RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>				
	<u>P. truncatus</u>	<u>R. dominica</u>	Dockage	Control	Cold Control
2	14.12±0.63	13.63±0.45	13.73±0.54	13.44±0.44	13.25±0.21
5	14.95±0.60	13.93±0.47	13.34±0.41	12.92±0.43	
8	16.45±1.39	13.69±0.48	13.06±0.56	12.91±0.43	
11	15.06±0.65	14.51±0.51	13.22±0.50	12.99±0.55	13.85±0.18
14	14.96±0.59	14.82±0.43	12.96±0.38	12.65±0.39	
17	14.84±0.66	16.47±0.48	13.08±0.39	12.81±0.43	
20	15.10±0.40	16.82±0.52	13.14±0.27	13.26±0.24	13.74±0.06

<sup>a</sup>Note: n=8

Appendix 5. Mean germination and standard error in percentages of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>				
	<u>P. truncatus</u>	<u>R. dominica</u>	Dockage	Control	Cold Control
2	32.5±8.6	28.7±4.8	28.7±8.9	42.5±5.9	43.7±6.2
5	20.0±6.0	20.0±3.8	20.0±4.6	38.7±5.8	
8	22.5±7.0	13.7±6.0	26.2±5.6	25.0±5.7	
11	7.5±3.7	1.2±1.2	20.0±5.3	23.7±7.8	57.5±6.7
14	8.7±4.4	0	30.0±8.2	30.0±6.0	
17	3.7±2.6	0	15.0±4.2	33.7±6.2	
20	2.5±2.5	0	16.2±3.2	21.2±6.4	51.2±6.4

<sup>a</sup>Note: n=8

Appendix 6. Mean percentage and standard error of infection by Aspergillus glaucus group of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>				
	<u>P. truncatus</u>	<u>R. dominica</u>	Dockage	Control	Cold Control
2	71.2± 6.4	72.5± 7.7	78.7± 2.3	71.2± 6.4	41.2±6.4
5	62.5±11.5	61.2± 5.8	70.0± 7.1	55.0±14.5	
8	57.5±11.6	63.7± 9.6	73.7± 9.2	68.7±11.1	
11	58.7±13.8	55.0±13.8	61.2±11.6	53.7±14.7	43.7±6.5
14	46.2±12.2	66.2±13.3	78.7± 9.5	72.5±13.5	
17	33.7± 8.6	56.2±15.0	72.5±11.1	70.0±11.6	
20	25.0± 5.0	71.2±12.2	63.7±13.2	55.0±14.3	60.0±7.8

<sup>a</sup>Note: n=8

Appendix 7. Mean percentage and standard error of infection by Penicillium spp. of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>				
	<u>P. truncatus</u>	<u>R. dominica</u>	Dockage	Control	Cold Control
2	17.5±5.6	11.2±5.8	23.7±9.4	13.7±6.5	13.7±9.8
5	10.0±6.0	8.7±4.0	0	7.5±4.1	
8	1.2±1.2	3.7±2.6	5.0±2.7	8.7±2.3	
11	1.2±1.2	0	2.5±2.5	2.5±2.5	10.0±6.0
14	2.5±2.5	2.5±1.6	1.2±1.2	2.5±2.5	
17	3.7±2.6	0	3.7±1.8	11.2±5.5	
20	1.2±1.2	0	1.2±1.2	2.5±1.6	11.2±6.1

<sup>a</sup>Note: n=8

Appendix 8. Mean percentage and standard error of infection by bacteria of insect-infested corn, uninfested corn and dockage, and uninfested corn control stored at  $30\pm 0.5^{\circ}\text{C}$  and  $70\pm 2\%$  RH for 20 wk.

Storage time (wk)	Treatment <sup>a</sup>				
	<u>P. truncatus</u>	<u>R. dominica</u>	Dockage	Control	Cold Control
2	6.2±3.2	13.7±4.6	7.5±2.5	3.7±2.6	3.7±1.8
5	12.5±3.7	11.2±4.0	6.2±2.6	16.2±4.6	
8	10.0±5.0	2.5±2.5	8.7±5.8	6.2±1.8	
11	10.0±4.2	10.0±3.3	2.5±1.6	8.7±4.4	5.0±3.3
14	23.7±3.2	15.0±4.2	12.5±2.5	11.2±3.0	
17	38.7±4.4	23.7±4.6	16.2±3.2	18.7±4.0	
20	21.2±4.8	22.5±4.5	12.5±4.5	5.0±1.9	2.5±1.6

<sup>a</sup>Note: n=8

MANUSCRIPT II. Bioenergetics of the larger grain borer, Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae), feeding on corn

Appendix 9. Mean energy content and standard error of individual P. truncatus dissected for implanted kernels at  $30 \pm 0.5^\circ\text{C}$  and  $70 \pm 2\%$  RH.

Storage time (days)	$\bar{n}$	Energy content (J)		
0	30	0.569	±	0.030
2	30	0.633	±	0.018
4	24	0.550	±	0.057
6	23	1.448	±	0.214
8	21	1.989	±	0.204
10	23	7.480	±	0.735
12	17	11.367	±	1.353
14	25	32.212	±	3.514
16	23	44.242	±	3.708
18	25	38.136	±	2.090
20	27	35.892	±	0.908
22	24	34.813	±	0.926
24	18	30.714	±	1.287
26	28	30.209	±	1.148
28	32	32.051	±	0.859
30	34	37.027	±	0.722
32	23	43.519	±	0.927

Appendix 10. Mean hourly oxygen consumption and carbon dioxide production with standard errors, and calculated respiratory quotient (RQ) values for P. truncatus as determined by a Warburg respirometer at  $30 \pm 1^\circ\text{C}$ .

Age (days)	Life stage	$\underline{n}^a$	O <sub>2</sub> consumed Mean $\pm$ SE ( $\mu\text{L} \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ )	CO <sub>2</sub> produced Mean $\pm$ SE ( $\mu\text{L} \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ )	RQ <sup>b</sup>
2	egg	8	2.21 $\pm$ 0.31	1.06 $\pm$ 0.27	0.48
4	egg	8	3.39 $\pm$ 0.34	2.28 $\pm$ 0.21	0.67
6	L <sub>1</sub>	8	16.40 $\pm$ 0.69	12.68 $\pm$ 2.00	0.77
8	L <sub>1</sub>	8	12.89 $\pm$ 1.19	9.45 $\pm$ 0.57	0.73
10	L <sub>2</sub>	8	15.11 $\pm$ 1.41	11.29 $\pm$ 0.51	0.75
12	L <sub>2</sub>	8	13.68 $\pm$ 2.14	11.31 $\pm$ 1.05	0.83
14	L <sub>2</sub>	8	11.21 $\pm$ 1.66	9.77 $\pm$ 0.85	0.87
16	L <sub>3</sub>	8	15.76 $\pm$ 0.91	12.76 $\pm$ 0.42	0.81
18	L <sub>3</sub>	8	14.08 $\pm$ 0.87	9.73 $\pm$ 0.41	0.69
20	prepupa	8	4.98 $\pm$ 0.23	4.16 $\pm$ 0.30	0.84
22	pupa	32	1.92 $\pm$ 0.07	1.58 $\pm$ 0.05	0.82
24	pupa	16	2.03 $\pm$ 0.08	1.68 $\pm$ 0.08	0.83
26	pupa <sup>c</sup>	16	3.17 $\pm$ 0.17	2.18 $\pm$ 0.10	0.69
28	adult	16	5.23 $\pm$ 0.24	3.91 $\pm$ 0.20	0.75
30	adult	16	9.42 $\pm$ 0.75	7.58 $\pm$ 0.62	0.80
32	adult	16	12.66 $\pm$ 1.10	9.85 $\pm$ 0.99	0.78

<sup>a</sup>Note:  $\underline{n}$  = number of hourly readings except for 16-18 day L<sub>3</sub> which had 1/2-hourly readings taken; groups of 8-200 individuals were used each day.

<sup>b</sup>Note: RQ = respiratory quotient = CO<sub>2</sub> produced/O<sub>2</sub> consumed.

<sup>c</sup>Note: pupae at this age showed some adult characteristics.

Appendix 11. Energy equivalents of oxygen and carbon dioxide for various respiratory quotient (RQ) values, due to utilization of different proportions of carbohydrates and fats.<sup>a</sup>

R.Q.	Oxygen J/L	Carbon Dioxide J/L	% O <sub>2</sub> consumed by carbohydrate component
0.70	19.62	28.02	0.0
0.75	19.80	26.45	14.7
0.80	20.10	25.12	31.7
0.85	20.36	23.95	48.8
0.90	20.61	22.90	65.9
0.95	20.82	21.96	82.9
1.00	21.13	21.13	100.0

<sup>a</sup>Note: modified from a table in Southwood (1966).

Appendix 12. Energy equivalents of oxygen, in joules, for various respiratory quotient (RQ) values calculated for P. truncatus as determined by a Warburg respirometer at 30±1°C.

Age (days)	Life stage	R.Q.	Energy used for consumption of 1 mL oxygen in joules <sup>a</sup> (J x 10 <sup>-3</sup> )
2	egg	0.48	18.50
4	egg	0.67	19.45
6	L <sub>1</sub>	0.77	19.95
8	L <sub>1</sub>	0.73	19.75
10	L <sub>2</sub>	0.75	19.85
12	L <sub>2</sub>	0.83	20.25
14	L <sub>2</sub>	0.87	20.45
16	L <sub>3</sub>	0.81	20.15
18	L <sub>3</sub>	0.69	19.55
20	prepupa	0.84	20.30
22	pupa	0.82	20.20
24	pupa	0.83	20.25
26	pupa <sup>b</sup>	0.69	19.55
28	adult	0.75	19.85
30	adult	0.80	20.10
32	adult	0.78	20.00

<sup>a</sup>Note: calculated from a regression line for calorific equivalents of oxygen for various values of RQ due to the utilization of different proportions of carbohydrates and fats (Appendix 11).

<sup>b</sup>Note: pupae at this age showed some adult characteristics.

Appendix 13. Mean energy and standard error, in joules, used for respiration, per milligram and per individual *P. truncatus* at  $30 \pm 1^\circ\text{C}$ .

Age (days)	Life stage	O <sub>2</sub> consumption		Energy for respiration <sup>a</sup>	
		( $\mu\text{L}/\text{mg}/\text{h}$ )	( $\mu\text{L}/\text{individual}/\text{h}$ )	( $\text{J}/\text{mg}/\text{h}$ $\times 10^{-3}$ )	( $\text{J}/\text{individual}/\text{h}$ $\times 10^{-3}$ )
2	egg	2.21 $\pm$ 0.31	0.071 $\pm$ 0.010	40.89 $\pm$ 5.74	1.31 $\pm$ 0.19
4	egg	3.39 $\pm$ 0.34	0.097 $\pm$ 0.010	65.94 $\pm$ 6.61	1.89 $\pm$ 0.19
6	L <sub>1</sub>	16.40 $\pm$ 0.69	0.505 $\pm$ 0.021	327.18 $\pm$ 13.77	10.07 $\pm$ 0.42
8	L <sub>1</sub>	12.89 $\pm$ 1.19	1.16 $\pm$ 0.11	254.58 $\pm$ 23.50	22.91 $\pm$ 2.17
10	L <sub>2</sub>	15.11 $\pm$ 1.41	2.42 $\pm$ 0.23	299.93 $\pm$ 27.99	48.04 $\pm$ 4.57
12	L <sub>2</sub>	13.68 $\pm$ 2.14	5.89 $\pm$ 0.92	277.02 $\pm$ 43.34	119.27 $\pm$ 18.63
14	L <sub>2</sub>	11.21 $\pm$ 1.66	7.68 $\pm$ 1.14	229.24 $\pm$ 33.95	157.06 $\pm$ 23.31
16	L <sub>3</sub>	15.76 $\pm$ 0.91	28.19 $\pm$ 1.63	317.56 $\pm$ 18.34	568.03 $\pm$ 32.84
18	L <sub>3</sub>	14.08 $\pm$ 0.87	26.49 $\pm$ 1.64	275.26 $\pm$ 17.01	517.88 $\pm$ 32.06
20	prepupa	4.98 $\pm$ 0.23	7.72 $\pm$ 0.35	101.09 $\pm$ 4.67	156.72 $\pm$ 7.11
22	pupa	1.92 $\pm$ 0.07	2.86 $\pm$ 0.10	38.78 $\pm$ 1.41	57.77 $\pm$ 2.02
24	pupa	2.03 $\pm$ 0.08	2.72 $\pm$ 0.10	41.11 $\pm$ 1.62	55.08 $\pm$ 2.03
26	pupa <sup>b</sup>	3.17 $\pm$ 0.17	4.21 $\pm$ 0.23	61.97 $\pm$ 3.32	82.31 $\pm$ 4.50
28	adult	5.23 $\pm$ 0.24	5.85 $\pm$ 0.26	103.82 $\pm$ 4.76	116.12 $\pm$ 5.16
30	adult	9.42 $\pm$ 0.75	11.54 $\pm$ 0.92	189.34 $\pm$ 15.08	231.95 $\pm$ 18.49
32	adult	12.66 $\pm$ 1.10	18.17 $\pm$ 1.58	253.20 $\pm$ 22.00	363.40 $\pm$ 31.60

<sup>a</sup>Note: calculated by multiplying O<sub>2</sub> consumption by energy used for consumption of 1 mL O<sub>2</sub>.

<sup>b</sup>Note: pupae at this age showed some adult characteristics.