A. VAN HUIS

INTEGRATED PEST MANAGEMENT IN THE SMALL FARMER'S MAIZE CROP IN NICARAGUA

633.15:632.93:632.78(728.5)

A. VAN HUIS

INTEGRATED PEST MANAGEMENT IN THE SMALL FARMER'S MAIZE CROP IN NICARAGUA

Proefschrift
ter verkrijging van de graad
van doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. H. C. van der Plas,
hoogleraar in de organische scheikunde,
in het openbaar te verdedigen
op woensdag 24 juni 1981
des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen.

H. VEENMAN & ZONEN B.V.–WAGENINGEN–1981

ERRATA

p.	6	Table 3	'Production ($\times 10^2$kg)' and 'Yield per ha ($\times 10^2$kg)'
p.	15	line 5	'3 to 4 and 4.5 to 5 metric tons'
		line 6	'2 to 2.5 metric tons'
p.	147	Table 46A	P and Q have been interchanged
p.	204	line 32	'bescherming' i.p.v. 'bestrijding'

A. van Huis

Integrated pest management in the small farmer's maize crop in Nicaragua

Wageningen, 24 juni 1981

STELLINGEN

1.

Het feit, dat de kleine boeren in de tropen technologische pakketten niet in hun geheel accepteren, is eerder een teken van creativiteit dan van achterstand in ontwikkeling.

S. Biggs, 1980. CERES(FAO), **76**: 24–26.

2.

De natuurlijke mortaliteit van plagen in de veelal onbespoten gewassen van de kleine boer in de tropen dient de basis te zijn voor de bestrijdingsprogramma's.

3.

Voordat veranderingen in de produktiemethoden van de kleine boer in de tropen worden aanbevolen, moet zorgvuldig de invloed hiervan op het optreden van plagen worden onderzocht.

4.

Waarborgen voor een optimale toepasbaarheid van het onderzoek naar geïntegreerde bestrijdingsmethoden van plagen zijn een interdisciplinaire werkwijze en een dynamische interactie met de landbouwvoorlichting.

5.

Het succes van toepassing van geïntegreerde bestrijding van plagen in katoen in Nicaragua, zoals beweerd door Falcon en Smith, is niet bewezen.

L. A. Falcon en R. F. Smith, 1973. FAO, AGPP: Misc/8. 92 pp.

6.

Het verdient aanbeveling om criteria op te stellen om de vooruitgang van geïntegreerde bestrijdingsprojekten te meten.

7.

Het verdient aanbeveling internationale normen vast te stellen waaraan de kwalifikatie 'geïntegreerde bestrijding' dient te voldoen.

8.

De Landbouwhogeschool te Wageningen zou in ruimere mate moeten bijdragen aan ontwikkelingssamenwerking dan momenteel het geval is.

9.

Men is zich onvoldoende bewust, dat roken van de vader risico's met zich mee kan brengen voor aangeboren afwijkingen bij zijn nakomelingen, hetzij door een nadelige invloed op de chromosomen van de zaadcel, hetzij door beïnvloeding van het milieu van de moeder tijdens de zwangerschap.

A. VAN HUIS
Integrated pest management in the small farmer's maize crop in Nicaragua
Wageningen, 24 juni 1981

Cover design:
Bolon Dz'acab, the Sky God in the centre of sprouting maize leaves.
Altar at Copan, Honduras. Drawing by W. C. T. Middelplaats. (See Robicsek, F., 1972. Copan, home of the Mayan Gods. The museum of the American Indian Heye Foundation, New York. 166 pp.)

AL CAMPESINO NICARAGÜENSE

CONTENTS

LIST OF ABBREVIATIONS AND SYMBOLS

Statistics

**	highly significant (P (= probability level) $\leqslant$.01)
*	significant (P $\leqslant$.05)
+	weakly significant (P $\leqslant$.10)
NS	not significant (P > .10)

The symbols **, *, +, and NS, used in tables and figures, relate to effects (F-test), differences of contrasts from zero, differences between means, in analysis of variance, regression analysis and other test procedures.

$\arcsin\sqrt{x}$	arcsine transformation (arc in radians) of fraction x
β	standardized regression coefficient (Nie et al., 1975)
df	number of degrees of freedom
r	correlation coefficient (Pearson)
R^2	squared multiple correlation coefficient (proportion of variation explained by the variables in the regression equation; Nie et al., 1975)
RFSC	regression factor structure coefficient (Cooley and Lohnes, 1971)
SD	standard deviation
SPSS	Statistical Package for the Social Sciences; a system of computer programmes (Nie et al., 1975)
V.C.	variation coefficient

Measures

cm	centimetre
ha	hectare
l	litre
m	metre
mm	millimetre
s	seconds

Technical terms

insecticide EC	emulsifiable concentrate
G	granular
SP	soluble powder
a.i.	active ingredients
IPM	Integrated Pest Management

Organizations

BCN	Banco Central de Nicaragua
BNN	Banco Nacional de Nicaragua
CIBC	Commonwealth Institute of Biological Control
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo, El Batán, Mexico
CONAL	Comisión Nacional del Algodón, Managua
DIPSA	Dirección Nacional de Planificación Sectorial Agropecuaria, Managua
FAO	Food and Agriculture Organization of the United Nations, Rome
IAN	Instituto Agrario de Nicaragua
ICTA	Instituto de Ciencia y Tecnología Agrícolas Guatemala
INCEI	Instituto Nacional de Comercio Exterior y Interior, Managua
INTA	Instituto Nicaragüense de Tecnología Agropecuaria
INVIERNO	Instituto Nicaragüense de Bienestar Campesino
IRRI	International Rice Research Institute, Los Baños, Laguna, Philippines
MAG	Ministerio de Agricultura y Ganadería, Managua
OECD	Organization of Economic Cooperation and Development, Paris
PCCMCA	Programa Cooperativo Centroamericana para el Mejoramiento de Cultivos Alimenticios
PNUD	Programa de Naciones Unidas para el Desarrollo (= UNDP)
UNASEC	Unidad de Analysis Sectorial (since 1975: DIPSA)
UNDP	United Nations Development Program, New York
UNEP	United Nations Environmental Program, Nairobi
USA	United States of America

1. GENERAL INTRODUCTION

Maize is an important food crop of the small farmer in Central America. The insect pests considerably reduce yields in this area; however an approach other than chemical control is lacking. In this publication an attempt is made to develop an integrated pest management program, taking into consideration the specific conditions under which the small farmer realizes his production.

The field work on which this book is based, was performed from 1974 to 1979 as a part of an integrated pest management project of the United Nations organizations FAO and UNDP together with the Nicaraguan Agricultural Research Institute INTA. The author was assigned to this project as a FAO entomologist.

1.1. AGRICULTURE IN NICARAGUA

1.1.1. *Agropolitics*

The data that follow pertain to the period before the Sandinistic revolution of July 1979. Although since the revolution considerable efforts have been made to improve the conditions of the small farmer (alphabetizing campaign, land reform by establishing cooperatives on expropriated land), the data reveal the many problems that still have to be solved before the peasant's living conditions will have been improved. The situation is typical for most countries in Latin America.

Nicaragua has an estimated population of 2.32 million inhabitants, 48 per cent of whom live in rural areas; of the economically active population (728,400), 43 per cent are employed in agriculture (BCN, 1978a).

There are two different agricultural sectors. On the one hand a small group of farmers whose activities are directed at products for the export market (cotton, coffee, sugarcane), who farm relatively large land units on the most fertile soils; the crops (except coffee) are grown at a relatively high technological level. On the other hand there is the large group of small farmers, whose products are sold on the domestic market (maize, sorghum, beans, upland rice), who use small land units on marginal soils with few technological inputs (WARNKEN, 1975). The export sector largely depends on the supply of labour by the domestic sector.

As the land resources are mainly in the hands of a limited number of producers (table 1A), a large proportion of the rural population (50 to 75%; WARNKEN, 1975) is unable to achieve an adequate level of production and as a consequence, their income remains insufficient. Therefore this section of the population lives at a minimum subsistence level (table 1B). Physically, socially and economically this group is isolated as the infrastructure is poor (table 1C) and the communities are inadequatly served by public services, such as education (table 1D) and health (table 1E). It is difficult for the small farmer to obtain credit facilities and

TABLE 1. Land tenure, standard of living, infrastructure and health conditions in Nicaragua before 1979.

A. Land tenure

- Number of farmer families, who do not own land: 93,821[1].
- Seventy-six per cent of the land and 51% of the farms are owned, the rest is under some form of land tenancy[2].
- Landless labourers: 33% of the rural population (data 1970; SIECA/FAO, 1974).
- Two per cent of the rural population benefitted directly from the agrarian reform and colonization programmes (accumulated figure 1977[1]).
- Distribution of land property (data 1971; Warnken, 1975):

	Farm sizes (ha)			
	< 4	4–35	> 35	Total
	percentages			
Number of farms	31.7	43.9	24.4	100
Land area	1.0	12.4	86.6	100

B. Standard of living.

- Standard of living of the rural population: 84% low (struggling for subsistence), 14% medium, 4% high (criteria: income, nutrition, housing, health, education; UNASEC, 1974).
- In the Central Interior 21% of the communities benefitted from a minimum total of selected social services (production services, physical accessibility, land tenure, education, health; DIPSA, 1977b).

C. Infrastructure

- Sixty-seven, 10 and 23% of the communities in the country have respectively a low, medium and high ratio of kilometres all-year roads to km^2 (DIPSA, 1977c).

D. Education

- Seventy per cent of the rural population is illiterate (data 1971[3]).

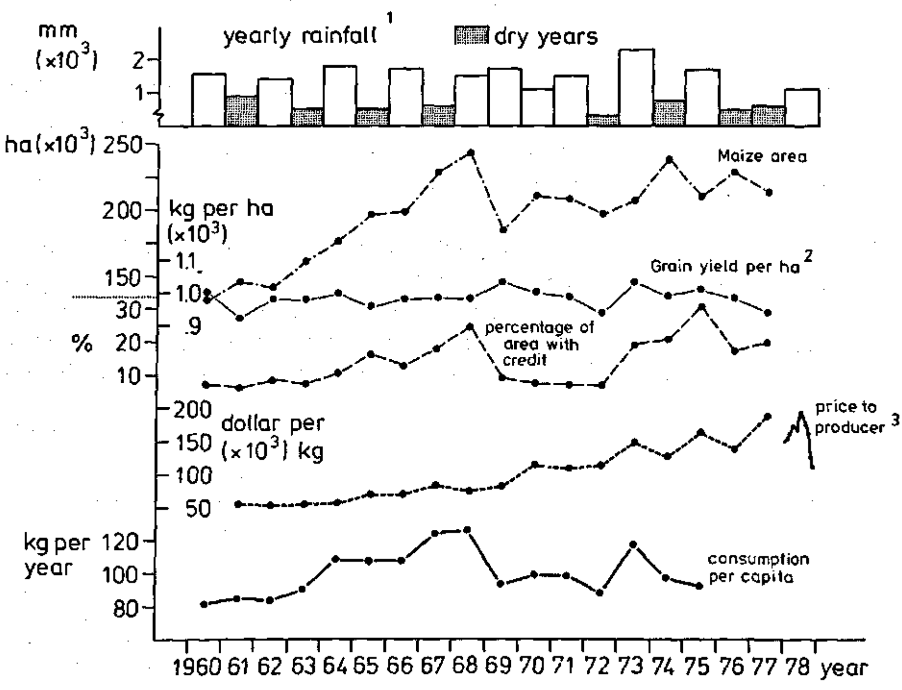
E. Human health

- Sixty per cent of the population shows signs of suffering from malnutrition due to a diet low in calories, proteins and vitamins and 90% suffers from parasites, only 6% has potable water; the health service in rural areas is inadequate, 1 medical doctor and .2 nurses per 5000 inhabitants (UNASEC, 1974).
- Only 10% of the communities in the Central Interior region has health posts (DIPSA, 1977b).

[1] Source: Instituto Agrario de Nicaragua (IAN).
[2] Source: DIPSA, Censo Nacional Agropecuaria, 1971.
[3] Source: Oficina Ejecutiva de Encuestas y Censos (OEDEC).

technical assistance (chapter 1.1.2.). About half of the farms are subject to some form of land tenancy (table 1A). The insecurity of fluctuating market prices and of the threat of droughts are other handicaps (for example, in 1976 and 1977 drought struck many small foodgrain farmers; in 1978 although there were no climatic set-backs the maize market collapsed (fig. 1), notwithstanding the efforts of the 'Instituto Nacional de Comercio Exterior y Interior' (INCEI) to stabilize the market price).

The development of the foodgrain sector must be envisaged within this socio-economic context. For that reason pest management should not be seen as an isolated effort. The degree to which all the above mentioned restrictions can be removed, will greatly help the success of the implementation of integrated pest management (OECD, 1977). In 1975 a national program for foodgrains was started (DIPSA, 1977a). The program formed an integral part of the national plan for rural development 1975–1980 (DIPSA, 1976). New technological inputs (e.g. new varieties, pesticides, fertilizer, irrigation) were introduced to stimulate productivity.



Source: BCN (1976, 1978b).

[1] La Calera, Managua. Source: Servicio Metereológica Nacional, Ministerio de Defensa, Managua.
[2] Refers to area harvested.
[3] Source: INCEI (1978)

FIG. 1. Data on maize production in Nicaragua from 1960 to 1978.

1.1.2. *Agricultural services*[1]

There are three organizations for research, credit and technical assistance in foodgrains (table 2). The 'Instituto Nicaragüense de Tecnologia Agropecuaria' (INTA) is responsible for research and – via their extension department – for technical assistance. The 'Instituto Nicaragüense de Bienestar Campesino' (INVIERNO) provides both credit and technical assistance. The 'Banco Nacional de Nicaragua' (BNN) gives most of the credit and some technical assistance. In 1978 BNN and INTA cooperated, the farmer target groups received credit from BNN and technical assistance from INTA. To extend their investment opportunities both INVIERNO and BNN also operate through farmer groups or groups of the farmer's leaders (each representing about 10 farmers).

In total 62 rural agencies provide technical assistance and credit, and 35 only technical assistance. These agencies are scattered throughout the country, which has about 75,000 foodgrain farmers; the ratio of extentionists to farmers is about 1 to 250. A survey in 1976 done in the Interior Central (fig. 2) showed that 60 per cent of the communities were reached by credit and technical assistance (DIPSA, 1977b). This shows that despite the great efforts the joint capacity of the institutions mentioned proved insufficient to reach all farmers.

1.1.3. *Foodgrain production*

The area, production and yield of export and foodgrain crops are presented in table 3. Cotton and maize are the dominant crops, about 200,000 ha each. Maize is produced throughout the Pacific and Interior regions, but particularly in the Interior Central and Interior South; cotton is produced mainly in the Pacific North (table 4, fig. 2).

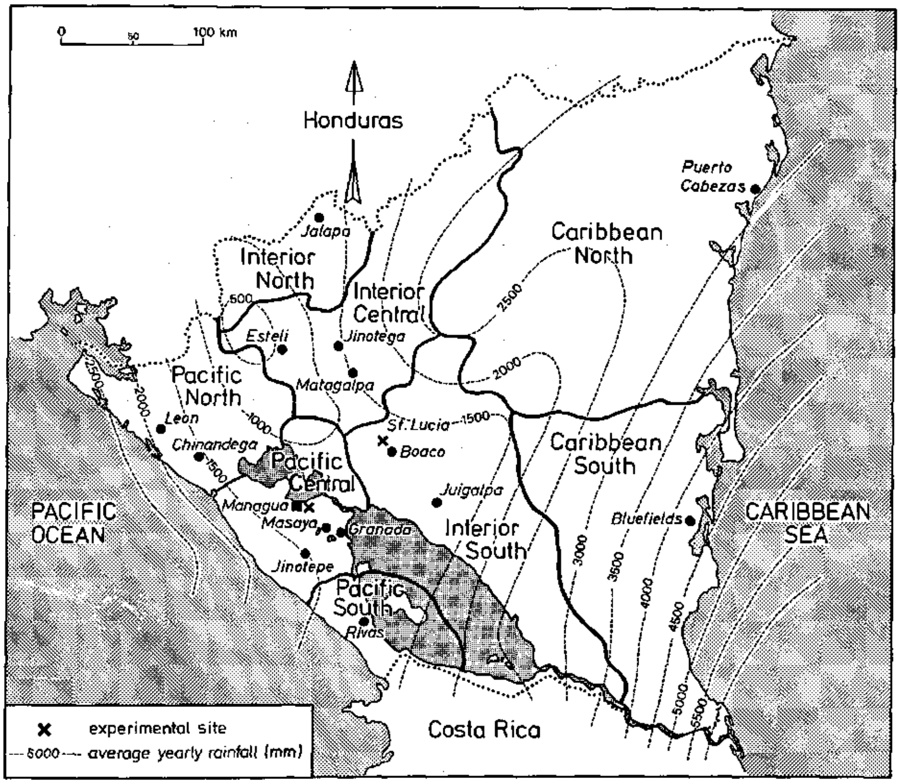
In Nicaragua the rainy season extends from mid-May to early November. During this season maize, beans and sorghum are sown in two successive periods (fig. 3). The maize area in the first growing period is 155,000 ha and in the second 45,000 ha. The acreage of sorghum and beans is much less. Beans are usually sown in the second half of the rainy season as harvesting is safer because there is

TABLE 2. Research, technical assistance and credit facilities in the foodgrain sector in Nicaragua (before July, 1979).

Institutions (semi-autonomous)	Service provided			Number of		Number of extension activities		
	research	technical assistance	credit	rural agencies	extensionists	meetings for farmers	demonstration plots	courses for farmers
INTA (1977)	X	X		35	147	–	9819	–
INVIERNO (1975/76)		X	X	5	91	2796	82	1
BNN (1977)		X	X	60	60	314	103	78

Source: BNN (1978), INTA (1978), INVIERNO (1977).

[1]) Before July 1979



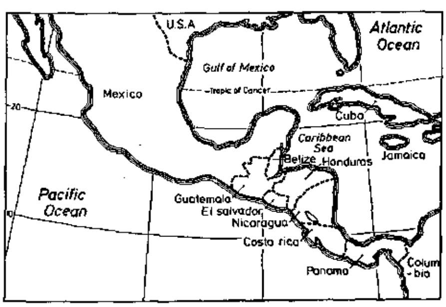


FIG. 2. Map of Nicaragua: production regions (see also table 4).

less danger of rot in the relatively dry months of November and December. The rain available in this second growing period is often not sufficient for maize; therefore beans, vegetables (shorter crop cycle) or sorghum (more drought-resistent) are sown, or the land is left fallow. The intercropping of maize with either beans or sorghum is common practice (no statistical data are available).

The maize area harvested increased from 150,000 ha in 1960 to 200,000 ha in 1965 and has since fluctuated at this level (fig. 1). It represents about 16 per cent of the total maize area in Central America (table 5). Maize yields in Nicaragua are low in comparison to the neighbouring countries El Salvador and Costa Rica

TABLE 3. Production indicators for export crops and foodgrains in Nicaragua (1977).

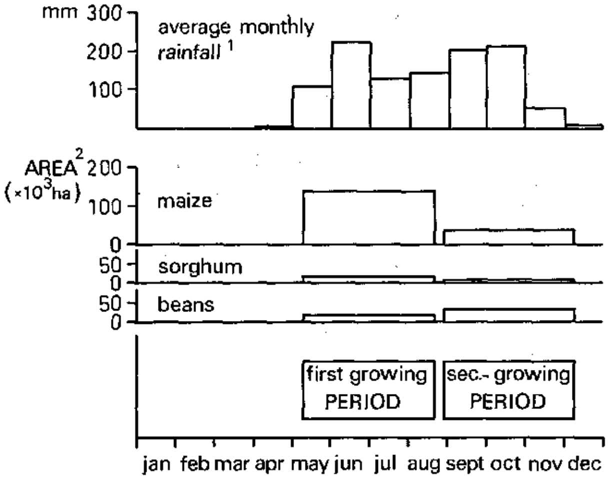
Crops	Area ($\times 10^3$ ha)	Production ($\times 10^3$ kg)	Price to producer (dollar per 10^3 kg)	Yield per ha ($\times 10^3$ kg)	Average farm size[1] (ha)
Export crops					
seed cotton	212	1,417	1,087	6.6	33.3
coffee	84	541	3,439	6.4	6.1
sugarcane	42	25,424	11.02	611	8.4
Foodgrains					
maize	212	1,788	157.5	8.4	2.5
sorghum	44	422	141.7	9.7	2.3
beans	62	406	346.4	6.6	1.3
rice	28	546	315.0	19.3	4.4

Source: BCN, 1978a.
[1]Source: DIPSA, Encuesta de Granos Básicos, 1973/74.

TABLE 4. Number of farms and areas under maize and cotton per production region in Nicaragua.

Production regions[1]		Maize		Cotton[2]	
		Number of farms	Area (ha)	Number of farms	Area (ha)
			($\times 10^3$)		
Republic		102.5	181.0	5.9	219.2
			percentages		
Pacific	North	13	12	95	83
	Central	21	15	5	16
	South	6	4		
Interior	North	11	10		
	Central	29	29		
	South	20	30	0	1
Total		100	100	100	100

Source: DIPSA, Encuesta de Granos Básicos, 1973/74.
[1]See figure 2.
[2]Source: CONAL (data 1977/78).



[1]Las Mercedes, Managua (1958–1977). Source: Servicio Metereológica Nacional, Ministerio de Defensa, Managua.
[2]Source: DIPSA, Encuesta Nacional de Granos Básicos 1973/1974.

FIG. 3. Average monthly rainfall and area sown with foodgrains per growing period in Nicaragua.

(table 5). This indicates that there are seed varieties and cultural practices present in Central America which should make it possible to increase grain yields. In Nicaragua only 12 per cent of the farmers used improved seeds, 8 per cent applied fertilizers and 8 per cent insecticides (data 1974: DIPSA, 1977a; see also table 6). Only 20 per cent of the total maize area benefitted from credit (fig. 1).

About 30 per cent of the maize area is sown on farms of between .7 and 3.5 ha, these farms represent more than 40 per cent of the farms growing maize (table 7). Yield increases with farm size (table 7), which may partly be due to the fact that

TABLE 5. Area and average maize yields in Nicaragua and other countries.

Country		Maize area (× 10^3 ha) 1975–1977	Grain yield (kg ha^{-1}) 1969–1971	Grain yield (kg ha^{-1}) 1975–1977
U.S.A.		28,167	5,164	5,546
Mexico		6,955	1,218	1,221
Columbia		608	1,251	1,291
Guatemala	(C.A.)[1]	539	1,118	1,315
Honduras	(C.A.)	357	1,117	963
El Salvador	(C.A.)	242	1,671	1,597
Nicaragua	(C.A.)	226	912	908
Panama		79	859	870
Costa Rica	(C.A.)	54	1,123	1,505

Source: FAO, 1978.
[1]C.A. = Central America.

TABLE 6. Use of insecticides in foodgrain crops in Nicaragua (1973–1974).

Production region[1]		Insecticide[2] use		
		fraction (%) of		kg per ha (where applied)
		farms	crop area	
			maize	
Pacific	North	29	34	9.7
	Central	22	38	13.8
	South	14	23	5.0
Interior	North	1.7	2.3	8.4
	Central	3.4	5.8	9.4
	South	6.0	3.6	1.9
Total (= Republic)		10.6	12.1	10.1
			sorghum	
Republic		6.7	41.8[3]	5.2
			beans	
Republic		6.0	9.5	12.8

Source: DIPSA, Encuesta de Granos Básicos, 1973/74.
[1] See figure 2.
[2] Commercial product (similar use per region).
[3] 44 percent of the farms are larger than 70 ha (WARNKEN, 1975); they mainly grow hybrids.

larger farms are situated on the more fertile soils and use more technological inputs. Since 1960 maize yields have remained almost constant (fluctuating between 950 and 1,000 kg per ha, fig. 1). Annual fluctuations in the national production are mainly related to changes in area harvested (fig. 1).

Maize is the staple food, especially in the rural areas. In Nicaragua maize is responsable for 17 per cent of the protein and 24 per cent of the total calorie intake per day (PINEDA, 1978). Only the white endosperm varieties are used for human consumption. Consumption level per capita depends largely on how much is produced annually (fig. 1).

Shortages in maize production, estimated at about 300,000 metric tons per year, meant that maize was imported causing strong price fluctuations. Unless yields can be increased an enlargement of the total maize area by 300,000 ha will be necessary to cover this deficit (UNASEC, 1974). Yield losses caused by insects in the field are estimated at about 20 per cent (McGUIRE and CRANDALL, 1966). Pest control is one of the means available of closing the difference between the actual maize production and consumer needs.

1.1.4. *Small farmers and insecticides*

Insecticides play an important role in pest management. However, great care

TABLE 7. Number of farms producing maize, the maize area, and yield, classified per farm size in Nicaragua.

Farm size classes (ha)	First growing period		Second growing period		Average grain yield per ha[1] (kg)
	Number of farms	Area (ha)	Number of farms	Area (ha)	
	(× 10^3)				
	74.8	140.9	27.7	40.1	
	percentages				
<.7	18	5	23	7	585
.7–3.5	41	27	43	32	653
3.5–7	10	10	8	11	760
7–14	8	8	6	7	767
14–35	11	14	10	15	793
35–70	6	11	5	11	834
70–141	3	10	3	6	890
>141	3	15	2	11	1028
Total	100	100	100	100	

Source: DIPSA, Encuesta de Granos Básicos, 1973/74.
[1] Average of both growing periods.

should be taken in recommending them especially in the case of the small farmer, these chemicals may have severe health, socio-economic and agroecological implications.

Poisoning may easily occur because: 1. the farmer is inexperienced in handling the chemicals (many farmers are not reached by the extension services and label instructions cannot be read due to illiteracy; the instruments that they use for handling chemical products are often spoons and mugs; 2. the lack of a safe place to store the chemicals in the small, overcrowded and low quality houses; 3. a higher toxicity, a lower lethal dose level, due to malnutrition (ALMEIDA, 1978).

The socio-economic position of the small farmer may be aggravated if the purchase of the insecticides and the application equipment (knapsack sprayer) is not fully renumerated because on the one hand climatical crop risks are high and on the other hand inexperience may lead to ineffective use of insecticides. The psychological impact on the farmer of the results of insecticides used on maize to control *Spodoptera frugiperda* (J. E. Smith) is very great, as they are able to see within a few days the dead larvae and the termination of whorl injury. *S. frugiperda* is the major pest of maize in Nicaragua so the farmer will be very tempted to use insecticides if he is able to afford them. However plant injury is often linked too easily with yield loss. This attitude complicates the implementation of a rational control of the insect. In the case of *Diatraea lineolata* (Wlk.), a common stalk borer of maize, the situation is reversed. Many farmers are not even aware that the insect weakens the plant by tunneling the stalk. They only notice the larvae in the ear centre, when removing the husks from the ears.

Agroecological implications are that the rich beneficial fauna that has developed over many years in the absence of insecticides can easily be disrupted by large-scale use of chemicals, creating an insecticide dependent agroecosystem (QUEZADA, 1973). An indication for such a disruption is the high incidence of *S. frugiperda* in maize in the Pacific region possibly due to the many applications of insecticides to cotton. This high level of *S. frugiperda* attack is mainly responsible for the greater use of insecticides on maize in the Pacific plain as compared to the country's Interior (table 6).

For these reasons insecticides should be used rationally and cautiously. This is the aim of integrated pest management which can be defined as:

'A pest management system that, in the context of the associated environment and the population dynamics of the pest species, utilizes all suitable techniques and methods in as compatible a manner as possible and maintains the pest population at levels below those causing economic injury'. (FAO panel of experts on integrated pest control; first session, Rome, 1967.)

Integrated pest management should as much as possible use other than chemical methods taking into account the small farmer's conditions.

1.1.5. *Adaptive research*

Field conditions in research stations are often very different from those prevailing in the majority of the small farms. This includes climatic conditions, soil types, slope of fields and occurrence of beneficial fauna. Research frequently does not take into consideration peasant's agricultural inputs (varieties, fertilizer, herbicides) and the traditional agronomic practices (cropping systems, soil preparation, plant density, weeding). Traditional pest control methods of the small farmer are often ignored, as well as his risk perception, and readiness to control pests and to accept alternative techniques.

The 'Instituto de Ciencia y Tecnología Agrícolas' (ICTA) of Guatemala developed a multi-disciplinary methodology of generating technology for small traditional farmers (HILDEBRAND, 1976). In this model the farmer is not a passive recipient of technology, but actively participates in the research. The model uses the following procedure (WAUGH, 1975).

1. Identifying the problems of the farmer.
2. Identifying and developing technology.
3. Testing of technology at farm level and adapting it to farmer's condition.
4. Evaluating technology, as managed by farmers.
5. Evaluating the acceptance of technology.
6. The general promotion of technology, together with the assurance of availability of inputs and services.

Social scientists are actively involved in this modelling and provide information on the effect of social and economic factors on the potential of increasing farm productivity in a target group.

To make integrated pest management appropriate to small farmer's conditions the peasant's concept of pests (pest knowledge, traditional control methods, agronomic practices related to pest control, risk perception) and the

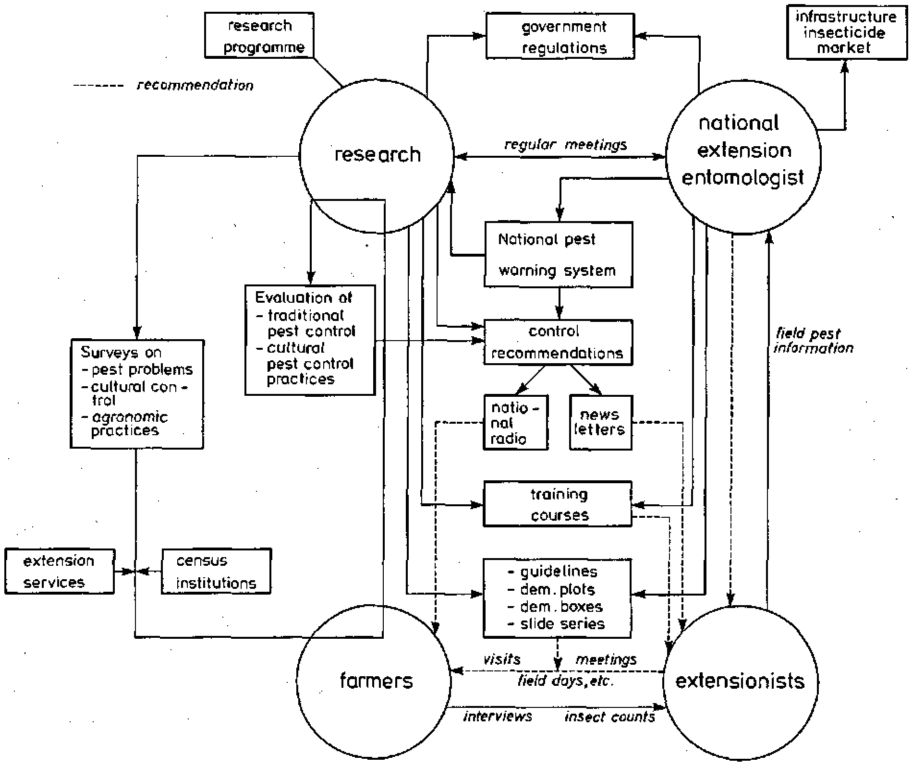


DIAGRAM 1. Development and implementation of integrated pest management in foodgrains. An organizational structure (in use in Nicaragua in 1978).

industrial factors involved in pest management (credit, technical assistance, physical infrastructure, marketing, land tenure) should be known[1].

Integrated pest management can only be appropriate if its implementation in the above mentioned context is considered in the development phase. This can best be achieved when the cooperation between research and extension is close. This cooperation was structured in Nicaragua in 1978 (diagram 1). A national extension entomologist was nominated and a national pest warning system established. It appeared, that 80 per cent of the recommendations on insecticide use given by extensionists during the first growing period in 1978, were incorrect, measured by the criteria of the extension service. This demonstrates the need for pest management training courses for extension workers.

In the development of cropping systems and agronomic practices other criteria than those of pest management may prevail. It should also be recognized that new technological inputs (e.g. new varieties, fertilizer) generally augment potential

[1] For these reasons a socio-technical survey of these factors was carried out in 1978 among 200 foodgrain farmers stratified to farm size in four major producing regions of Nicaragua. Some results are given in this paper. The subject will be dealt with in detail in a separate publication.

loss of yield by pests (OECD, 1977). Therefore a multi-disciplinary approach to the development of integrated pest management for the small farmer is necessary.

1.2. INTEGRATED PEST CONTROL PROJECT[1]

1.2.1. *History*

In Nicaragua the integrated pest management approach was started in cotton in 1967 (PETERSON et al., 1969; FALCON and SMITH, 1973). The excessive use of insecticides in this crop affected human health (intoxications, pesticide residues, cross resistance by the malaria transmitting mosquito, *Anopheles albimanus*), the economy (high production costs, decrease of foreign exchange), the environment (release of non-target pests in cotton and other crops by environmental disruption, pest resistance and resurgence, hazards to wildlife species). These factors have been extensively discussed by FALCON and DAXL (1973).

The Ministry of Agriculture in Nicaragua requested technical assistance from the FAO, as a result the project Nic/70/002 in cotton was started in 1970. The integrated pest management approach has since then been strongly advocated by the 'Proyecto Algodonero de Asistencia Técnica' (PAAT) of the National Bank of Nicaragua (BNN). A comprehensive approach was made involving research, extension and training at all levels. This approach served as a model for the FAO/UNEP Cooperative Global Programme for the development and application of integrated pest control in agriculture (FAO/UNEP, 1975).

Although postponement of the first insecticide applications was accepted (cotton leaf surface area before fruit formation may be reduced up to 50 per cent without economic injury, the regulatory impact of beneficial species is maintained, preventing pest resurgence; see FALCON and SMITH, 1973), no breakthrough in reducing the number of insecticide applications (from 1971 to 1976: 19 to 22)[2] was achieved. The problem was not so much technical, but organizational. PAAT was understaffed, lacked an autonomous status with a national responsibility and judicial power and could not control its own budget.

In 1972 the severe drought and the earthquake that afflicted the country stimulated interest in the socio-economic development of the foodgrain sector. The rural development plan (DIPSA, 1976) was designed to alleviate the constraints mentioned in chapter 1.1.1.. In this context the development and implementation of integrated pest control in foodgrains was included in the extension of project Nic/70/002 in 1974.

1.2.2. *Project activities*

One of the activities the project initiated was collecting local information and literature about the foodgrain pests of Nicaragua. General recommendations

[1] The final report of the project FAO-UNDP/NIC/70/002 recently appeared: FAO/UNDP (1980).
[2] Source: Comision Nacional del Algodon (CONAL), Memorias 1971/76.

were formulated and published (in keeping with a resolution of the plenary meeting of foodgrain research in Central America and Panama, PCCMCA, at San José, Costa Rica, in 1976) as a guideline to the integrated pest control in maize, sorghum and beans (MAG/FAO/PNUD, 1976). The booklet was distributed to the extension services and research departments of all Central American countries and Panama. The issue of the guidelines fulfilled a need, as control recommendations used by the national extension services appeared to be out-dated or deficient (VAN HUIS, 1977). It showed that an integrated pest management program can be drawn up by carefully evaluating and integrating known techniques without previous lengthy and detailed research. BRADER (1979) indicated that in this way effective programmes may be implemented. In 1979 an updated version of the guideline on integrated pest control in beans was published and another for maize and sorghum was prepared and will soon be published (R. DAXL, 1980, pers. communic.).

Integrated pest management is usually adopted under pressure after intensive and indiscriminate use of pesticides has created severe problems, as was the case in cotton. In foodgrains however the use of insecticides was very limited (table 6). The project's approach here was the development of a pest control system appropriate to small farmer's conditions, while avoiding the failures and disasters brought about by a total reliance on chemical pesticides, in an increasing effort to boost food production.

1.2.3. *Research program*

The research concentrated mainly on the two major pests of maize in Nicaragua viz. the whorl defoliator *Spodoptera frugiperda* and the neotropical corn borer, *Diatraea lineolata*. In particular the ecology and economic importance of these lepidopterous pests were studied, taking into account the small farmer's method of farming and his socio-economic conditions.

The ecological studies were carried out on the fields of a small farmer at St. Lucia, a village situated on the border of the Interior South and the Interior Central (fig. 2), both important regions for maize production (table 4). Attention was directed towards the abundance of insect pests in the traditional maize-bean intercropping systems. The frequently occurring system of maize with interjacent weeds was also evaluated. The role of natural enemies (predators and parasites) and rainfall as natural mortality factors of both pests was investigated. Oviposition by the pests was studied in relation to plant development at the experiment station 'La Calera', Managua.

At the same research station experiments on aspects of crop loss assessment were also carried out. Pest damage was studied in relation to plant density and the use of fertilizer. Drought, one of the main limiting factors in maize production, was simulated and its effect on the damage by *S. frugiperda* measured. The sensitivity of the plant at various growth stages to whorl injury by *S. frugiperda* was determined, also by simulating the injury with artificial defoliation. A first approach was made to assess crop loss by *D. lineolata*.

Several chemical control methods appropriate to small farmer's conditions were tested and traditional control methods were evaluated. Prospects of biological and cultural control methods are discussed, as well as plant breeding for insect resistance.

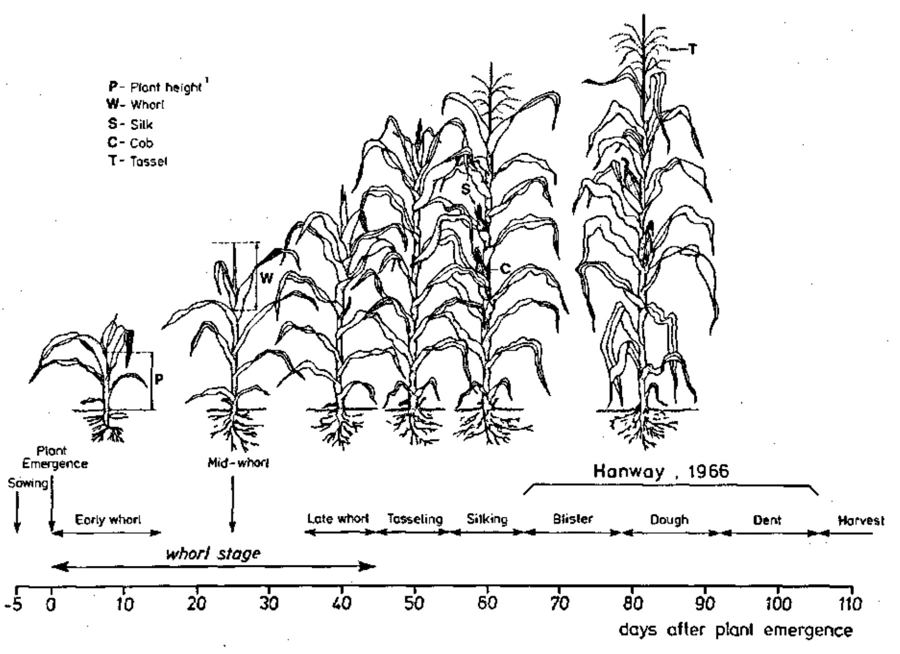
An experimental approach and an extensive review of the literature aimed at the establishment of an integrated pest management program for maize.

2. MAIZE AND THE ARTHROPOD PESTS

2.1. THE MAIZE CROP

The inland ('criollo') varieties are much used by the small farmer. These open-pollinating varieties are highly appreciated as food by the rural population, the yields however are low. Of the more than 20 inland varieties 'Tuza Morada' ('Violet Husk') is the most cultivated. Open-pollinating varieties and commercial hybrids yield better (yield potential: 30 to 40 and 45 to 50 metric tons per ha respectively) than the inland varieties (yield potential: 20 to 25 metric tons per ha) (PINEDA, 1978). The varieties Salco, NB-2 and Nic-Synt-2 are produced by the breeding department of INTA. Nic-Synt-2 is a short-season variety, specially suited to regions with a low precipitation (second growing period in the Pacific plain). Of the commercial hybrids, X-105-A had been recommended the most, and was most widely used.

Land preparation after the dry season is either absent or consists of ploughing by oxen. Maize stubble in the dry season is used for cattle feeding, the remnants are burned in April-May just before the start of the rainy season. When sown by plantstick 2 or 3 seeds are deposited per planting hole. Plant densities vary from a



[1] Plant height was measured from the soil surface to, where the leaves of the whorl still form a cone.

FIG. 4. Stages of plant development of maize (example: hybrid X-105-A) as used in this publication.

minimum of 30,000 plants per ha for the inland varieties to a maximum of 80,000 plants per ha for the hybrids. Soil preparation and plant densities further depend on soil conditions (slope, stones, soil type).

INTA recommended for the two methods of maize farming (i.e. the 'plant-stick' and 'oxen'), applications of 130 kg NPK fertilizer (10–30–10 or 15–30–8) per ha and two gifts of 65 kg urea, one at sowing and one 5 weeks after plant emergence[1]. Recommendations vary for the different production regions (fig. 2).

Weeding is by hand about twice during the growing period. Weeding is very laborious and costly, and during the peaks in the growing season labour is often difficult to obtain. The method of minimum tillage that uses herbicides was studied lately.

The plant developmental stages as referred to in this publication are presented in figure 4.

2.2. ARTHROPOD PESTS[2]

McGUIRE and CRANDALL (1966) estimated field losses caused by insects in maize in Central America at 20 per cent in dry grain weight. For Nicaragua such a percentage would be equivalent to 47,200 metric tons, worth 7.2 million dollars (average production figures over 1975 to 1977; BCN, 1978a). LEON and GILES (1976) estimated that there was a yearly loss of 15 per cent in dry weight for maize, caused by storage insects, equivalent to 35,400 metric tons and worth 6 million dollars.

ESTRADA (1960) listed a number of insects encountered on maize plants in Nicaragua. From 1974 to 1979 extensive collections were made of foodgrain insects. Material was sent for identification. Table 8 summarizes the most important maize insects that generally occur in Nicaragua.

Since investigation primarily concentrated on *Spodoptera frugiperda* and *Diatraea lineolata* these maize pests will be discussed first, followed by a brief review of the other pests.

2.2.1. *Spodoptera frugiperda (J. E. Smith)*

S. frugiperda, formerly recorded as *Laphygma frugiperda* (Smith and Abbot) occurs throughout Latin America and is a permanent resident in the Southern USA. It is considered as one of the most destructive insect pests of maize in Latin

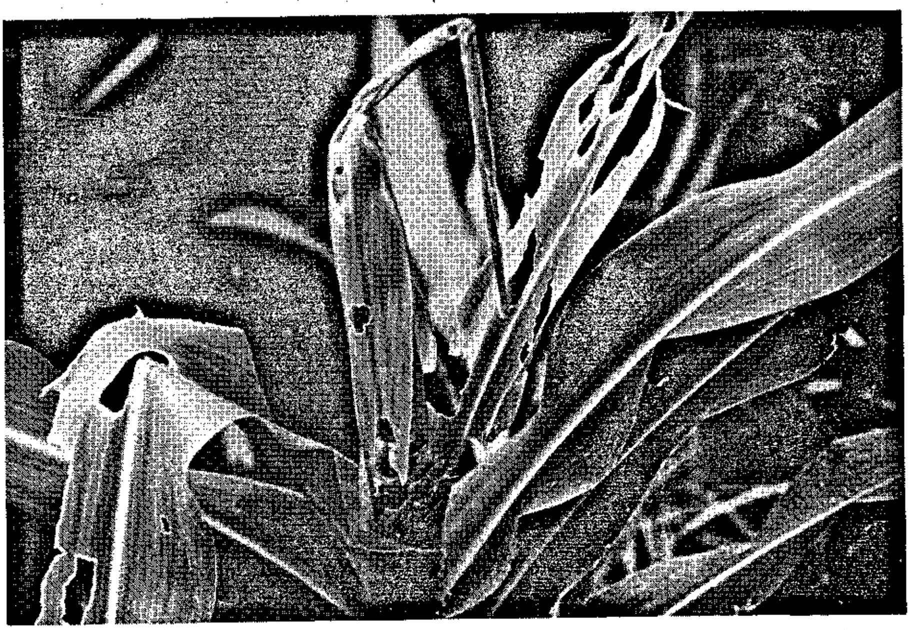
[1] Source: INTA, 1978

[2] Identifications provided by:

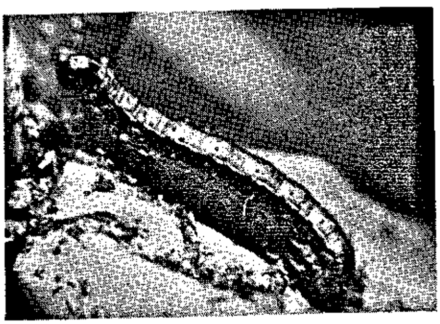
E. W. Baker	Acarina	M. B. Stoetzel	Aphididae *(S. flava)*
T. L. Erwin	Carabidae	T. J. Spilman	Cerambycidae
D. C. Ferguson	Pyralidae	G. Steyskal	Diptera
J. L. Herring	Miridae	E. L. Todd	Noctuidae *(M. latipes)*
J. P. Kramer	Cicadellidae	R. E. White	Chrysomelidae
L. M. Russell	Aphididae *(R. maidis)*	D. R. Whitehead	Curculionidae

America (ORTEGA, 1974; CHIANG, 1977). It is generally known as 'cogollero', as its injury consists mainly in the defoliation of the whorl (Spanish: 'cogollo') (photo 1). There are several other *Spodoptera* species besides *S. frugiperda* in Nicaragua, viz. *S. sunia* (Guenée), *S. exigua* (Hübner), *S. latisfacia* (Walk.), *S. eridiana* (Cramer) and *S. dolichos* (F.) (VAUGHAN, 1975). The mature larvae of the various species can be identified with the key provided by LEVY and HABECK (1976). *S. frugiperda* has a wide range of hosts. Other host crops in Nicaragua are sorghum, sesame, sugarcane, rice, cotton, tobacco, potato and vegetable crops, such as tomato, cucumber, cabbage. Some of the weed hosts are listed in chapter 3.3..

The oviposition by the moths on maize is described in chapter 3.1. and the dispersal behaviour of first instar larvae in chapter 3.2.. ESTRADA (1960) reported from Nicaragua an average duration of the larval stage (6 instars) of 11.1 days under natural conditions ranging from 9.6 to 20.0 days, when grown on maize



A



B

PHOTO 1. *Spodoptera frugiperda* (J. E. Smith)
A. Injured whorl
B. Fullgrown larva

leaves. RANDOLPH and WAGNER (1966) reported from Texas, USA, an average larval development period of 14.7 days (range 8 to 26 days), when grown on a wheat germ diet at 27 °C. The average duration of the pupal stage as reported in both references is 8.8 and 7.9 days respectively. In Surinam seven larval instars were distinguished, the total duration of larval development was 19 days and the pupal stage lasted 7 to 9 days (VAN DINTHER, 1955). One female may oviposit between 97 and 2,407 eggs (average 1,281) (RANDOLPH and WAGNER, 1966). Last larval instars are cannibalistic (WISEMAN and MCMILLIAN, 1969). This may explain why normally only one last instar larva per maize whorl remains.

Whorl defoliation is the most common type of injury, but 'dead heart' also occurs when at an early growth stage the larvae tunnel into the stalk (BURKHARDT, 1952) and feed on the meristematic tissue of the bud. After tasseling the larvae may attack the ear, entering through the silk channel or through the leaves of the husk. In Nicaragua loss of yield because of ear feeding is negligible.

During the whorl stage *S. frugiperda* may destruct the tassel partially or completely, but the incidence of this injury is low. According to SOZA et al. (1975) the producers of maize hybrids utilize only 25 per cent of the tassels to obtain complete pollinization of a whole field (2 rows ♂♂ alternated with 6 rows ♀♀).

In the Interior South of Nicaragua (fig. 2) maize seemed to be attacked less by *S. frugiperda*. Natural mortality by parasites and predators was higher in this region. When maize was grown under irrigation in the Pacific North after the cotton harvest in February, *S. frugiperda* attack was very severe. This probably results from the *S. frugiperda* population build-up in cotton at the end of the growing season (VAUGHAN, 1975).

The percentage of injured whorls is generally used as a criterion for insecticide applications against *S. frugiperda*. SILGUERO (1976) mentioned that there were no differences between the samplings of 5, 10, or 15 consecutive maize plants in each of 16 evenly distributed sampling sites per ha, CLAVIJO (1978) suggested that plants could be randomly sampled.

2.2.2. *Diatraea lineolata (Wlk.)*

The first record of the neotropical corn borer, *D. lineolata* was made in 1856 from Venezuela (BOX, 1949). The insect is known in the Bahamas, Cuba, Grenada, Tobago, Trinidad, Mexico and most of Equatorial South America North of the River Amazone, but oddly enough not in Jamaica, Hispaniola, Puerto Rico and the lesser Antilles, North of Grenada (BOX, 1950). *Diatraea saccharalis* (F.) and *D. lineolata* are respectively the first and second most widespread *Diatraea* species. BOX (1949) mentioned 10 different *Diatraea* species from Central America, those that attack maize are *D. saccharalis*, *D. grandiosella* Dyar and *D. lineolata*.

Borer material from maize and sorghum was regularly collected from different parts of Nicaragua. Occasionally adults were sent for identification, but usually they were identified with the help of DYAR and HEINRICH'S (1927) determination tables; only *D. lineolata* was found. In Nicaragua *D. saccharalis* has been occasionaly reported in maize fields adjacent to sugarcane (ESTRADA, 1960); in sugarcane its incidence is low.

In contrast to *S. frugiperda*, *D. lineolata* has a very limited range of hosts. BOX (1950) mentioned besides maize *(Zea mays)*, teosinte [*Zea(= Euchlaena)mexicana*] and guatemala grass *(Tripsacum laxum)*. *Sorghum vulgare* Pers. was a host plant for *D. lineolata* in Nicaragua.

Oviposition by *D. lineolata* on maize is described in chapter 3.1.. Eggs are deposited in batches, in which they are arranged like roof tiles. The egg stage lasts about 5 days. After two days two to three irregular, red, transverse bands appear over the cream-coloured eggs. A day later the black head capsule of the U-shaped embryo is clearly visible.

The sizes of head capsules and lengths of the larvae of the various instars are:

(L: $\bar{x}$ $\pm$SD, $\bar{y}$ $\pm$SD,z, n; L = larval instar, $\bar{x}$ = avg. head capsule width (mm), $\bar{y}$ = avg. larval length (mm), SD = standard deviation, z = avg. duration of larval stage (days), n = number of larvae; L_1: .31 $\pm$.01, 1.50 $\pm$.00, 2.5, 28; L_2: .43 $\pm$.02, 2.53 $\pm$.18, 2.8, 25; L_3: .66 $\pm$.04, 4.78 $\pm$.59, 3.5, 25; L_4:.94 $\pm$.07, 7.33 $\pm$.87, 3.9, 21; L_5: 1.29 $\pm$.13, 11.11 $\pm$1.05, 4.5, 15; L_6: 2.33 $\pm$.24, 14.11 $\pm$3.06, 7.0, 13; $L_1 - L_5$: population of May 1978; L_6: population of October 1978).

Although there was no overlap between the widths of head capsule or lengths of the larvae between subsequent instars, measurements of other populations produced intermediate values, therefore caution is needed in using these figures.

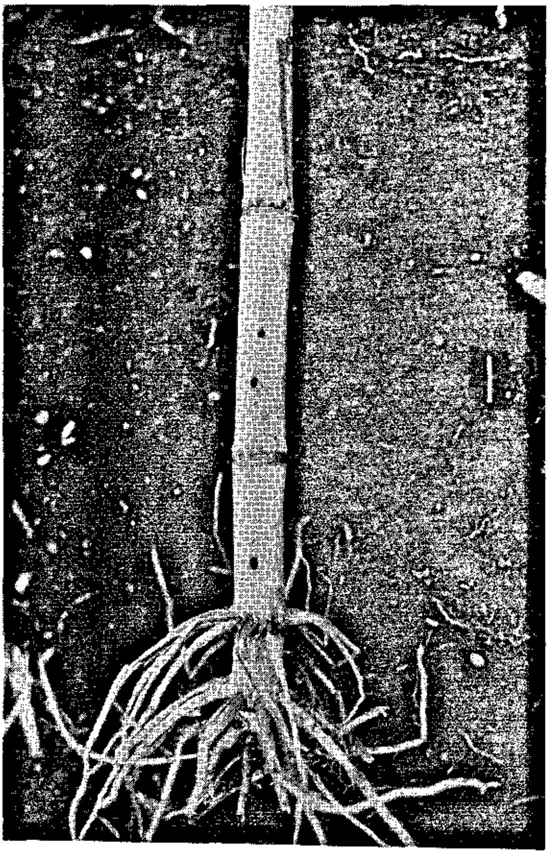
DYAR'S rule (DYAR, 1890) did not hold for these data. For the european corn borer, *Ostrinia nubilalis* (Hbn.), BECK (1950) found that the correlation between head-capsule width and instar number is subject to considerable variation, depending on nutritional conditions. GIRLING (1978) found for the maize borer *Eldana saccharina* Walk. that when head capsule widths were plotted against accumulated life time, a good linear relationship was obtained. This was also the case for *D. lineolata*.

KEVAN (1944) reported 6 to 8 larval stages (average 7) for *D. lineolata*. HYNES (1942) mentioned an extra mould of this borer during the resting stage; this was not observed by us. The pupal stage of *D. lineolata* took 9.1 days.

At whorl stage the newly hatched first instar larvae penetrate the whorl of the maize plant deeper than larvae of *S. frugiperda* of the same age. The first lesions (skeletonized leaf patches) cannot be distinguished from those of *S. frugiperda*. Seven days after egg emergence the typical leaf injury by *D. lineolata* becomes apparent: a transverse row of tiny holes on the leaf, caused by the larva boring into a rolled up whorl leaf. Larvae from the fourth larval instar onwards may start boring into the stem. Whorl feeding after the fifth larval instar was not observed. During and after tasseling larvae can be observed on the husk leaves and the leaf-sheaths.

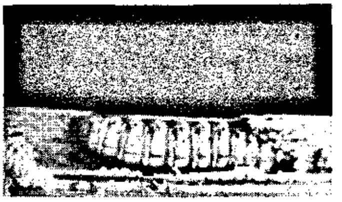
The injury by the boring larvae can be observed from the outside as small holes in the stemwall (perforations), which occur at intervals in the internodes (photo 2A) and in the ear shank. Before pupating or entering the resting stage an exit hole is made, leaving only the thin epidermis intact. Different types of injury by *D. lineolata* are discussed in chapter 4.4..

When the larva enters diapause it changes from a spotted to an immaculate



A

B



C

PHOTO 2. *Diatraea lineolata* (Wlk.)
A. Injury: small holes in the stemwall (perforations)
B. Fullgrown larva
C. Larva in diapause

morph (photo 2B and C). The diapausing larva is often found in the lowest stem internodes at the root zone. In the first growing period some larvae may enter diapause. In the second growing period almost all larvae enter into this resting condition; only a few pupate, the resulting generation probably succumbs due to the absence of hosts.

The diapause is correlated with the growing stage of the plant at the time of infestation. From November 12, 1978 to January 19, 1979 irrigated maize (hybrid X-105-A) from six sowings (at two-weekly intervals from Aug. 14 to Oct. 23, 1978) was dissected weekly and spotted and immaculate larvae were recorded. It appeared that from tasseling (45 days after plant emergence) until about 90 days after plant emergence the percentage of immaculate larvae increased about linearly from 0 to 100 for all sowings. The growth stage of the plant is probably one of the factors responsible for the induction of the diapause.

From January to May, 1979 a monthly attempt was made to break the diapause artificially by soaking (daily spraying for a week with water) maize stalks, collected in the second growing period of 1978 just before treatment from one experimental maize field. The stalks were dissected, by mid-April 20% of the borers encountered had pupated and by mid-May 50% (R. OBANDO, 1979, pers. communic.). This may indicate that a minimum period of diapause is required before it can be broken. KEVAN (1944) found that contact moisture rather than humidity was the initiating factor to break dormancy in *D. lineolata* larvae.

D. lineolata occurs throughout Nicaragua. Its incidence in the second growing period, especially in the Pacific plain is considerably higher than in the first growing period, indicating that the population builds up in the rainy season.

2.2.3. *Other maize pests*

In table 8 the most important maize insects that occur generally in Nicaragua, are listed.

Mocis latipes occasionally causes severe defoliation before midwhorl stage. The larvae move like a looper. The later instar larvae feed on the leaf margins in a characteristic undulating way. The density of the population may become so high, that much damage is caused and chemical control seems to be the only remedy.

Adult chrysomelids, predominantly *Colaspis* sp. may occasionally occur in high numbers during the early whorl stage, they feed on the whorl leaves, but the injury (roundish holes) cannot be expected to affect the yield (see chapter 6.2.). Control of chrysomelids by chemicals was often (erroneously) recommended, as the injury may look alarming.

Leaf injury by the leaf miner *Liriomyza sorosis* (Williston) (Diptera: Agromyzidae) is common, but of no importance (see also chapter 3.3., fig. 21)

The lesser cornstalk borer, *Elasmopalpus lignosellus* occasionally reaches

TABLE 8. Important maize arthropods in Nicaragua.

Type of pest	Order	Family	Species
Defoliators	Lepidoptera	Noctuidae	*Spodoptera frugiperda* (J. E. Smith) *Mocis latipes* (Guen.)
Stem borers	Lepidoptera	Pyralidae Phycitidae	*Diatraea lineolata* (Wlk.) *Elasmopalpus lignosellus* (Zell)
Leaf suckers	Hemiptera (Homoptera)	Cicadellidae Aphididae	*Dalbulus maidis* (Delong & Wolcott) *Rhopalosiphum maidis* (Fitch)
	Acarina	Tetranychidae	*Oligonychus pratensis* (Banks)
Cob feeders	Lepidoptera	Noctuidae	*Heliothis zea* (Boddie) *S. frugiperda*
Soil insects	Lepidoptera	Noctuidae	*Feltia subterranea* (F.) *Agrotis* sp.
	Coleoptera	Scarabaeidae Elateridae Tenebrionidae	*Phyllophaga* spp. *Aeolus* sp. *Epitragus* sp.

damaging densities in maize, but more frequently in sorghum, especially in dry growing periods.

When dissecting stalks at harvest small larvae of *Leptostylus* sp. (near *gibbosulus* Bates) (Coleoptera: Cerambycidae) were sometimes observed.

The direct damage by leaf sucking of the cicadellid *Dalbulus maidis* is very low. *D. maidis* is however, a vector of corn stunt spiroplasma and rayado fino virus (GÁMEZ, 1980). In the second growing period corn stunt incidence in the Pacific plain is so high that the National Bank of Nicaragua (BNN) does not provide credit during this period. Investigations into host plant resistance, alternative host plants, and the biology of the vector are carried out mainly in El Salvador.

The aphid *Rhopalosiphum maidis* is occasionally observed in high numbers on whorl or tassel, mostly just before or at tasseling stage. Its injury to maize however is negligible. It does attract many predators like sirphids, cantharids, caribids, coccinellids and parasites such as tachinids and sarcophagids. Aphid populations as such may have an indirect beneficial effect in controlling maize pests. The aphid *Sipha flava* (Forbes) was only sporadically found. ORTEGA (1974) mentioned that aphid species, mainly *R. maidis* spread the sugarcane mosaic virus complex.

Injury by *Collaria oleosa* (Distant) (Heteroptera: Miridae) hardly occurs (see chapter 3.3.). *Oligonychus pratensis* is an occasionally serious mite pest, when maize is grown under irrigation (by inundation) in the dry season (maize is sown as an intermediate crop between two cotton crops by large landowners). Since infestation often occurs in spots in the field, spraying of these areas only, is recommended.

Heliothis zea is a common cob feeder. The moth oviposits its eggs on the silk. Hatched larvae feed on the silk and enter the cob, where they start feeding on the grains. Cannibalism by *H. zea* larvae has been noticed frequently (see also WISEMAN and MCMILLIAN, 1969). Cultivars with a low husk tightness proved vulnerable to ear damage by this noctuid. The common inland variety Tuza Morada, characterized by a very tight husk has a high resistance to cob feeders. Larvae of *Estigmene acrea* (Drury) (Lepidoptera: Arctiidae), a common pest of beans, and larvae of the subfamily Phycitinae (Lepidoptera: Pyralidae) (species not identified) have occasionally been observed feeding on the silk. Cob feeders encourage subsequent infestations by secondary insects such as Otitidae (e.g. *Eumecosomyia nubila* (Wiedemann), see also ESTRADA, 1960) and storage insects.

Economic thresholds of soil insects (table 8) were established empirically (see MAG/FAO/PNUD, 1976). Cut maize roots caused by *Anisocnema validus* Chd. (Coleoptera: Carabidae) were also once observed. In Costa Rica this insect has also been reported on maize (T. L. ERWIN, 1976, pers. communic.)

Stalk feeding in damaging populations by the curculionids *Geraeus senilis* (Gyll) (ESTRADA, 1960), *Hyperodus* sp. and *Centrinaspis* sp. sometimes occurred.

3. AGROECOLOGY OF MAIZE PESTS

3.1. OVIPOSITION BY *D. lineolata* AND *S. frugiperda* ON MAIZE

3.1.1. *Stage of plant development*

3.1.1.1. Introduction

KEVAN (1944) reported from Trinidad that eggs of *D. lineolata* are laid in egg masses on the upper leaves of the maize plant. Under laboratory conditions the average number of eggs per mass ranged from 2.7 to 21.3 with a mean of 9.0. Judging by the occurrence of the young externally feeding larvae, he concluded that the moth preferred to oviposit just before tasseling and stopped egg laying almost completely when the cobs were formed (KEVAN, 1943).

A positive correlation between plant height of maize and oviposition was found for *Ostrinia nubilalis* (Hbn.) in an experiment where the moth was given a choice between five developmental stages and four varieties (PATCH, 1929). By sampling a number of maize fields in different areas PATCH (1942) found most of the egg masses of this borer in fields with the tallest plants. TURNER and BEARD (1950) studied the relationship between oviposition by *O. nubilalis* and the stage of growth of different maize inbreds; at the whorl stage first generation oviposition was more associated with leaf area than with the height of the plant, second generation eggs were deposited more in relation to the growth stage than to plant height.

The number of eggs from freshly emerged moths of *Diatraea grandiosella* Dyar, caged with maize in different developmental stages was correlated directly with the leaf surface area available to the moths; plants with a larger leaf area, received more eggs (STEWART and WALTON, 1964). The authors concluded that the moth showed no preference for any stage or age of the plants. In the same experiment 47 per cent of all eggs were laid on the upper leaf surfaces of plants at the tasseling stage and 62 per cent at the dough stage (see fig. 4); 36 and 31 per cent respectively were laid at the same stages on the lower leaf surfaces; the rest was laid on the stem. Most eggs were deposited 1.3. to 1.8 m above ground level on tasseling and dough stage plants. Only 9 per cent was oviposited in the lower .6 m interval on dough stage plants, where leaves were deteriorating. The authors suggested that the moisture content of plant parts influenced the height of oviposition sites.

Little has been published on oviposition patterns by *S. frugiperda* on maize, but some data on first instar larval behaviour will be presented, to better understand oviposition behaviour. MORRILL and GREENE (1973a) studied the distribution of the larvae of *S. frugiperda* on the maize plant. In pretassel field maize they found most larvae in the plant whorls, but at tasseling the number of larvae per plant decreased. In their opinion this was an indication of high larval mortality, because most larvae were too young to pupate succesfully and mass movements of the larvae from the fields were never seen. When the tassel emerges from the plant, larvae were observed leaving the tassel and moving to the leaves or the ears. Larvae attack ears by entering through the silk channel or more commonly through the husk or sheath surrounding the ears. Young ears with soft silk contained larvae in the ear tips, in the middle of the ears and in the silks. The spreading roughly corresponds with our observations in Nicaragua.

MORRILL and GREENE (1973b) reported that first instar larvae of *S. frugiperda* have a prevalent negative geotactic and/or positive phototactic response, which declines during the second instar. They assumed that it is this behaviour which causes first instar larvae to move to the top of the maize plant, where they can be dispersed by the wind, but they gave no experimental evidence.

More information about oviposition by both pests in relation to the growth stage of the plant is essential to develop control methods such as, the introduction of egg parasites, the timing of insecticide applications and the establishment of economic thresholds. Because larvae of maize stem borers are hidden in the plant's tissue, their incidence during plant development is difficult to estimate. Therefore the number of egg masses has been used as a criterion for economic thresholds (*O. nubilalis:* CHIANG and HODSON, 1952 and 1959).

Oviposition by *D. lineolata* and *S. frugiperda* was investigated in an open field experiment. The moths were given a choice between maize plants at different stages of development, each about 2 weeks apart in time. The experiment was carried out in the second growing period when the natural populations of *D. lineolata* are abundant.

3.1.1.2. Material and methods (Exp. A I)

From August 14 to October 23, 1978, the maize hybrid X-105-A was sown on 6 dates at two-weekly intervals in a split-plot design with 4 replicates, the 6 developmental stages in the main plots and 2 fertilizer treatments in the subplots. Of each pair of subplots one subplot (a half-row main plot) was fertilized at sowing with NPK fertilizer (10–30–10) and urea at a rate of 130 and 65 kg per ha respectively, the urea treatment was repeated after 25 days; the other subplot was not fertilized. Each plot consisted of 11 rows, 10 m long and .9 m apart. Between plots a space of 2 m was left open. The plots were irrigated after sowing and this was repeated weekly if necessary. Germination was noted at about two-weekly intervals. Between the first and the second week after germination plants were thinned to .15 m in the row.

Sampling was carried out when all 6 developmental stages were present in the field. Due to the amount of work involved in the egg and egg mass counts the samples were taken at two 3-days periods (2 blocks were sampled the first day of each period and each of the remaining 2 blocks on one of the other days). The first sampling period was from October 31 to November 2 and the second a week later from November 7 to 9, 1978. The plants sampled in the second period, a week after the first samples were taken, were at a growth stage exactly half way between the growth stages of the plants at the beginning of sampling. In figures and tables the second day of a sampling period of 3 days is noted. The sampling unit consisted of 2 inner rows of 5 m taken from each subplot, it was reduced when a very high number of *D. lineolata* egg masses was encountered.

In the field the following data were recorded: number of plants sampled, height of 6 consecutive plants, number of fully extended leaves, number of egg masses of *D. lineolata* and *S. frugiperda*. Number of eggs per egg mass and number of black egg masses (parasitized by *Trichogramma* *pretiosum* Riley) of *D. lineolata* were counted. *S. frugiperda* egg masses were collected and in the laboratory the number of egg layers and of eggs per egg mass were counted. The distribution of egg masses on successive leaves and on the upper or lower side of the leaf was recorded. Leaves were the only plant parts sampled. On the second day of both sampling periods, 2 plants of average height were selected from each plot and the total green leaf area was determined by drawing green leaf contours on paper, which were cut out; these stencils were weighed and compared with the paper weight of a fixed surface.

The fertilizer treatment hardly influenced plant phenology, probably because the experimental plot had been fallow for a year. Fertilized plants grew only an insignificant 2 to 3% taller. Because oviposition was also not influenced by the fertilizer treatment, the experiment was analyzed as a randomized block design with 6 developmental stages in 4 replicates. The number of egg masses and eggs (converted to 100 plants) were logarithmically transformed, because estimated standard deviations were about proportional to the mean. The two-tailed sign test was used to analyze differences between upper and lower leaf surfaces, with regard to the percentage of egg deposition and the number of eggs per mass. When differences were only small statistical analysis was omitted. In the analysis of variance the effect of the developmental plant stages (and therewith the treatment sum of squares) was partitioned into linear, quadratic and cubic components.

3.1.1.3. Results and discussion

D. lineolata

Oviposition by *D. lineolata* simultaneously recorded from maize in six developmental stages shows the following pattern (fig. 5B). Egg deposits increased with more advanced whorl stages; main oviposition occurred at late whorl and tasseling stages; after tasseling oviposition declined rapidly. In the analysis of variance (table 9) of the number of egg masses (logtransformed) both sampling periods showed a highly significant quadratic (spherical) effect of the age of the plant (days after plant emergence). Between plant stages there was no consistent difference in the number of eggs deposited per egg mass (table 10).

Plant height, number of fully extended leaves and green leaf area correlated significantly with the number of eggs deposited (Pearson correlation coefficients are .89, .90, and .98, respectively), when considering only plant stages up to silking (before 55 days after plant emergence). After tasseling oviposition declined more rapidly than the green leaf area of the maturing plant of which the lower leaves deteriorated (fig. 5).

Green leaf area correlated almost perfectly with oviposition and therefore seems an excellent explanatory variable for the amount of oviposition up to silking. This has also been found for *D. grandiosella* (STEWART and WALTON, 1964) and for *O. nubilalis* (TURNER and BEARD, 1950). Until silking the eggs were distributed proportionally to the amount of green leaf area available for oviposition and during this time there was no preference for one of the different growth stages. However if the growth stages after silking were taken into account there was an oviposition preference for the stages before silking.

The results described above deal with oviposition when all stages of plant development are present and can be expected to play a role when maize fields are sown over a prolonged period. These results should also be taken into account in maize breeding programmes (using lines or varieties of maize with a different maturity and/or leaf area), aiming at borer resistance and utilizing natural infestations.

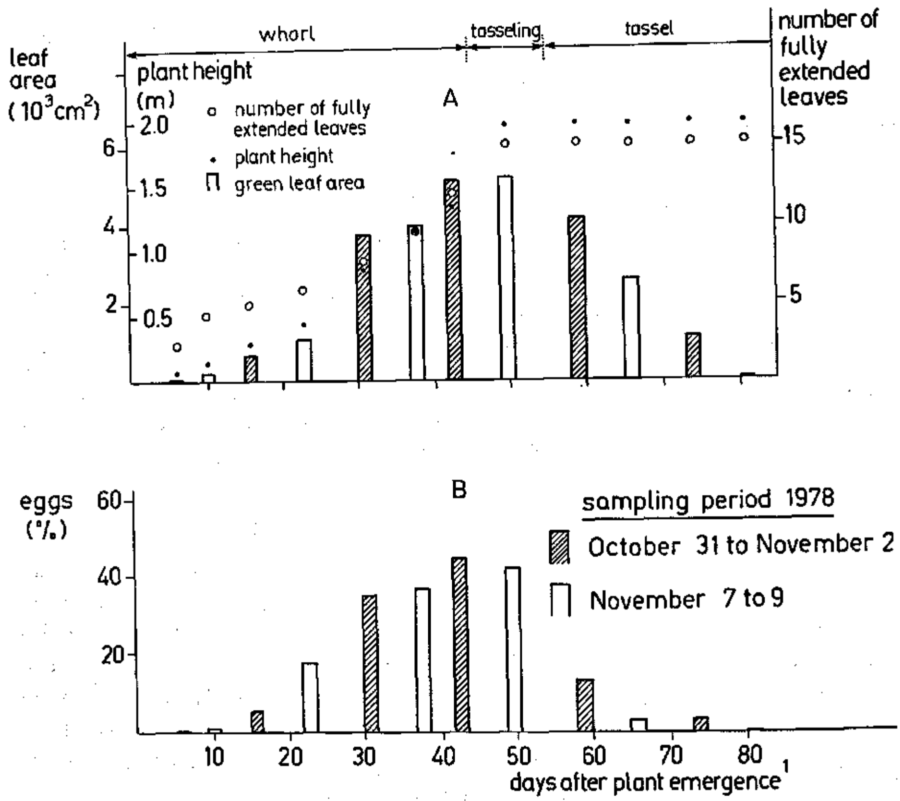


FIG. 5. Plant development and egg numbers of *D. lineolata* for six stages of development and two sampling periods. (Exp. A I)
A. Plant development (days after plant emergence): number of fully extended leaves, plant height and green leaf area.
B. Frequency distribution of egg deposition by *D. lineolata* over six stages of plant development, for each of two sampling periods.

[1] Days after plant emergence is a time scale for six stages of plant development and two sampling periods.

In several of our experiments, differences in oviposition by *D. lineolata* between blocks were significant or weakly significant (table 9, table 20). Apparently moth flight was limited during oviposition, neighbouring maturing maize fields acting as a source of infestation. This means that the moth, when not having a choice for oviposition between maize fields in various stages of plant development, might deposit more eggs on a certain stage than it would have done otherwise e.g. figure 6 shows a high oviposition at the early whorl stage.

From midwhorl stage onwards 60 to 70 per cent of all egg masses were deposited on the upper leaf surface, significantly more than 50 per cent (by sign test; table 10). Moreover the size of the egg mass was significantly larger on the upper leaf surface than on the lower. However, at early whorl stage lower leaf

TABLE 9. Maize in six stages of plant development in two sampling periods. The effect on the average number of egg masses (ln(x + 1)) of *D. lineolata* on maize. Analysis of variance: F-values, significancies, means. (Exp. A I)

Source of variation	df	Sampling period: Oct. 31–Nov. 2		Nov. 7–9	
		F-values			
Blocks	3	2.63^{+}		1.37	
Treatments	5	32.5^{**}		28.8^{**}	
Linear	1	10.7^{**}		17.0^{**}	
Quadratic	1	$150.^{**}$		$121.^{**}$	
Rest	3	.78		3.70^{+}	
Error: V.C.	15	21.1		24.0	
Total	23			means	
			ln(x+1)		ln(x+1)
Grand mean			2.74		3.30
		date[1]		date[1]	
		3	.36	10	1.67
		16	2.49	23	4.56
		31	4.32	38	5.32
		43	4.60	50	5.47
		59	3.25	66	2.37
		74	1.43	81	.38
Total number of egg masses		667		1157	

[1] Date (= days after plant emergence) is a time scale for six stages of plant development.

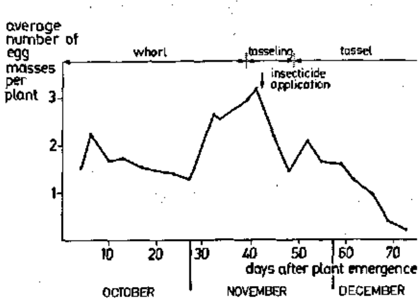


FIG. 6. Average number of egg masses of *D. lineolata* on field maize during plant development. (Five random sites, each composed of 10 consecutive plants in a row, sampled twice weekly; variety Nic-Synt-2 sown September 30, 1975 at the experimental station La Calera, Managua.)

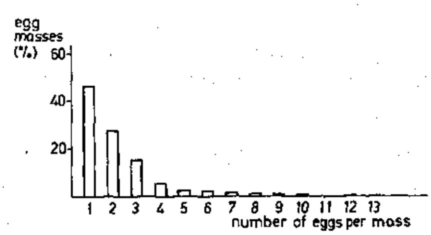


FIG. 7. Frequency distribution of egg masses over the number of eggs per mass of *D. lineolata* on field maize at early whorl stage. (Samples taken 6 and 10 days after plant emergence; 392 egg masses involved; variety Nic-Synt-2 sown September 30, 1975 at the experimental station La Calera, Managua.)

TABLE 10. Oviposition by *D. lineolata* on upper and lower leaf surface of the maize and the occurrence of black eggs (parasitized by *Trichogramma pretiosum*). Sampling was carried out on five developmental stages of maize in two sampling periods. (Exp. A I)

	Sampling period									
	Oct. 31–Nov. 2 days after plant emergence					Nov. 7–9 days after plant emergence				
	16	31	43	59	74	10	23	38	50	66
Leaf surface	fraction (%)									
deposited on upper side										
egg masses	36	**68**[1]	**66**	**62**	**74**	20	**60**	**64**	**55**	**55**
eggs	36	**68**	**70**	**69**	**73**	14	**61**	**67**	**59**	**54**
eggs per mass deposited on:	average number of eggs									
upper side	2.1	1.9	2.1	2.3	2.6	1.7	*2.1*[2]	*2.1*	*2.1*	*1.8*
lower side	2.1	1.9	1.7	1.7	2.7	2.5	*1.9*	*1.9*	*1.8*	*1.9*
T. pretiosum	fraction (%)									
sampled as black eggs										
egg masses	2	31	35	29	61	0	7	22	11	22
eggs	2	30	37	29	57	0	7	18	10	19
eggs per mass	average number of eggs									
black	2.0	1.8	2.1	2.1	2.4	–	2.1	1.6	1.8	1.6
normal appearance	2.1	2.0	1.9	2.1	2.8	2.5	2.0	2.2	1.9	2.0
Eggs per mass	2.1	1.9	2.0	2.1	2.6	2.5	2.0	2.1	1.9	1.6
Total number involved	number of egg masses and eggs									
egg masses	61	187	278	100	34	12	217	396	485	49
eggs	125	358	555	210	89	30	436	810	935	89

[1] Bold type figures: different from 50% (P ≤ .01; two-tailed sign test).
[2] Italic figures: upper different from lower (P ≤ .05; two-tailed sign test).

surfaces were preferred (table 10). Apart from this experiment samples taken from a field of maize seedlings (variety Nic-Synt-2, October 1975), confirms these findings: 69, 21 and 10 per cent were oviposited on lower, upper leaf surface and stem, respectively.

A frequency distribution of eggs per mass from this sample is presented in figure 7, almost half the amount of egg depositions consisted of only one egg. In our experiment the average size of an egg mass fluctuated around 2 (table 10). This is much less than the egg mass size in the field, as reported for *O. nubilalis* (average size of 15 eggs; CHIANG and HODSON, 1959). Therefore the use of the inconspicuous egg masses as a criterion for economic thresholds for *D. lineolata* is less suitable than for *O. nubilalis*. We found that when under laboratory conditions moths reared from larvae collected in the field were forced to oviposit in plastic cages on wax paper, the size of the egg mass increased greatly. Therefore the observation of KEVAN (1944), in which he mentioned averages from 2.7 to 21.3 in Trinidad may not be true for field conditions.

Parasitization of eggs by *Trichogramma pretiosum* Riley, constitutes a high mortality factor for *D. lineolata* (chapter 3.4.). Among the egg masses which had been visited by parasites, the eggs were nearly always parasitized.

The lower percentage of black egg masses (those parasitized by *T. pretiosum*) before midwhorl compared to developmental stages after midwhorl was not significant (table 10). The percentage of black egg masses decreased from the first to the second sampling period, possibly because the number of deposited egg masses increased by a factor 1.7 (table 10).

The distribution of the number of egg masses on the successive leaves of the maize plant seems to be fairly symmetric and unimodal (fig. 8). Oviposition on the lower leaves decreased with plant development, especially after tasseling when the lower leaves deteriorated.

The number of black eggs before tasseling diminished with plant height (fig. 8). However a black egg mass remains on the plant longer than a non-parasitized egg mass (chapter 3.4.). The top leaves had relatively more recently deposited eggs, which were exposed for a shorter period to parasite attack. Besides it takes

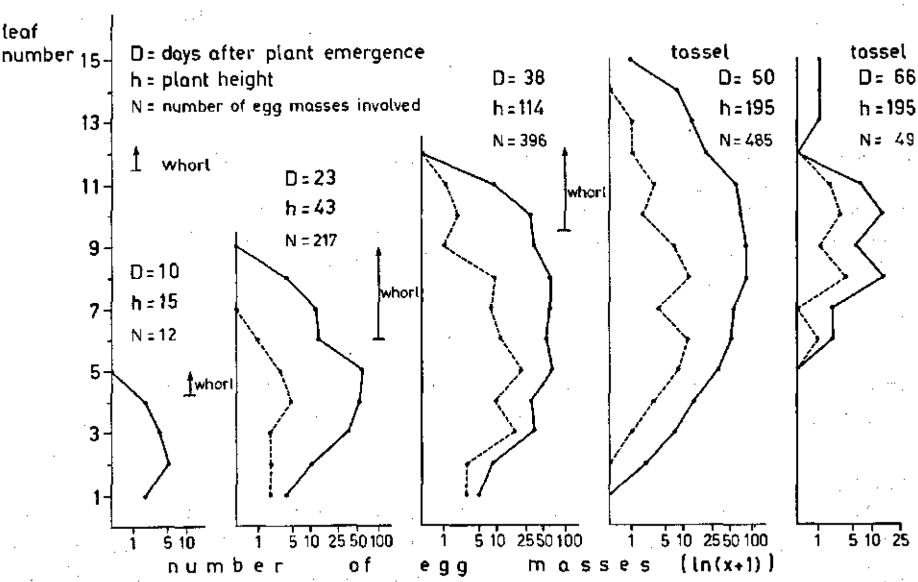
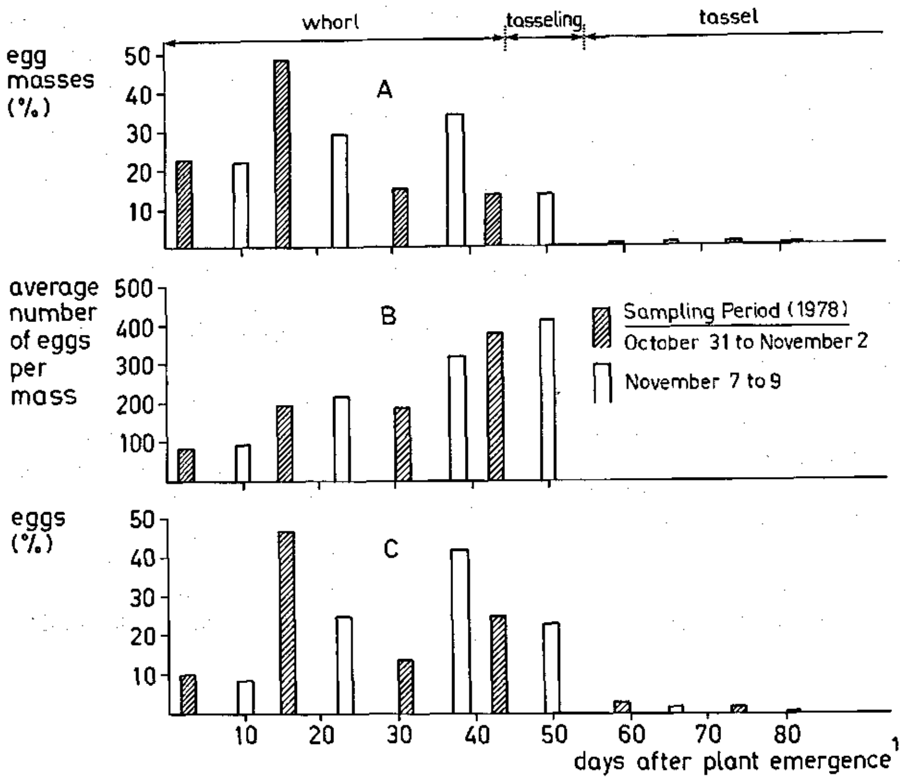


FIG. 8. Total number of egg masses (————) and black egg masses (– – – – – – –, parasitized by *Trichogramma pretiosum*) of *D. lineolata* deposited on succeeding leaves of maize plants at five stages of plant development (sampling period: Nov. 7–9). (Exp. A I)



[1] Days after plant emergence is a time scale for six stages of plant development and two sampling periods.

FIG. 9. Oviposition by *S. frugiperda* on maize at six stages of plant development, sampled in two periods. (Exp. A I)
A. Frequency distribution of egg masses over six growing stages for each of the two sampling periods.
B. Average number of eggs per mass for four growing stages in two sampling periods.
C. Frequency distribution of eggs over six growing stages, for each of the two sampling periods.

about 2 days before parasitized eggs turn black. Therefore from our observations it cannot be assessed if parasitism by *T. pretiosum* diminished with plant height.

S. frugiperda

Oviposition by *S. frugiperda* occurred mainly at the whorl and tasseling stage, after tasseling very few egg masses were found (fig. 9A). Preference for oviposition in the different stages of whorl development and tasseling differed slightly in the two sampling periods:

In the first sampling period the developmental stages before midwhorl received more egg masses than those after midwhorl (significant linear component, table

TABLE 11. Maize in six stages of plant development in two sampling periods. The effect on natural oviposition by *S. frugiperda* on maize. Analysis of variance: F-values, significancies and means. (Exp. A I)

Sampling period: Oct. 31–Nov. 2						Sampling period: Nov. 7–9					
Developmental stage (date)[1]	Number x of egg masses[2] (ln(x+1))	Number x of eggs (ln(x+1))	Egg masses[4]: Number x of eggs per mass (lnx)	Egg masses[4]: Number of egg layers per mass	Egg masses[4]: Number	Developmental stage (date)[1]	Number x of egg masses[3] (ln(x+1))	Number x of eggs (ln(x+1))	Egg masses[4]: Number x of eggs per mass (lnx)	Egg masses[4]: Number of egg layers per mass	Egg masses[4]: Number
3	1.92	6.15	4.2 ± .2	2.0 ± .6	25	10	2.92	7.37	4.3 ± .1	2.2 ± .2	34
16	2.53	7.69	5.0 ± .1	3.0 ± 1.0	48	23	3.16	8.48	5.3 ± .1	3.4 ± .6	28
31	1.56	6.55	5.0 ± .3	3.0 ± .8	10	38	3.17	8.87	5.5 ± .1	3.2 ± .3	22
43	1.22	5.47	5.5 ± .3	3.0 ± 1.1	8	50	2.41	8.34	6.0 ± .2	3.9 ± .3	13
59	.13	1.59				66	.36	1.86			
74	.17	1.50				81	.53	1.57			
Grand mean	1.63	6.47	4.80				2.92	8.27	5.10		
Standard error	.22	.89					.24	.24			

Analysis of variance (first 4 dates)

Source of variation	df	F-value	F-value	df	F-value	df	F-value	F-value	df	F-value
Block	3	2.93^{+}	1.10			3	.47	.47		
Treatment	3	6.68*	1.43	3	5.88**	3	2.58	7.19**	3	36.5**
Linear	1	10.0*	.64	1	5.16*	1	2.39	9.55*	1	99.9**
Quadratic	1	4.85^{+}	2.19			1	5.05^{+}	12.0**		
Cubic	1	5.15*	.48			1	.30	.03		
Rest				2	6.24**				2	4.84*
Error: V.C.	9	26.5	27.4	87	17.5	9	16.3	5.74	93	11.4
Total	15			90		15			96	

[1]Date = days after plant emergence.
[2]Number of egg masses involved: N = 105.
[3]Number of egg masses involved: N = 186.
[4]Means ± SD.

11). An oviposition peak occurred 16 days after plant emergence (weakly significant quadratic and significant cubic component, table 11). The number of eggs also showed a peak at 16 days (fig. 9C), but differences were not significant (table 11).

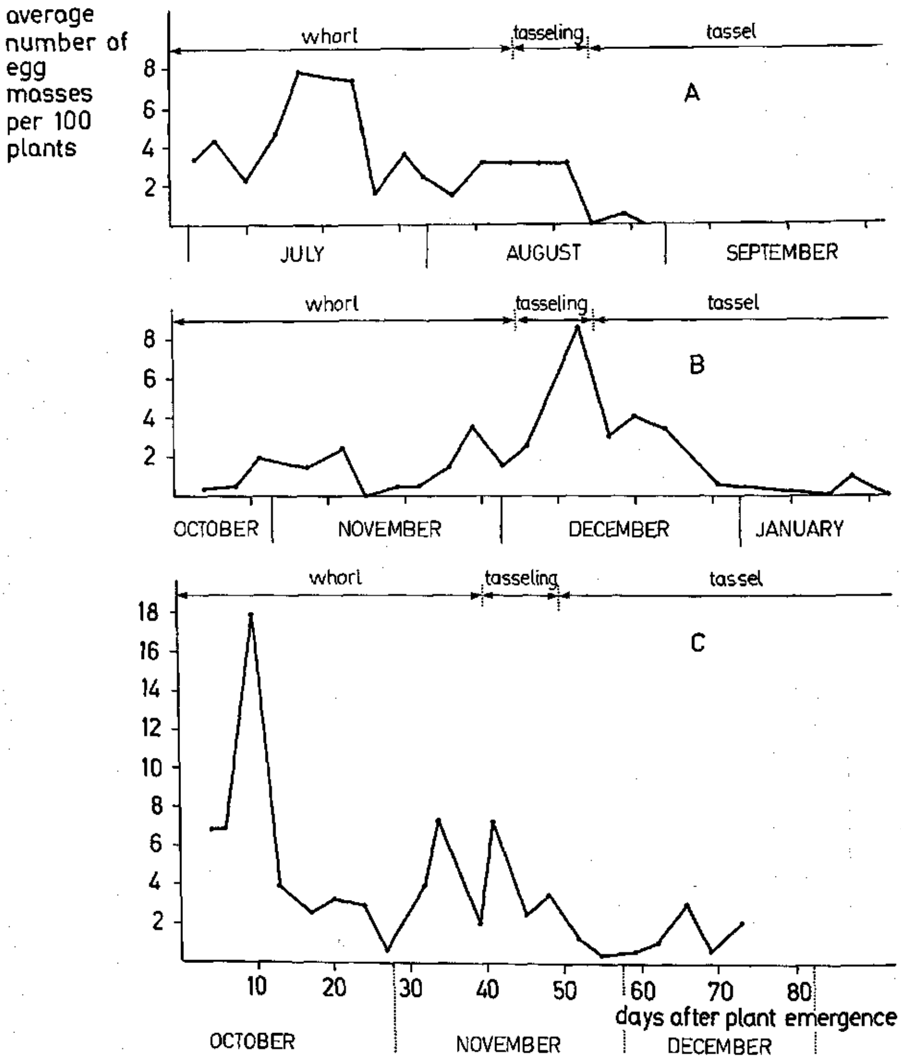


FIG. 10. *S. frugiperda* egg masses, sampled during the development of the plant of different maize crops.
A. Variety Salco, first growing period 1975, at the Experimental Station La Calera, Managua.
B. Variety Salco, second growing period 1975, at the Experimental Station Campos Azules, Dept. of Jinotepe.
C. Variety Nic-Synt-2, second growing period 1975, at the Experimental Station La Calera, Managua.

In the second sampling period the number of egg masses increased a little during the advanced whorl stage and decreased at tasseling (fig. 9A; weakly significant quadratic component, table 11). The number of eggs, however, showed a definite increase during the more advanced whorl stage and reached a peak 38 days after plant emergence, a week before tasseling; oviposition in the tasseling stage was less (fig. 9C) (significant linear and quadratic components, table 11).

Considering the total pattern of egg mass deposition (fig. 9A) there were two oviposition peaks: the first two weeks after plant emergence and the second just before tasseling, there was a depression just after midwhorl stage. Egg mass size increased nearly linearly (significant components, table 11) from less than a 100 eggs per egg mass during the earliest stage of plant development to about 400 at tasseling (fig. 9B). Considering the relative preference as expressed by the total number of eggs for each growing stage, the two-peaked curve as discussed above becomes even more pronounced (fig. 9C).

Similar oviposition patterns were observed when these results were compared to those obtained by taking regular samples of egg masses in maize fields in different parts of Nicaragua in 1975 (fig. 10): early whorl stage shows a high oviposition as well as during the late whorl and/or tasseling stage, whereas there was a drop during the stage just after midwhorl. The eggs of the second peak could have been laid by moths of the next generation. However the depression at midwhorl stage found in this experiment would not be explained. The following is suggested. Oviposition at early whorl stage provides the larvae with protection until pupation. Oviposition at late whorl stage or tasseling, enables the young larvae to 'shelter' in leaf sheaths and cobs. However if oviposition takes place just after midwhorl the larva will not be able to complete its development in the whorl and will be less protected at tasseling e.g. more exposed to biological control agents (chapter 3.4.). MORRILL and GREENE (1973a) mentioned a high mortality of the larvae at tasseling. High mortality of larvae, developed from eggs deposited just after midwhorl, selects against this behaviour.

At whorl stage egg masses were deposited on the leaves just below the whorl (fig. 11). Besides the fact that the whorl is the main infestation area it is also the highest part of the plant from which dispersal (predominantly by wind, Exp. B V, chapter 3.2.) takes place. The prevalent negative geotactic and/or positive phototactic behaviour of first instar larvae (MORRILL and GREENE, 1973b) makes them move to the whorl. Oviposition just below the whorl is of advantage to both infestation and dispersal.

At the early whorl stage all egg masses were deposited on the lower leaf surface (fig. 12). As the plant developed, a higher percentage of the egg masses were deposited on the upper leaf surface, reaching 40 per cent at tasseling.

One of the reasons for the increase in the size of the egg masses as the plant develops (fig. 9B) could be the following. At the early growth stage the risk for the larvae hatched from a few large egg masses deposited on a few plants is probably higher, than for those from many small egg masses deposited on many plants, because the colonization of new plants by wind-dispersing first instar

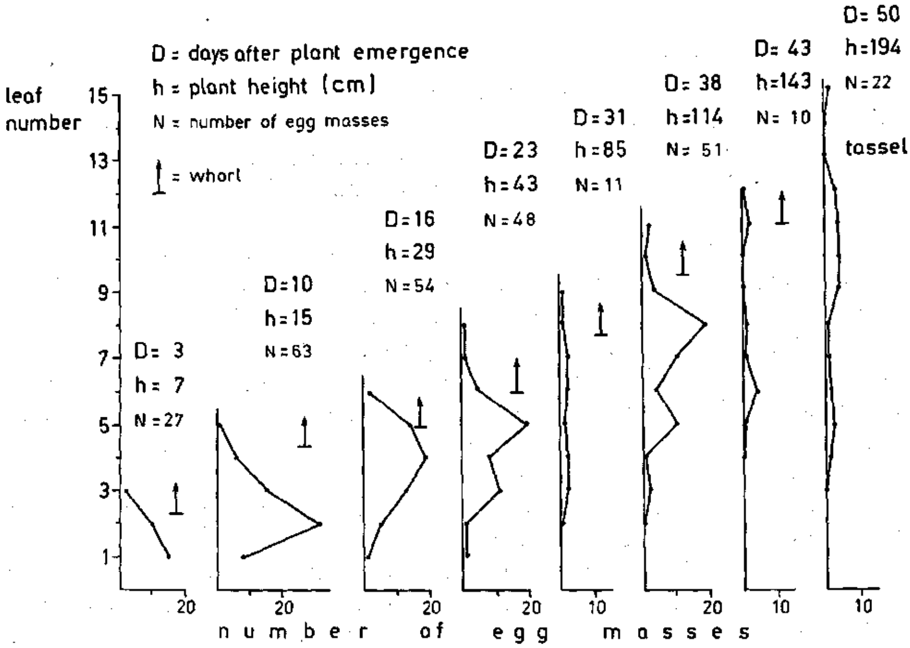
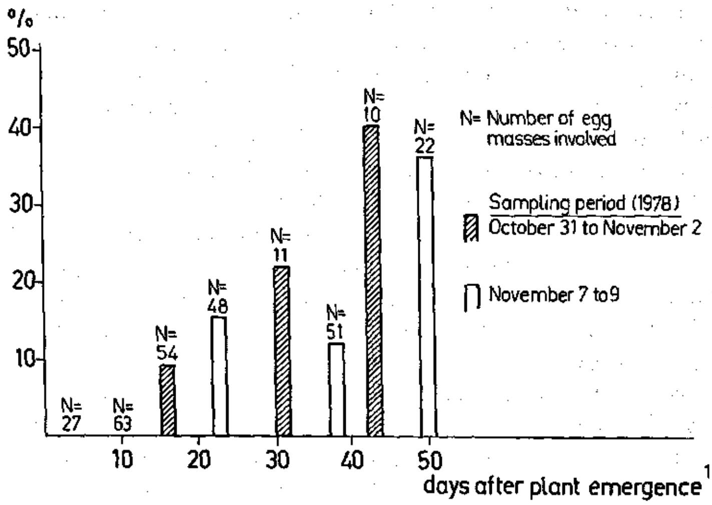


FIG. 11. Number of egg masses of *S. frugiperda* on successive (numbered) leaves of maize plants at four stages (see fig. 12) of plant development for the two sampling periods. (Exp. A I)



[1]Days after plant emergence is a time scale for four stages of plant development and two sampling periods.

FIG. 12. Fraction (%) egg masses of *S. frugiperda* on the upper leaf surfaces of maize at four stages of plant development in two sampling periods. (Exp. A I)

larvae, will be lower on smaller plants.

Apart from the above experiment, the oviposition preference for certain leaf surfaces and the increase of egg mass size during plant development were also apparent in other years with at least two other maize varieties, namely Nic-Synt-2 and Salco.

3.1.2. *Alternative host (sorghum), fertilizer and bean intercropping*

3.1.2.1. Introduction

Infestations by *S. frugiperda* in sorghum were generally lower than in maize. The use of fertilizer increased injury in maize by *S. frugiperda* and by *D. lineolata* (Exp. F, chapter 4.1.). Bean intercropping decreased maize injury by both pests, compared to a maize monoculture (Exp. B I, B II, B III; chapter 3.2.).

The varying infestation levels of both insects in maize and sorghum under these different production regimes may be caused by an oviposition preference of *S. frugiperda* and *D. lineolata*. This assumption was tested in a cage experiment.

3.1.2.2. Material and methods (Exp. A II)

The experiment was sown in nylon-screen cages of 1.8 × 3.6 × 1.8 m. on August 29, 1978 at the experimental station La Calera, Managua. The design was a split-split-plot with 3 replicates. The main plot, subplot and sub-subplot were for the bean intercropping, fertilizer and host (maize and sorghum) treatments respectively. An example of the layout of a cage is presented in diagram 2. The following varieties were used: the maize hybrid X-105-A; the open pollinating sorghum variety Guatecau, its height being about the same as of the maize hybrid used; the commonly used bean variety Honduras-46. Fertilizer treatment consisted of N-P-K fertilizer (10–30–10) and urea at rates of 160 and 65 kg ha^{-1} respectively. The urea treatment was repeated 2 weeks after plant emergence. Granular phoxim (Volaton 2.5%) was applied at sowing at a rate of 33 kg ha^{-1} to control soil insects (mainly *Agrotis* sp.). On October 4, 1978 maize and sorghum with and without fertilizer were sown on the same field and leaf areas were determined 32 and 39 days after plant emergence (methodology, see Exp. A I). *S. frugiperda* and *D. lineolata* pupae were reared from field collected larvae. Pupae in petri-dishes were placed in the middle of the cages one day prior to adult emergence. *S. frugiperda* egg masses were counted from 5 to 38 days after plant emergence. To diminish foliar injury by *S. frugiperda*, methomyl (Lannate 90% a.i. SP, .25 kg ha^{-1}) was applied with a knapsack sprayer 17 days after plant emergence. *D. lineolata* egg masses and eggs per mass were counted, 32 to 38 days after plant emergence.

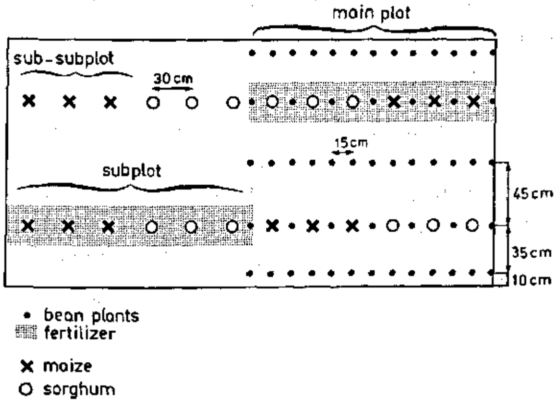


DIAGRAM 2. Layout of the planting system (a cage) in Experiment A II (a split-split-plot design).

All data on insect numbers were logarithmically transformed. Because the main plot error and subplot error were much lower than the sub-subplot error, all F-values were calculated using the sub-subplot error. The significance of each effect was however tested with the number of degrees of freedom of the actual error mean square. F-values for the main plot error and subplot error are also presented in this way.

3.1.2.3. Results and discussion

D. lineolata

The effect of the three factors, host, fertilizer and bean intercropping, on oviposition by *D. lineolata* will be dealt with in the following three paragraphs.

Host. *D. lineolata* deposited significantly more eggs and egg masses on maize than on sorghum (table 12). Leaf area was found in the foregoing experiment A I to be an excellent explanatory variable for the amount of oviposition by *D. lineolata* in maize. In this experiment maize had a leaf surface area of about twice that of sorghum, but had 3 to 3.5 times more eggs than were found on sorghum (table 13). This suggests that leaf area is not only responsible for the lower oviposition by *D. lineolata* on sorghum.

Fertilizer. *D. lineolata* deposited on fertilized plants significantly more egg masses and eggs per mass than on unfertilized plants (table 12). Fertilizer about doubled plant height in both maize and sorghum, the height of both crops was the same with and without fertilizer (table 14). The leaf area of maize and sorghum was about 4 times higher on fertilized plants, however the number of eggs deposited on fertilized plants was 8 to 9 times higher than on unfertilized plants (table 13B). Other effects (e.g. visual), were probably responsible for higher oviposition on plants when fertilized (the dark green colour of the fertilized plants contrasted sharply with the yellow light green colour of the unfertilized plants).

Bean intercropping. Numbers of egg masses and of eggs of *D. lineolata* on maize and sorghum plants were lower when intercropped with beans than with monocultures of these crops. However the difference was not significant. Bean intercropping decreased the egg mass size of *D. lineolata* in sorghum, but not in maize. This interaction was weakly significant (table 12).

S. frugiperda

S. frugiperda deposited in the cage considerably more egg masses on maize than on sorghum (table 12). Probably this also occurs in the field when both crops are grown in the same area. However it has been observed that sorghum fields are heavily infested when there are no maize fields nearby (preferential resistance). Bean intercropping diminished and fertilizer increased egg mass deposition on maize and sorghum, the differences were however not significant (table 12).

TABLE 12. Host (maize and sorghum), bean intercropped and as monoculture, with and without fertilizer. The effect on oviposition by *D. lineolata* and *S. frugiperda*. Analysis of variance (split-split-plot design): F-values, significancies and means. (Exp. A II)

Source of variation	df	*D. lineolata* (number x of) egg masses (ln(x+1))	eggs (ln(x+1))	eggs (lnx) per mass	*S. frugiperda* (number x of) egg masses (ln(x+1))
			F-values[1]		
Blocks	2	15.8^{+}	2.94	55.6*	1.86
Bean Intercropping (B)	1	3.43	2.85	1.22	3.34
Error (a)	2	.28	.04	5.80	1.80
Fertilizer (F)	1	41.6**	41.2**	21.1*	2.45
B × F	1	2.72	2.80	2.54	.15
Error (b)	4	.62	.94	.17	4.12
Host (H: maize or sorghum)	1	22.4**	14.0**	.84	41.6**
B × H	1	.86	1.19	3.60^{+}	.47
F × H	1	1.20	.00	.03	2.67
B × F × H	1	.02	.13	1.18	.07
Error (c): V.C.	8	40.4	51.9	19.5	41.6
Total	23				
			means		
Grand mean		2.35	3.34	1.24	1.25
Monoculture		2.58	3.67	1.30	1.42
Bean Intercropping		2.12	3.01	1.19	1.08
Unfertilized plants		1.53	2.10	1.02	1.10
Fertilized plants		3.16	4.58	1.47	1.40
Host: maize		2.95	4.06	1.29	1.86
sorghum		1.75	2.40	1.20	.64
Standard error		.18	.27	.07	.13
Treatment combinations B × H					
Monoculture : maize				1.45	
sorghum				1.15	
Bean intercropping : maize				1.50	
sorghum				.88	
Standard error				.10	
Number of egg masses and eggs involved		533	1830	–	95

[1] All F-values against their relevant error denominator (a, b or c); error (a) and (b) expressed by their F-values against error (c).

TABLE 13. Oviposition by *D. lineolata* on maize and sorghum, fertilized and unfertilized. (Exp. A II)

A. Total number of egg masses and eggs deposited, and leaf area, of maize and sorghum.

Fertilization	Maize			Sorghum		
	Egg masses	Eggs	Leaf area(cm^2)[1]	Egg masses	Eggs	Leaf area(cm^2)[1]
Unfertilized	56	137	1066	25	46	644
Fertilized	365	1279	4438	87	368	2383
Total	421	1416		112	414	

B. Number of times that the egg masses, eggs and leaf area is higher on maize as compared to sorghum, and on fertilized plants in comparison to unfertilized plants (derived from table A).

Ratio maize/sorghum	Un-fertilized	Fertilized	Ratio fertilized/unfertilized	Maize	Sorghum
Egg masses	2.2	4.2	Egg masses	6.5	3.5
Eggs	3.0	3.5	Eggs	9.3	8.0
Leaf area[1]	1.7	1.9	Leaf area[1]	4.2	3.7

[1] Average of 33 and 39 days after plant emergence.

TABLE 14. Height (cm) of maize and sorghum plants (33 days after emergence), unfertilized and fertilized, in monoculture or bean intercropped. (Exp. A II)

Fertilization	Maize		Sorghum	
	Mono-culture	Bean inter-cropped	Mono-culture	Bean inter-cropped
Unfertilized	49	46	50	47
Fertilized	98	96	94	97

3.1.3. *Summary and conclusions*

In a field experiment *D. lineolata* deposited its eggs proportionally to the available green leaf area and showed no preference for a developmental stage until tasseling. The moth preferred stages before silking to those after silking. An average egg mass deposited on maize in the field contained two eggs and the size was not influenced by the stage of plant development. These small egg masses are not easily visible and this makes it less suitable to be used as a criterion for economic thresholds. From midwhorl stage onwards (significantly) more eggs (60 to 70%) were deposited in (significantly) larger masses on the upper leaf surface, as compared to the lower surface. The vertical distribution of the egg masses over the plant was symmetric and unimodal. It may be that the survival rates of the larvae were higher near the cob, as was found for *O. nubilalis* by CHIANG (1964) (see also chapter 4.4.).

S. frugiperda hardly deposited any egg masses after the tasseling stage. There was a drop in the number of egg masses in the stage just after midwhorl. Selection against oviposition at this growth stage might have occurred as the larvae, which develop from these eggs, are not ready to pupate before tasseling and become exposed to natural mortality factors, when the whorl disappears. Egg mass size increased significantly from about 80 at early whorl stage to about 400 at tasseling.

At early whorl stage oviposition by *S. frugiperda* occurred only on lower leaf surfaces. As the plant developed, increasing percentages of the total number of egg masses were deposited on the upper leaf surface, reaching a 40 per cent at tasseling. The leaves just below the whorl seemed to be favoured for oviposition.

In a cage experiment bean intercropping in maize and sorghum decreased oviposition by *D. lineolata* and *S. frugiperda*, although not significantly. *D. lineolata* oviposited significantly more on maize than on sorghum and more on fertilized than on unfertilized plants. As leaf area only in part explained these differences, there may be a preference. *S. frugiperda* deposited significantly more eggs on maize than sorghum. Fertilized plants received more egg masses than unfertilized, but this difference was not significant.

The results obtained in this experiment will also be dealt with in chapters 4.1., 5.1. and 6.2..

3.2. ABUNDANCE OF PEST INSECTS IN MAIZE-BEAN POLYCULTURES

3.2.1. *Literature*

3.2.1.1. Polycultures

'Growing two or more useful plants simultaneously in the same area' is common practice by small farmers in the tropics. KASS (1978) named this practice *polyculture*. *Multiple cropping* has been defined by HARWOOD (1975) as growing more than one crop on the same land in one year. When two or more crops are grown simultaneously it is called *mixed cropping* when they are intermingled and not in rows, and *intercropping* when they are sown in alternate rows in the same area (RUTHENBERG, 1971). The latter cropping system was used in the following investigations. When weeds are regulated within a crop, weeds will be given the crop status in this paper and the above definitions apply.

Literature generally indicates that polycultures, for small farmers in the tropics, are good practice. The advantages of polycultures compared to monocultures are of an agronomic, socio-economic and nutritional character and have been extensively reviewed by KASS (1978), NORTON (1975) and PERRIN(1977). They can be summarized as follows.

Agronomic advantages

Higher productivity in terms of gross returns per ha, identified as Land

Equivalent Ratios[1] (LER) greater than unity. This has been shown for a wide range of crops and experimental conditions (KASS, 1978). Higher productivity is obtained by:

1. a more efficient use of solar radiation, or beneficial mulching or shading;
2. a more efficient use of soil water and soil nutrients because of a greater degree of root zone exploitation;
3. growing cereals with legumes increases soil fertility and decreases competition for nitrogen;
4. reduction of autotoxic effects of certain plants and the possibility of high plant densities;
5. a dense canopy of plants smothers weed species and provides protection against erosion;
6. favourable changes in the incidence of pests and diseases.

Socio-economic and nutritional advantages

1. The production risk is less and therefore the returns are more dependable. Traditional cropping systems have been selected over the years, which lead to a stable productivity. Also the uncertainty of the unstable market in tropical countries can be alleviated by having more crops to offer.
2. An improvement in human and animal nutrition, especially the combination of cereals with grain legumes, because the latter provide much protein.
3. Reduction of unemployment and underemployment in this capital scarce and labour intensive agriculture.
4. Optimal use of limited land resources.
5. Less dependence on agrochemicals.

With regard to ease of harvest and (other) mechanized operations polyculture presents some problems but recent research, aimed at reducing these difficulties has been surprisingly succesful (KASS, 1978).

The 'Centro Agronómico Tropical de Investigación y Enseñanza' (CATIE), Turrialba, Costa Rica, investigates which crop combinations are most suitable for Central America.

3.2.1.2. Pest abundance in polycultures

Pest regulation in multiple cropping systems has been reviewed by a number of authors (PERRIN, 1977; VAN EMDEN, 1977; PERRIN AND PHILLIPS, 1978; NORTON, 1975; LITSINGER AND MOODY, 1976), and more specifically in maize and bean polycultures by ALTIERI et al. (1978). Reviews of the effect of weeds on the abundance of pests have been given by ALTIERI et al. (1977), VAN EMDEN (1965)

[1] Land Equivalent Ratio is defined as the total land required using monoculture to give total production of the same crops equal to that of 1 hectare of the intercrop. It is calculated by determining the ratio of the yield of a crop in a mixture to its yield in monoculture under the same management (weeds, fertility, etc.) level. The optimum monoculture population is used as a comparison. The ratios of all crops in the mixture are then added to give the land equivalent (IRRI, 1974).

and ZANDSTRA and MOTOOKA (1978); ALTIERI and WHITCOMB (1979) reviewed the manipulation of beneficial insects.

The effect of polycultures on insects may occur during the plant colonization phase (invasion and settling) or the plant development phase (population development and survival), of the insect.

Plant colonization

The densities of individual plant species in polycultures are usually lower than in monocultures. ROOT (1973) suggested that herbivores are more likely to find hosts growing in dense or nearly pure stands ('the resource concentration hypothesis').

The visual effects of the cropping systems on the host location by insect pests may be important. A crop background effect was reported for *Ostrinia furnacalis* Guence in maize by RAROS (1973). The borer preferred to oviposit on maize plants with a brownish background rather than those with a solid green background, which may partly explain the reduced infestation in maize by the borer when intercropped with peanuts. The aphid *Brevicoryne brassicae* L. was more attracted to Brussels sprouts *(Brassica oleracea* var. *gemmifera)* when grown on bare soil than when it was grown with an artificial green background (SMITH, 1976a), while for some syrphids *(Melanostoma* sp., *Platycheirus* sp., *Spaerophoria* sp.) the opposite was true (SMITH, 1976b). In polycultures the plant density or the plant itself (size or colour spectrum) may have a visual effect.

Olfactory camouflage of *Brassica oleracea* by tomato *(Lycopersicon esculentum)* attacked by *Phyllotreta cruciferea* Goetze was demonstrated by TAHVANAINEN and ROOT (1972). MONTEITH (1960) showed that non-food plants masked olfactorily, the host larvae and host plant for a tachinid fly. This effect on predators or parasites could be a disadvantage of polycultures. Grass weeds, mainly *Eleusine* sp. and *Leptochloa* sp. probably contained a chemical which repelled the leafhopper *Empoasca kraemeri* Ross and Moore from beans (ALTIERI et al., 1977).

A familiar example of diversionary hosts is the strip cropping of alfalfa *(Medicago sativa)* with cotton. The presence of alfalfa, an attractive habitat for *Lygus hesperus*, deterred the migration of this insect to cotton and in this way acted as a trap crop (STERN, 1969). Maize rather than sorghum was preferred for oviposition by *S. frugiperda* (Exp. A II, chapter 3.1.); in Nicaragua sorghum was only heavily infested in the absence of adjacent maize crops.

Insect development

A changed nutritional value of the host plant because of competition in the polyculture or a change in microclimate by the non-host plant may affect insect development and survival (see also chapter 4.1.). Laboratory findings by TAHVANAINEN and ROOT (1972) suggest that confusing olfactory stimuli received from non-host plants reduced insect feeding.

Another factor of polycultures concerns the mortality of insect pests by natural enemies. The increased canopy of a polyculture may provide shelter for predators. Cruciferous crops undersown with clover seemed to increase the number of predators, notably carabids (DEMPSTER and COAKER, 1974). Groundnuts intercropped with maize provided a favourable habitat for spiders *(Lycosa* sp.), which showed significant predatory effects on the borer *(Ostrinia furnacalis)* larvae (IRRI, 1974). Maize, sorghum and alfalfa intercropped with cotton may act as a predator reservoir for cotton (JIMENEZ and CARRILLO, 1976; FYE and CARRANZA, 1972; VAN DEN BOSCH and STERN, 1969).

Non-hosts may have alternative prey and/or supplementary food, such as pollen and nectar, for beneficial insects; this has been reviewed by ALTIERI and WHITCOMB (1979). An example is the wide range of natural enemies, which develop because of the presence of a harmless aphid of the weed *Urtica dioica* L., before the harmful aphids appear on the cultivated plants (PERRIN, 1975). BEIRNE (1967) mentioned the possible benefits of regulating non-crop vegetation within the crop area.

Level of pest abundance

The above mentioned effects may reduce pest incidence in polycultures. Polycultures however may also escalate pest problems e.g. by providing alternative host plants either in space or time. It depends on the specific herbivores and their natural enemies whether the pest level will be lower than in monocultures. Additional pest control methods will still be necessary, depending if this level is less or more than the economic threshold.

3.2.2. *Introduction*

3.2.2.1. Experimental site

The experiments were carried out in 1977 and 1978 at St. Lucia, Dept. of Boaco, located on the border of two regions both important for foodgrains, the Interior Central and Interior South (fig. 2). The community is situated in a valley 500 m above sea level. A traditional maize-bean intercropping system was predominant in the first growing period. In the second growing period tomatoes were sown next to the maize stem, the latter being used as a support. The use of agrochemicals was sporadic, except for fungicides to protect the tomato crop.

A real problem of the ecological studies was to choose the size of the experimental plots. The areas had to be large enough to sustain a 'natural population' as defined by HUFFAKER and MESSENGER (1964) (DE LOACH, 1970). At St. Lucia the lack of efficient and cooperative farmers on the one hand and the statistical requirements for the design on the other hand resulted in an arbitrary minimum plot size of 20 × 20 m. It remains to be seen whether this plot size can be taken as an ecological unit, especially with such mobile parasites as adult tachinids.

An advantage of working directly with the small holder on his field is that one acquires information on traditional farming technology and the socio-economic environment of the peasant, which cannot be obtained at the experimental stations (VERSTEEG and MALDONADO, 1978). Another advantage is that the agroecosystems are undisturbed in contrast to the artificial conditions at the experimental stations, especially with regard to natural enemies.

3.2.2.2. Maize-bean intercropping

In Latin America 60 per cent of maize and 80 per cent of beans are grown in multiple cropping. A combination of these crops is the most common (FRANCIS el al., 1978). In maize intercropped with beans ALTIERI et al. (1978) reported a reduced whorl infestation of 23 per cent by *S. frugiperda*, they also found 14 per cent reduction in *S. frugiperda* as cutworms. The incidence of *Diabrotica balteata* LeComte, a common pest in maize and beans was reduced by 45 per cent. Principle predators were *Condylostylus* sp. (Diptera: Dolichopodidae) and some Hemiptera (Reduviidae and Nabidae), the populations were higher in the polyculture. RYDER (1968) reported from Cuba a reduced incidence of *S. frugiperda* in maize alternated in eight-row strips with the non-host sunflower, compared to a monoculture of maize.

In our experiments bean intercropping in maize was investigated for its effects on the grain yield, the plant development of both crops and on the incidence of the maize pests *S. frugiperda* and *D. lineolata*. In the first experiment the injury to maize by both pests was significantly reduced, in subsequent experiments the possible causes were investigated: reduced oviposition, less dispersal of first instar larvae (for *S. frugiperda* only), higher natural mortality due to parasites and predators.

3.2.3. *Material and methods*

Three field experiments (B I, B II, B III) with maize as a monoculture and intercropped with beans were conducted in succession in 1977 and 1978 at St. Lucia, Dept. of Boaco (table 15). Insects and injury were regularly counted. The following numbers of plants were sampled: B I 2880, B II 960, B III 640; and per planting system: B I 960, B II 320, B III 320. In experiment B I only, data on maize and bean yield, the incidence of *D. lineolata* and insects on beans were collected. In experiments B II and B III the effect of bean intercropping on *S. frugiperda* in maize was of primary interest. In the second growing period of 1978 the effect of the presence of beans in the maize crop (cage Exp. A II, chapter 3.1.) and the effect of a wider spacing of the maize rows (Exp. B IV) on oviposition by *S. frugiperda* and *D. lineolata* were investigated at the research station La Calera, Managua. In Experiment B V the dispersal of the first instar larvae of *S. frugiperda* in different planting systems was investigated. Table 15 lists the experiments.

All agricultural practices were carried out by the local farmer, such as soil preparation, sowing (with plantstick), weeding and earthing-up.

3.2.3.1. Experiment B I

In the first growing period of 1977 maize and beans were sown in dry soil on May 12 to 14 at St. Lucia; germination started with the first rains on May 14 and was completed by May 18.

Treatments consisted of 3 planting systems (P), 2 maize cultivars (C) and 2 different fertilizer gifts (F). The planting systems are presented in diagram 3. P_0 is the traditional local method of intercropping beans with maize, in which besides the 3 intercropped bean rows, beans were also planted within the maize row. P_1 is a planting system with 2 bean rows intercropped and no beans in the maize row. P_2 is a maize monoculture. The treatments C consisted of 2 maize cultivars: the open pollinating traditional local variety Tuza Morada (C_0) and the hybrid X-105-A(C_1). The bean variety used was Honduras-46. The treatments F were no fertilizer (F_0) and fertilizer application (F_1). The soil was chemically analysed and fertilizer applied accordingly. F_1 consisted of NPK fertilizer (15-30-15) and ammonium sulphate (32% N) at the rate of 90 and 70 kg ha^{-1} respectively at sowing, and 65 kg

Table 15. List of the maize-bean intercropping experiments

Experiment (code)	Year/ Growing period/ Locality[1]	Materials and methods (chapter)	Results: Subject investigated (chapter)	Results: Tables (Tb) and Figures (Fg) (Exp. code)
B I	1977/1st/SL	3.2.3.1. (diagram 3)	Yield and plant development (3.2.4.1.)	Tb: 16, 17 (B I); 18 (B II, B III). Fg: 13, 14 (B I)
B II	1977/2nd/SL	3.2.3.2. (diagram 3)	Incidence of pests (3.2.4.2., 3.2.4.3.) and predators (3.2.4.6.)	Tb: 16 (B I). Fg: 15, 18, 19 (B I); 16 (B II); 17 (B III)
B III	1978/1st/SL	3.2.3.3.	Incidence of parasites (3.2.4.6.)	Tb: 23, 25 (B I); 24 (B III)
			Oviposition (3.2.4.4.)	Tb: 19 (B I, B II, B III)
A II	1978/2nd/Mg	3.1.2.2. (diagram 2)	Oviposition (3.1.2.3.)	Tb: 12 (A II)
B IV	1978/2nd/Mg	3.2.3.4.	Oviposition (3.2.4.4.)	Tb: 20 (B IV)
B V	1978/1st/SL	3.2.3.5. (diagram 4)	Dispersal of *S. frugiperda* larvae (3.2.4.5.)	Tb: 21, 22 (B V)

[1] SL = St. Lucia; Mg = Managua.

ha^{-1} urea 28 days after plant emergence. Ammonium sulphate and urea were applied to the maize only at rates which apply to the monoculture (P_2), while quantities proportional to the number of plants per ha were applied to the intercropping plots (P_0, P_1). Several urea treatments were applied in error so it was decided to put it on all plots. Differences due to fertilizer therefore were only brought about by the applications at sowing.

The experiment was laid out according to a 3×2^2 (P × C × F) factorial design in 3 replicates making a total of 36 plots. The interactions C × F and P × C × F were partially confounded in 6 blocks (YATES, 1937). The plots of 20 × 20 m were separated by paths 1.5 m wide.

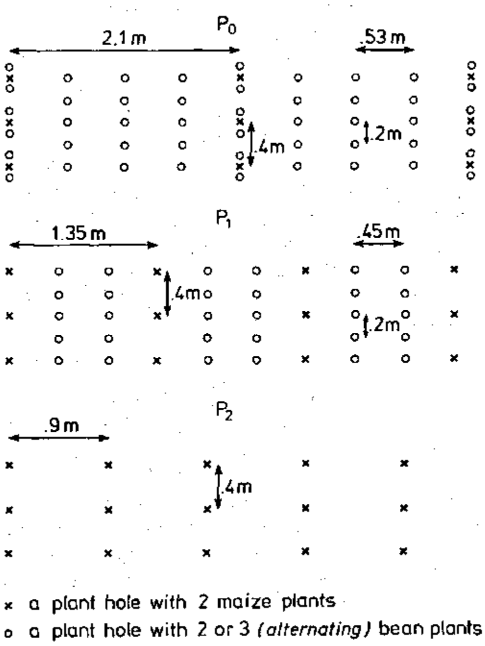


DIAGRAM 3. Maize: bean intercropped (P_0, P_1) and as monoculture (P_2). Lay-out of the planting systems in Experiment B I and B II.

Twice a week a random sampling site of 20 consecutive maize plants was taken at least 2 m from the border in each quarter of a plot. The number of injured whorls was counted and the height of the 3 last plants per site was measured. The start of tasseling was checked by counting the number of tasseling plants. Once a week all insects on the maize plant were counted, such as egg masses of *S. frugiperda* and *D. lineolata*, spiders and earwigs.

D. lineolata injury to the hybrid X-105-A was determined 111 and 112 days after plant emergence. At each of two random sites per plot, 20 consecutive plants were dissected and scored for the number of injured internodes, perforations, exit holes, larvae (normal and diapausing), pupae, pupal skins and parasites. The cultivar Tuza Morada matured later so the sampling was postponed till 130 days after plant emergence and because of heavier infestation only 10 plants per site were sampled.

The bean plants were sampled twice a week in a random site per plot quarter. In the P_0 plots there were 2 sites of a pair of adjacent rows (a bean and a maize-bean row) and 2 of a pair of adjacent bean rows, all 1.33 m long. In the P_1 plots each site included a pair of adjacent bean rows 1.54 m long. With this methodology (see FALCON and SMITH, 1973) a fixed portion of a 'manzana' (1 mz = .7 ha), was sampled, namely 4×10^{-4} mz^{-1}. At each sampling site the height of a representative bean plant was measured. Leaf injury and incidence of chrysomelids, other insects and slugs were scored.

A pair of adjacent rows were harvested to estimate maize and bean yield (in P_0 a maize or bean and a maize-bean row at two random sites per plot). The number of harvested plants were counted. Beans started to flower 35 days after plant emergence. The plants were uprooted 70 days after emergence, left to dry and threshed at 82 days. The maize hybrid X-105-A was harvested at 110 days, and the local variety Tuza Morada 127 days after plant emergence. Grain weight was adjusted to 15% moisture.

In the analysis of variance of the main effects and interactions, the effect of 6 blocks was first eliminated as a set of covariables. Corrected means of the product classification C × F were obtained. The SPSS computer program was used.

3.2.3.2. Experiment B II

In the second growing period of 1977 the maize hybrid X-105-A and the bean cultivar Honduras-46 were sown on September 26 in a randomized block design with 3 treatments and 4 replicates. The treatments consisted of the same planting systems (P_0, P_1, P_2) as used in experiment B I (see diagram 3). The plot size was 25 × 20 m. Germination was completed by September 30. NPK fertilizer (10-30-10) and urea were applied at sowing at a rate of 130 and 65 kg per ha. The urea treatment was repeated 3 weeks after plant emergence. The urea treatments were applied at the same rates as described for experiment B I. Plots were weeded 14 days after plant emergence.

In each plot 2 fixed sampling sites were used with 20 labelled consecutive plants each and 2 random sampling sites each consisting of 20 consecutive plants in a row. Whorl injury by *S. frugiperda* was scored twice a week using the injury index, designed by WISEMAN et al. (1966). A moderate attack of the whorls, probably by bacteria of the genus *Erwinia*, interfered with the injury ratings. Plant height was measured twice a week on one representative plant per sampling site.

Five weeks after plant emergence the experiment was abandoned due to severe drought, which caused an accelaration of tasseling. Yield data were therefore not considered.

3.2.3.3. Experiment B III

In the first growing period of 1978, the maize hybrid X-105-A and the bean variety Honduras-46 were sown on May 18 in a randomized block design with 2 treatments and 4 replicates. Two planting systems, P_0 and P_2 were compared. P_0 was maize intercropped with 3 bean rows. Maize rows were 2.1 m apart and the distance between plant holes was .4 m. The spacing for the beans was .53 m between rows and .2 m between plant holes. Treatment P_2 was a monoculture of maize, with spacing .9 m between rows and .4 m between plant holes. Maize plants received 2, and beans 3 to 4 seeds per plant hole. Plot size was 18 × 22 m. Germination was completed by May 24. NPK fertilizer (10-30-10) and urea were applied at a rate of 130 and 65 kg per ha respectively. The urea treatment was repeated 3 weeks after plant emergence. The dosages of urea treatments were those as described for experiment B I.

Maize plants were sampled weekly in a random site consisting of 20 consecutive plants in the row, per plot quarter. The height of the last 3 consecutive plants per site were measured. Each plant was examined for egg masses, whorl injury by *S. frugiperda* and the incidence of spiders and earwigs. The start of tasseling was checked by counting the number of tasseling plants.

S. frugiperda larvae are not easily visible in the whorl and can only be counted by dissecting the plant. Larval presence therefore was estimated by examining the whorl for injury. The index used for measuring the intensity of injury in maize whorls (only in Exp. B III) is:

0 – no visible injury
1 – less than 3 leaf lesions
2 – number of leaf lesions more than 2 and less than 8
3 – more than 7 leaf lesions
4 – less than 3 holes smaller than 2 cm
5 – more than 2 holes smaller than 2 cm
6 – less than 3 holes larger than 2 cm
7 – more than 2 holes larger than 2 cm
8 – whorl almost completely eaten away
9 – whorl completely eaten away

This index proved to be more practical than the one used by WISEMAN et al. (1966) for plant resistance studies. The index is such, that it contains a qualitative aspect with regard to larval size and a quantitative aspect with regard to larval density per plant. The three injury types (lesions, holes smaller and larger than 2 cm) may lead to different scores by varying larval densities per plant. The changes in the larval population will appear in the injury score 1 to 3 days later.

3.2.3.4. Experiment B IV

On November 1, 1978 a randomized block design with 4 replicates was sown with the maize variety Nic-Synt-2 in plots of 20 × 16 m with two treatments: a row spacing of 1 m and 2 m. Egg counts were made 7 and 13 days after plant emergence and then stopped because of a severe *S. frugiperda* attack, which defoliated the plants leaving only the midribs and killed many plants by stem tunneling and feeding on the meristematic tissue of the bud, causing 'dead heart'. In each plot 4 sampling sites consisting of rows 4 m long were taken at random. Results are presented for the totals of the sampling dates. Differences for *D. lineolata* oviposition between blocks may be due to differences in immigration from maturing maize fields nearby. In the analysis of variance the distance from the source of infestation was introduced as a covariable in order to eliminate this bias from the treatment effect.

3.2.3.5. Experiment B V

The maize hybrid X-105-A and the bean cultivar Honduras-46 were sown on May 24, 1978. The 5 treatments consisted of different planting systems and plant densities (see diagram 4). Plant density of system IA and IB was 95,200 plants per ha and of system IIA and IIB 23,800 plants per ha. Treatments A and B had one and 2 plants per plant hole respectively. System III was maize intercropped with beans. The 5 planting systems were laid out in a randomized block design with 3 replicates.

Plants completed germination on May 30. On 20, 30 and 39 days after germination one plant per plot was infested with several egg masses of *S. frugiperda* collected in maize fields of the experimental station, La Calera, Managua. Three days before each infestation, methomyl (Lannate 90% a.i. SP, .25 kg ha^{-1}), a very short-working insecticide, was applied with a knapsack sprayer to obtain plots free from *S. frugiperda*. Care was taken to ensure that plots received egg masses of similar size and age (colour). Egg masses were attached to the lower side of a whorl leaf of one labelled plant located in the middle of each plot, in the first two placements 2 to 3 egg masses and in the last infestation 5 to 6 egg masses, these egg masses were checked daily.

Three to 5 days after each infestation, when larval dispersal was assumed to have ended, the position of the infested plants in relation to the infestation source was mapped. Data on wind direction and velocity were obtained from the Meteorological Institute.

In order to analyse the larval distribution in relation to wind, each plot was divided in 4 quadrants (diagram 4). Quadrant 3 (downwind) was tested against quadrant 1 (upwind) and quadrant 2 was tested against quadrant 4 (both at right angles to the wind) with the sign test. For the analysis of the effect of planting systems on larval dispersal only the last infestation, which was rather succesful, was taken into consideration.

3.2.4. *Results and discussion*

3.2.4.1. Yield and plant development

The results are only from Exp. B I, in which many data about the maize plant were collected.

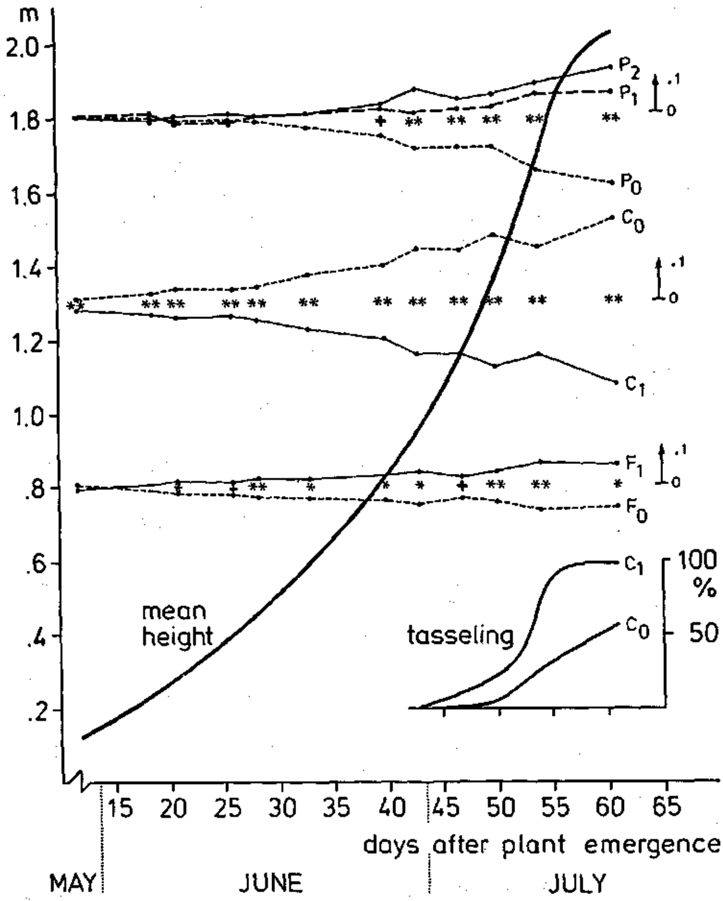
Maize plants in planting system P_0 with beans sown in the maize row were significantly shorter than in planting systems without beans sown in the maize row (P_1, P_2) (table 16, fig. 13). This may be explained by the interspecific competition for soil nutrients. This competition probably also reduced the number of plants in P_0 by 16–20 per cent as compared to P_1 and P_2 (table 16). Grain yield per plant was highest in planting system P_1, although the difference was not significant (table 16). Maize plants in P_1 could receive more solar radiation because of its wider spacing than those in P_2. This was also the case

TABLE 16. Maize: bean intercropped (P_0, P_1) and as monoculture (P_2). Maize cultivars (C_0, C_1), both without and with (F_0, F_1) fertilizer application. The effect on yield and plant development in maize and beans and on the incidence of and injury by, *D. lineolata* in maize. Analysis of variance: F-values, significancies and means. (Exp. B I)

Source of variation		df	Maize: Grain yield per row length	Grain yield per plant	Number per row length: plants	Number per row length: ears	Number of ears per plant	Plant height[1]
Blocks (covariables)		5	2.83*	1.59	2.00	3.73*	1.24	7.69**
Main effects								
Bean intercropping	(P)	2	11.4**	2.12	5.41*	7.29**	1.20	19.1**
Cultivar	(C)	1	96.8**	44.0**	12.7**	60.5**	35.0**	128.**
Fertilizer	(F)	1	1.74	.27	.40	1.42	.60	11.5**
Two-way interactions								
P × C		2	.30	.01	.72	.62	.46	1.92
P × F		2	.89	.37	.80	1.41	.16	.43
C × F		1	1.22	.20	.43	.98	.04	2.06
Three-way interactions								
P × C × F		2	.05	1.27	1.01	.81	.22	1.88
Error: V.C.		19	15.5	15.1	15.2	12.8	7.90	5.34
Total		35						
			gram		number			cm
Grand mean			4897	123.	39.6	40.4	1.02	167.
Bean intercropping	P_0		−15	−3	−12	−10	1	−8
	P_1		15	7	8	9	2	3
Monoculture maize	P_2		−0	−4	4	1	−3	5
Cultivar	C_0		−25	−17	−9	−17	−8	11
	C_1		25	17	9	17	8	−11
Fertilizer at sowing	F_0		−3	−1	−2	−2	−1	−3
	F_1		3	1	2	2	1	3

[1]Average of three sampling dates (50, 54 and 61 days after plant emergence).
[2]Sum of encountered larvae, pupae and pupal skins.
[3]Means are presented in figure 19.
[4]Percentage deviations of ln backtransformed values do not add up to zero.

D. lineolata					df	Beans			
Number per plant				Egg masses (ln(x+1))		Grain yield per		Number of plants per row length	Plant height at 34 days
injured internodes	perforations	larvae[2]	injured ears			row length	plant		
		F-values							
2.13	1.92	.85	1.76	1.14	5	1.15	1.30	2.16	2.07
10.5**	14.7**	7.14**	.10	2.83+	1	1.57	16.1**	9.20*	3.65+
134.**	149.**	68.8**	36.9**	5.14*	1	11.0**	.71	1.78	.17
.71	1.93	.22	6.55*	1.58	1	.01	1.28	1.25	.00
6.36**[3]	11.5**[3]	5.53*[3]	1.21	1.87	1	7.77*	1.39	.60	4.95*
.96	.96	.35	1.63	.02	1	.15	.39	.26	1.32
.57	1.36	1.01	3.87+	.65	1	.42	.55	.04	.86
.99	1.53	.22	1.76	1.25	1	.79	1.50	1.29	.18
20.0	21.2	26.2	69.5	89.9	11	18.5	20.3	21.9	12.8
					23				
		means							
number per plant			number per 100 plants[4]			gram		number	cm
2.20	3.05	1.17	9.38	.897		543.	7.44	76.8	67.9
percentage deviation from grand mean									
−18	−23	−18	31	26		5	17	−14	−5
−1	−1	−3	−19	−58		−5	−17	14	5
19	24	21	−12	45					
38	43	36	−70	49		−12	−3	−6	−1
−38	−43	−36	70	−41		12	3	6	1
−3	−5	−2	30	−24		0	−5	5	0
3	5	2	−30	26		−0	5	−5	−0
						some treatment combinations			
					P_0 C_0	3			−12
					P_0 C_1	7			2
					P_1 C_0	−28			10
					P_1 C_1	18			0



Note: For planting systems significant effects concern all treatments.

FIG. 13. Plant height (as deviation from the mean) of two maize cultivars (C_0, C_1) without and with fertilizer (F_0, F_1), bean intercropped (P_0, P_1) and as monoculture (P_2). (Exp. B I)

with the widely spaced maize plants in P_0, but they competed with beans in the same row. Therefore maize plants in P_0 and P_2 produced about the same yield although the plants in P_0 were significantly shorter than in P_2. Maize yield per row was significantly different for planting systems and cultivars (table 16). The grain yield per row of maize was highest in system P_1 and lowest in P_0. This can be concluded from the discussed effect of the planting system on the yield per plant and the number of plants per row.

The plant heights of both maize cultivars differed significantly (fig. 13). Sixty-one days after plant emergence the local variety Tuza Morada (C_0) measured 2.22 m and the maize hybrid X-105-A (C_1) only 1.78 m. The number of ears produced was significantly higher for the maize hybrid C_1 (table 16). Fertilizer at sowing caused a small significant increase in plant height of 9 cm at 61 days (fig. 13).

Tuza Morada (C_0) was probably too tall (shading) for beans in planting system P_1: yield decreased and plant parts elongated (significant two-way interactions $P \times C$ for bean plant height and bean yield per row, table 16). The increased shading and the slightly narrower distance between bean rows in planting system P_1, probably lowered significantly bean grain yield per plant compared to planting system P_0 (table 16). In planting system P_0 beans competed with the maize plants within the maize row. This probably caused the significant loss of bean plants (table 16).

Based on the number of plants sown and on the final number of plants at harvest, the expected and actual yields per ha of maize and beans could be compared (table 17). Tuza Morado (C_0) produced a bigger maize yield in planting system P_1 than was expected. Firstly because maize plants in P_1 did not have to compete with bean plants in the same row as in P_0. Secondly C_0 is a tall variety that needs to be widely spaced to make efficient use of solar radiation; this is absent in P_2. Thirdly the number of grains formed by variety C_0 in planting system P_0 was significantly less than in P_1, because of inadequate pollination due to the wider plant spacing. For bean yield planting system P_1 was inferior, because of too much shade, especially with the tall variety C_0 (table 17).

The returns in dollars per ha for the maize variety Tuza Morada (C_0) were highest in the P_1 system (fig. 14). However the bean yield was low, which is a disadvantage for the subsistence farmer. The returns for the hybrid X-105-A

TABLE 17. Plant densities and yields per ha of maize and beans using two maize cultivars (C_0, C_1), bean intercropped (P_0, P_1) and as monoculture (P_2). (Exp. B I)

	Bean intercropping		Mono-culture	Ratios ($P_0 = 1$)		
	P_0	P_1	P_2	P_0	P_1	P_2
Maize	plants per ha ($\times 10^3$)			plant density		
Sown	23.8	37.0	55.6	1	1.50	2.33
Sampled	16.7	31.6	45.7	1	1.89	2.74
Maize cultivar	yield (kg per ha) ($\times 10^3$)			yield		
Tuza Morada (C_0)	1.39	3.35	3.91	1	2.40	2.81
X-105-A (C_1)	2.58	5.01	6.94	1	1.95	2.69
Beans	plants per ha ($\times 10^3$)			plant density		
Sown	190.5	148.1	–	1	.78	–
Sampled	126.5	129.3	–	1	.98	–
Maize cultivar	yield (kg per ha) ($\times 10^3$)			yield		
Tuza Morada (C_0)	1.06	.58	–	1	.55	–
X-105-A (C_1)	1.10	.95	–	1	.86	–

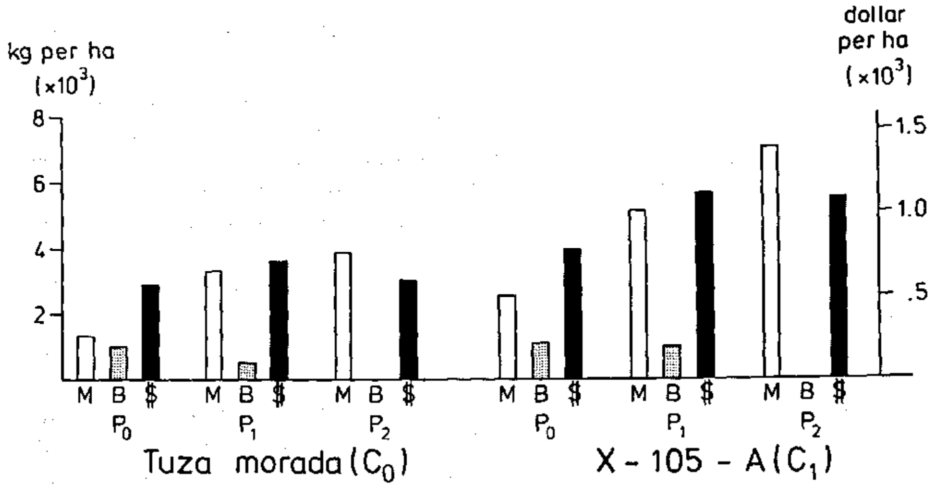


FIG. 14. Bean intercropping systems (P_0, P_1) and a monoculture (P_2) of two maize cultivars (C_0, C_1). The effect on grain yield of maize (M) and beans (B), and on returns ($). (Prices to producer in dollars per 10^3 kg: maize 157.5, beans 346.4; BCN, 1978b). (Exp. B I)

(C_1) were highest in the intercropping system P_1 and the monoculture P_2. The difference between the two cultivars C_0 and C_1 was very large both in yield and returns. In the intercropping systems the hybrid C_1 increased returns by 45%. Replacing the local variety C_0 in the traditional planting system P_0 by the hybrid C_1 increased returns by 20%. Viewed economically using the hybrid C_1, system P_1 increased returns per ha by 42% compared to the traditional planting system P_0; the bean yield per ha was only 14% less and the maize yield increased by 95% per ha.

Data collected on the maize plants in Exp. B II and B III related only to plant height. Although the same planting systems were used in Exp. B II as in Exp. B I, no significant differences were found in plant height, due to the high degree of variation caused by drought (table 18). In Exp. B III no beans were interplanted in the maize row to reduce the effect of competition, plant height was the same for both planting systems (table 18).

TABLE 18. Maize: bean intercropped (P_0, P_1) and as monoculture (P_2). Plant height of maize in the second growing period of 1977 (Exp. B II) and the first growing period of 1978 (Exp. B III).

Cropping system		Plant height (cm)	
		Exp. B II[1]	Exp. B III[2]
Bean intercropping	P_0	87 ± 16	110 ± 12
	P_1	69 ± 13	–
Monoculture	P_2	78 ± 17	110 ± 7

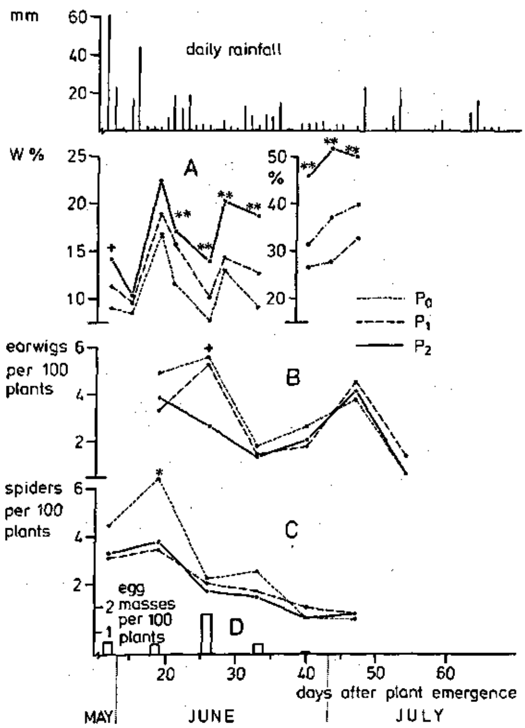
[1] Means ± SD, average of 31 and 34 days after plant emergence.
[2] Means ± SD, average of 41 and 48 days after plant emergence.

3.2.4.2. *S.frugiperda* and *D. lineolata* in maize

In assessing the effect of the planting system on maize pests, it has to be taken into account that the plants differ physiologically because of bean competition and different maize plant densities. Although in this experiment it is not possible to separate this effect, the result of the plant density experiment F in chapter 4.1. suggests that the effects on the larvae of *S. frugiperda* and *D. lineolata* by physiologically different plants are small.

S. frugiperda

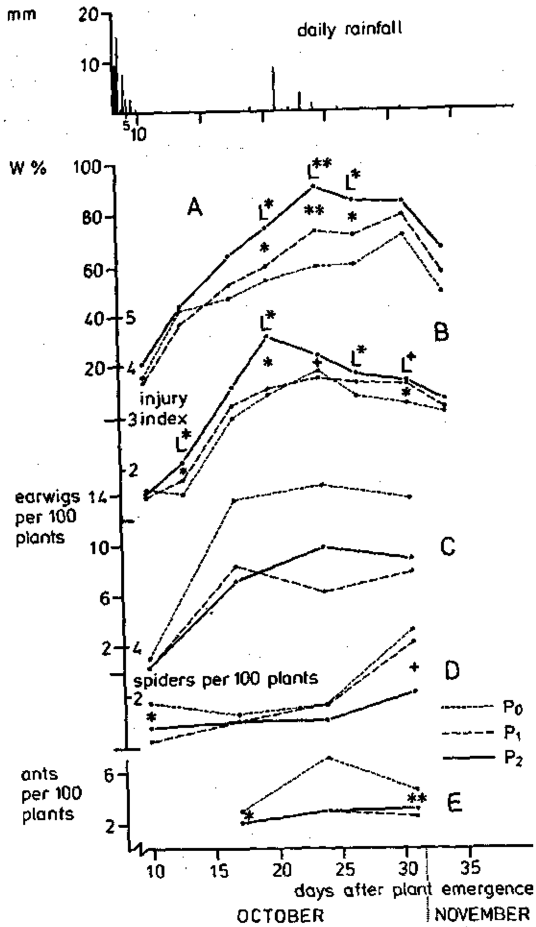
The significant effects of maize-bean intercropping on the percentage of whorls injured[1] by *S. frugiperda* can be seen in figure 15A (Exp. B I), figure 16A



Note: significant effects concern all treatments.

FIG. 15. Maize: bean intercropped (P_0, P_1) and as monoculture (P_2). The effect on injury by *S. frugiperda* and on the incidence of predators. (Exp. B I)
A. Percentage of whorls injured (W) by *S. frugiperda*.
B. Average number of earwigs (*Doru taeniatum*).
C. Average number of spiders (Araneae).
D. Average number of egg masses of *S. frugiperda* (P_0, P_1 and P_2 combined).

[1] As the same number of plants was used per sampling site the same results would have been obtained with the number of injured whorls.



Note: L*-significant linear component.

P_2

* Treatment P_2 is significantly different from treatments P_0, P_1 (also tested P_0 versus P_1, P_2).

P_0

P_1

FIG. 16. Maize: bean intercropped (P_0, P_1) and as monoculture (P_2). The effect on injury by *S. frugiperda* and on the incidence of predators. (Exp. B II)
A. Percentage of whorls injured (W) by *S. frugiperda*.
B. Average injury score of whorls injured by *S. frugiperda*.
C. Average number of earwigs (Doru taeniatum).
D. Average number of spiders (Araneae).
E. Average number of predatory ants (*Ectatomma ruidum*).

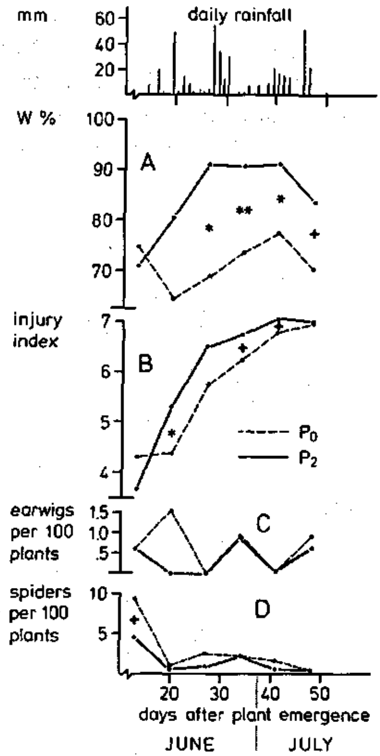


FIG. 17. Maize: bean intercropped (P_0) and as monoculture (P_2). The effect on injury by *S. frugiperda* and on the incidence of predators. (Exp. B III)
A. Percentage of whorls injured (W) by *S. frugiperda*.
B. Average injury score of whorls injured by *S. frugiperda*.
C. Average number of earwigs (*Doru taeniatum*).
D. Average number of spiders (Araneae).

(Exp. B II) and figure 17A(Exp. B III).

In Exp. B I (fig. 15A) the differences between the planting systems were larger when the bean plant density increased. Up till 33 days after plant emergence the level of infestation was low (between 8 and 22%), after 37 days, the population increased and the difference between the monoculture P_2 and the intercropping system P_0 (with the highest density of bean plants) was 20% (namely 50 and 30% of injured whorls respectively). Because of the very consistent differences between planting systems it seems that one or more factors acted continuously, such as oviposition by the moths and/or dispersal by first instar larvae. Parasitism and predation effects seem less plausable as they normally change in the course of plant development.

In Experiment B II (fig. 16A) the percentage of injured plants did not differ in the three planting systems on the first sampling dates. Later the percentage of injured whorls was significantly higher in the monoculture P_2 than in the polycultures P_0 and P_1 (80–90% versus 50–70%). The planting systems differed from the start in the intensity of whorl injury (fig. 16B). The lower injury scores for the bean intercropped maize plants probably reflects a lower number of larvae per infested plant (= injured whorl). This indicates that the lower number of larvae per plant and the lower number of infested plants had a common cause. Whether besides this process, bean odour deterred the larvae from feeding on the maize, was not investigated.

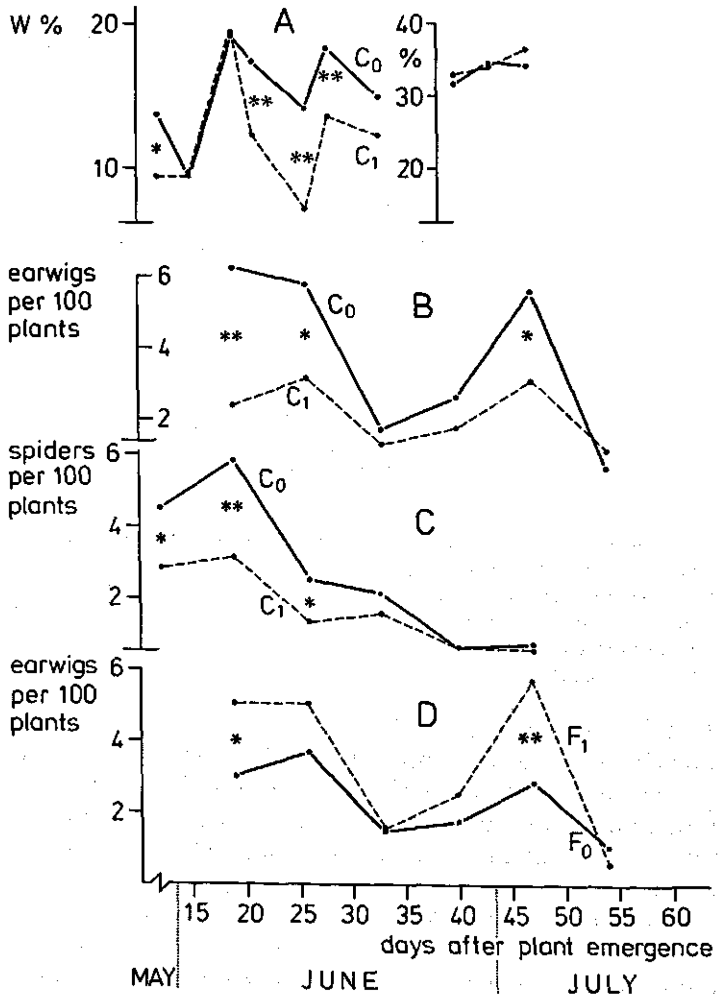


FIG. 18. Two maize cultivars (C_0, C_1). The effect on injury by *S. frugiperda* and on the incidence of predators. (Exp. B I)
A. Percentage of whorls injured (W) by *S. frugiperda*.
B. Average number of earwigs (*Doru taeniatum*).
C. Average number of spiders (Araneae).
Fertilization (F_1) and a control (F_0). The effect on the incidence of earwigs. (Exp. B I)
D. Average number of *D. taeniatum*.

In Experiment B III (fig. 17A) the maize was heavily infested by *S. frugiperda* from the start. After the 13th day the percentage of injured whorls was 90% for the monoculture P_2 and 70 to 80% for the intercropping system P_0. The intensity of whorl injury was also reduced by intercropping, probably because there were less larvae per infested plant (fig. 17B). The curves of the percentage of injured whorls and injury scores in figure 17A and 17B suggest that these differences between the planting systems were partly caused by the changes in infestation that occurred between 13 and 20 days after the plant emerged, but there are no indications for the reason.

The hybrid X-105-A (C_1) was less infested than the variety Tuza Morada (C_0) at the 2nd, 4th and 5th week of plant development (fig. 18A). The cause of the small but significant differences is not known.

D. lineolata

The number of larvae of *D. lineolata* and the degree of stalk injury in the maize hybrid C_1 were not affected by the planting system; however in the local variety C_0 injury increased by 30% when using the intercropping system P_1 and 60% in the monoculture P_2, as compared to the planting system P_0 which had the most intercropped beans (fig. 19; significant two-way interaction for the number of injured internodes, perforations and larvae, table 16).

The local variety C_0 compared to hybrid C_1 had more than twice the injury and the larvae per plant. This may be partly due to the fact that sampling in C_0 occurred two weeks later than in the earlier hybrid C_1. However oviposition may also be involved, because this seems to be closely related to leaf area (Exp. A I, chapter 3.1.) and C_0 is a tall variety with abundant foliage. The few egg masses of

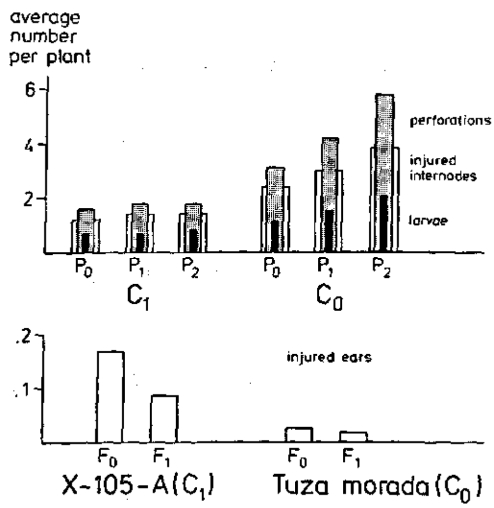


FIG. 19. Bean intercropping systems (P_0, P_1) and a monoculture (P_2) of two maize cultivars (C_0, C_1) without and with fertilizer (F_0, F_1). The effect on the incidence of and the injury by *D. lineolata* (two-way interactions C × P and C × F, table 16). (Exp. B I)

D. lineolata found were significantly more on C_0 than on C_1 (table 16).

The number of injured ears was higher in C_1, although stalk injury in C_1 was less than in C_0 (table 16). Fertilizer increased (not significantly) the number of larvae and the degree of stalk injury. It diminished (significantly) ear injury, the most in the hybrid C_1 (weakly significant two-way interaction, table 16; fig. 19).

3.2.4.3. Bean pests

In Experiment B I the bean crop hardly suffered from attacks by pests. Only the chrysomelid *Nodonata* sp. and the slug *Vaginulus plebeius* Fisher caused some leaf injury in about 4 plots situated on a small elevation in the experimental field; although the estimates made of the incidence of *Nodonata* sp. and of the injury by this crysomelid and the slug were accurate, the results of the analysis of variance were not reliable. Also in Experiments B II and B III the bean plants were hardly injured.

3.2.4.4. Oviposition by *S. frugiperda* and *D. lineolata*

Intercropping by beans may alter the visual and/or olfactory insect cues in such a way that it may lead to diminished oviposition. Therefore attempts were made to ascertain whether the different levels of *S. frugiperda* and *D. lineolata* infestation in maize as a monoculture and intercropped with beans, could be attributed to differences in the oviposition pattern. In the field experiments B I to B III more egg masses of *S. frugiperda* were found in the monoculture of maize, but differences were not significant (table 19). The size of the egg masses was not investigated. The number of *D. lineolata* egg masses found was too low to be significant.

If oviposition by *S. frugiperda* and *D. lineolata* is influenced by bean in-

TABLE 19. Maize: bean intercropped (P_0, P_1) and as monoculture (P_2). Oviposition by *S. frugiperda* on maize. (Exp. B I to B III)

Experiment	Number of replicates	Monoculture	Bean Intercropping	
		(P_2)	(P_0)	(P_1)
		average number of egg masses[1]		
B I	3	12.3 ± 4.9	11.1 ± 1.0	6.3 ± 3.5
B II	4	2.0 ± 1.2	2.0 ± 1.6	1.3 ± .5
B III[2]	3	9.0 ± 3.2	5.0 ± 3.6	–
		average number of minutes searched for an egg mass[1,3]		
B II	3	4.4 ± 1.7	5.0 ± 1.0	12.3 ± 15.3

[1]Means ± SD.
[2]19 and 23 days after plant emergence each plot was searched for half an hour for egg masses.
[3]26 days after plant emergence, the time taken to encounter 3 egg masses per plot within a maximum of half an hour was recorded. Total of 24 egg masses sampled. Only in one plot (of P_1) less than 3 egg masses (none) were found.

TABLE 20. Row spacing (1 and 2 metre) in maize. The effect on oviposition by *S. frugiperda* and *D. lineolata*. Analysis of variance: F-values, significancies and means, without (–C) and with (+C) a covariable which represents a possible gradient of infestation from an adjacent maize field. (Exp. B IV)

Source of variation	df		*D. lineolata* (number x of)						*S. frugiperda* (number x of)	
	–C	+C	Egg masses (lnx)		Eggs (lnx)		Eggs per mass (lnx)		Egg masses (lnx)	
			–C	+C	–C	+C	–C	+C	–C	+C
						F-values				
Blocks	3	3	6.38^{+}	16.0^{+}	27.9*	44.4*	16.0*	12.7^{+}	2.32	.25
Treatments	1	1	16.1*	2.82	23.4*	19.5*	35.6**	18.5*	.85	1.63
Covariable		1		.93		2.68		.37		.22
Error: V.C.	3	2	3.77	3.82	2.91	2.33	6.67	7.49	3.99	2.30
Total	7									
						means				
Grand mean			4.25		5.01		.75		3.50	
Row distance: 1 metre			4.40	4.37	5.25	5.22	.86	.85	3.55	3.60
2 metre			4.11	4.14	4.76	4.80	.65	.65	3.46	3.40
Standard error			.08		.07		.03		.07	
Number of egg masses and eggs involved			487		1152				210	

tercropping there may be two causes. Firstly the presence of the beans and secondly the wider spacing of the maize rows. The effect of beans only was investigated in a field cage experiment (for results see Exp. A II, chapter 3.1.). The effect of wider row spacing was investigated in field experiment B IV sown at the experimental station La Calera, Managua.

The effect of the row spacing on oviposition by *S. frugiperda* was absent (table 20), whereas the effect of the presence of beans gave some indications for lower oviposition (Exp. A II, table 12). For *D. lineolata* the wider maize row spacing and the presence of beans meant that less egg masses were deposited, but the effects were not significant (table 20 and 12). The size of the egg masses however was (significantly) smaller with the wide row spacing and (weakly significantly) lower when beans were present. As a result the number of eggs deposited showed the same tendency.

For both insects oviposition on maize seemed to be less in the bean intercropping systems, but the effect was not very pronounced.

3.2.4.5. Aerial dispersal of *S. frugiperda* larvae and planting system

MORRILL and GREENE (1973b) mentioned the negative geotactic and positive phototactic behaviour of the first instar and to a limited extent of the second instar larvae of *S. frugiperda*. Newly hatched larvae move upwards to the highest leaf and would then be transported by wind by means of their silk threads. BAREL (1973) found for *Adoxophyes orana* F. v. R. the same tactic responses and newly hatched larvae could be transported by wind over a distance of 45 metres in a bare field. For *Porthetria* (= *Lymantria*) *dispar* the spread in Eastern North America is mainly due to wind-blown first instar larvae (LEONARD, 1971). Female gypsy moths, although winged, do not fly. COLLINS (1917) showed that first instar larvae could be transported by air a distance of 48 km over water. He trapped larvae of the gypsy moth at wind velocities of .9 m s^{-1} but found that most dispersal occurred at velocities of 3.5 m s^{-1} or more (COLLINS, 1915; cited by LEONARD, 1971).

Experiment B V was designed to ascertain whether first instar larvae of *S. frugiperda* disperse by wind and whether this dispersal was influenced by bean intercropping and plant density.

3.2.4.5.1. Wind direction

Wind direction in Nicaragua is predominantly East. It was rather constant when this experiment was carried out (table 21). Most of the whorls injured by *S.*

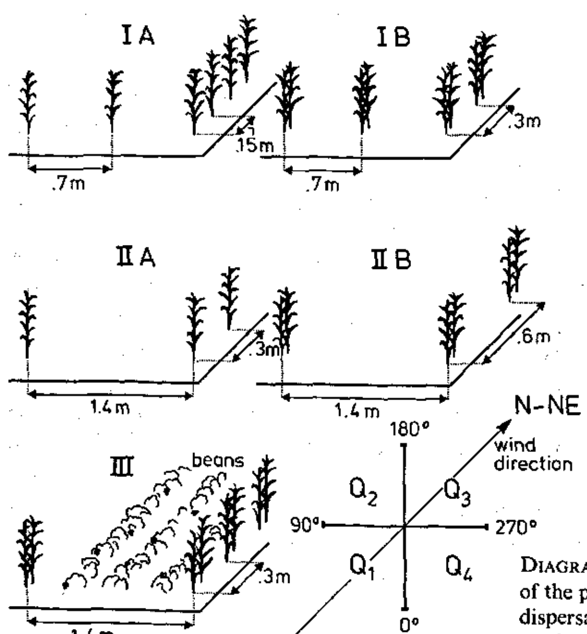


DIAGRAM 4. Layout with maize and beans of the planting systems, used to study the dispersal of first instar larvae of *S. frugiperda*. (Exp. B V)

TABLE 21. Wind direction and velocity during experiment B V (dispersal of first instar larvae of *S. frugiperda*).

Date (1978)	Days after plant emergence	Wind direction	Wind velocity (m s^{-1}) (ranges)		
			maximum	minimum	average
June 19–22	20–23	N-NE	2.6–4.3	1.1–1.3	1.4–2.4
June 29–July 3	30–34	N-NE	4.4–8.4	1.1	2.0–3.1
July 8–13	39–44	N-E	3.3–7.1	1.1–1.6	1.9–2.9

frugiperda were in quadrant 3, downwind (table 22, diagram 4). Distribution by wind probably determined the final spread. The distribution is facilitated by a thread spun by the first instar larvae, that increases its buoyance (see BAREL, 1973). The number of larvae per injured plant was not ascertained. If one reckons that the egg masses contained 100 to 200 eggs, the average success of newly hatched larvae in colonizing new plants was about 1 to 2 per cent.

3.2.4.5.2. Planting system

On 44 days after plant emergence (as explained before only this infestation was taken into consideration) the number of infested maize plants was significantly lower for the bean intercropped maize (plant system III versus I and II, diagram 4, table 22). Thus bean intercropping reduced dispersal of the first instar larvae.

There are several factors which could account for this effect:

1. wider row spacing of maize,
2. the larvae being trapped by bean plants when dispersing,
3. olfactory effect of the beans,
4. natural enemies.

The first factor can be excluded as the increase in row distance by a factor 2 in the monocultures (IA and IB versus IIA and IIB) did not show any effect, there was however an effect between the monoculture and the bean intercropping system with the same maize row distance (IIA and IIB versus III). The second factor seems the most probable. The bean crop 'trapped' the larvae when spreading aerially by their silk thread and prevented them in this way from reaching the other maize plants. This trapping capacity of the bean crop should be studied further (row direction at right angles to the prevailing winds could provide shelter for the air-borne insects; LEWIS, 1969). No indications are available for the third factor. The fourth factor seems unlikely as natural enemies were almost absent (the plots were sprayed a few days before the introduction of the egg masses).

The lower incidence of *S. frugiperda* injury to maize alternated in eight-row strips with sunflowers compared to a monoculture of maize (RYDER, 1968) may also have been caused by the trapping of first instar larvae by sunflower, a non-host; however the wind component was not investigated.

Between the different plant densities of the monocultures (IA and IB versus II

TABLE 22. Number of whorls injured by *S. frugiperda* in maize per plot quadrant (after dispersal of hatched larvae from an infestation scource in the middle of each plot) under different regimes of plant density and plant arrangement and when intercropped with beans. (Exp. B V; diagram 4; table 21.)

Planting system	Replicate	Number of injured whorls: $D^1 = 23$ June 22, 3 days after infestation — Quadrant 1	2	3	4	D = 34 July 3, 4 days after infestation — Quadrant 1	2	3	4	D = 44 July 13, 5 days after infestation — Quadrant 1	2	3	4	Total per plot	Total per planting system: Tot.	M^2
	1	2	1	4	1	0	1	6	0	5	6	6	2	19		
IA	2	2	1	6	1	0	0	2	0	0	2	9	1	12	38	38
	3	–	–	–	–	0	1	6	0	0	0	7	0	7		
	1	0	0	1	0	0	2	5	0	2	2	10	2	16		
IB	2	–	–	–	–	0	0	2	0	1	2	3	1	7	50	35
	3	–	–	–	–	0	0	4	0	3	8	15	1	27		
	1	0	0	2	0	0	0	4	0	1	1	3	3	8		
IIA	2	0	1	2	0	–	–	–	–	1	4	2	1	8	23	23
	3	–	–	–	–	0	2	2	0	1	1	5	0	7		
	1	0	1	8	0	–	–	–	–	2	3	15	9	29		
IIB	2	0	3	3	2	–	–	–	–	1	0	2	2	5	44	31
	3	–	–	–	–	1	1	4	0	0	6	4	0	10		
	1	1	0	4	0	0	1	1	0	0	0	4	0	4		
III	2	1	0	9	0	0	0	1	2	0	0	0	0	0	7	6
	3	–	–	–	–	0	0	6	0	0	0	3	0	3		
Total		6	7	39	4	1	8	43	2	17	35	88	22			

Distribution of injured whorls tested in relation to prevailing wind direction[3]		June 22 N	K	sign test	July 3 N	K	sign test	July 13 N	K	sign test
Downwind	: α	6	6	*	5	5	*	12	12	**
	: ß	9	9	*	12	12	**	14	14	**
At right angles to the wind	: γ	3	3	NS	7	6	NS	10	7	NS

[1]D = days after plant emergence.
[2]Modified total: two injured whorls per plant hole is considered as one unit injury.
[3]α – number of plots with the number of injured whorls ⩾ 5.
K = number of plots with the number of injured whorls in Quadrant 3 > Quadrant 1.
ß – total number of plots.
K = number of plots with the number of injured whorls in Quadrant 3 > Quadrant 1.
γ – total number of plots.
K = number of plots with the number of injured whorls in Quadrant 2 > Quadrant 4.
N = total number of plots reduced by the number of plots with an equal number of injured whorls in the tested quadrants.

A and IIB) there were no significant differences (table 22), although the plant density of IA and IB was four times as high as that of IIA and IIB and both I and II received the same number of egg masses. The spacing between plants probably did not affect the dispersal distance of the larvae.

When comparing the planting systems with one and two plants per plant hole (IA with IB and IIA with IIB), the results indicate that more plants were infested in the 'two plants per plant hole' system (B) (table 22). However when the whorls of both plants per plant hole were injured and are considered as a one unit injury, there is no difference between the planting systems of the same plant density (table 22). The trapping capability of one or two plants per plant hole was probably very similar. The wider spacing within the rows of planting systems B provided a chance for dispersing larvae to colonize the same number of 'two plants per plant hole' combinations as single plants in A and therefore more plants were attacked. If this effect was not caused by one larva injuring two plants, when grown together, then with a certain plant density the sowing of one plant per hole should be preferred to two plants per hole.

3.2.4.6. Predators and parasites

Predators

The earwig *D. taeniatum* preys on egg masses and the three first larval instars of *S. frugiperda* (Exp. D, chapter 3.4.). In the field experiments B I, B II and B III the earwigs were most frequent on maize, when intercropped with beans, although differences were not significant (fig. 15B, 16C, 17C). In the first growing periods (Exp. B I and B III) earwig populations were rather low as few as 6 per 100 plants (fig. 15B and 17C). In the second growing period (Exp. B II) populations were much higher, as many as 14 earwigs per 100 plants (fig. 16C) and in several plots an average of one earwig per plant was found. These figures are underestimates, because earwigs often hide deep in the whorl or behind sheath collars.

Several spiders collected from maize plants preyed on the first larval instars of *S. frugiperda* in the laboratory. Bean intercropping significantly increased the number of spiders on maize in the field experiments B I, B II, B III (fig. 15C, 16D, 17D). Less spiders were found in the later samples, possibly because it is difficult to find them on the larger plants.

Because the earwigs and spiders only preyed on the first larval instars of *S. frugiperda* the greatest effect can be expected soon after the oviposition peaks of the moths, which occur mainly at an early growth stage of the maize plant. Specific studies however will be necessary to quantify this effect.

In the second growing period the predatory ant *Ectatomma ruidum* Rogar was frequently observed on the maize plants and occurred significantly more on the bean intercropped maize plants (Exp. B II, fig. 16E). Other predators, such as Pentatomidae, Reduviidae, *Nabis* sp., *Geocoris* sp., *Polistes* sp. and *Chrysopa* sp. have been observed, but their effects were not quantified because the correct methodology to sample the populations accurately in the planting systems was not available.

TABLE 23. Maize, bean intercropped and as a monoculture. Natural mortality of *S. frugiperda* in two adjacent maize fields by parasites and pathogens at St. Lucia, Dept. of Boaco. Larvae collected at late whorl stage (July 6 and 13, 1977).

Cropping system	Number of larvae collected	Length of larvae (cm)		Number of larvae reared to adult		
		average	range		Unknown causes	Parasites and pathogens (total)
Monoculture	57	2.9	1.6–3.9	30	2	25(44)
Bean Intercropping	55	2.8	1.0–4.1	25	1	29(53)

Parasites

S. frugiperda

To get an impression of the effect of bean intercropping on the parasites of *S. frugiperda*, two adjacent farmer's maize fields at St. Lucia were sampled at the midwhorl stage on July 6 and 13, 1977. One field was a monoculture and the other a polyculture with beans. There were no substantial differences in levels of parasitism attributable to planting systems, tachinid fly parasites seemed more abundant in the bean intercropping systems, namely 31% as against 16% in the monoculture (table 23).

In experiment B III, larvae were collected in the two planting systems 27, 35 and 45 days after plant emergence (table 24), because larvae were collected per plot differences between treatments could be tested statistically. The braconid *Rogas laphygmae* was only frequent at an early growth stage of maize, because this parasite only attacks the first larval stages and ecloses during the fourth larval instar of the host. Bean intercropping diminished parasitism on *S. frugiperda* by *R. laphygmae*, but the difference of 20% between planting systems was only weakly significant. The tachinid fly *Lespesia archippivora* was most frequent on all three collection dates in the maize plots, that were intercropped with beans. For the last sampling date, just before tasseling, this difference was significant. Bean intercropping nearly doubled the incidence of this parasite.

These findings indicate that parasites were not responsable for the lower incidence of *S. frugiperda* in maize, when bean intercropped. *R. laphygmae* does eliminate the larvae before they are able to cause much defoliation, however this parasite seems to prefer larvae on maize grown in a monoculture. Tachinid fly parasites were most frequently reared from larvae collected in the maize-bean intercropping system, but because the parasitized larva completes its development before dying, whorl defoliation cannot be prevented. The following generation of *S. frugiperda* will however be reduced.

D. lineolata

Parasitism in the different planting systems was evaluated only in Experiment

Number of larvae killed by (percentages between brackets)

Pathogens	*Hexamermis* sp.	Insect parasites					Larvae double parasitized by *Hexamermis* sp. and *L. archippivora*
		Total	Tachinidae		Hymenoptera		
			L. archippivora	*A. marmoratus*	*C. insularis*	*Ophion* sp.	
1	12	14(25)	9	0	3	2	2
0	10	20(36)	11	6	2	1	1

B I. About 40 larvae per planting system were collected at harvest from one cultivar and reared in the laboratory (table 25A). Additionally, parasitism was recorded during the samplings of *D. lineolata* in the two maize cultivars (table 25B).

With the low number of parasites there was no marked difference between planting systems. Bean intercropping did not increase the degree of parasitism.

TABLE 24. Maize: bean intercropped and as monoculture. The effect on the natural mortality of *S. frugiperda* in maize (at midwhorl, late whorl and tasseling stage) by parasites and pathogens, at St. Lucia, Dept. of Boaco. (Exp. B III)

Number of larvae of *S. frugiperda* (percentages between brackets)	Sampling date, 1978 (days after plant emergence)					
	June 20 (27) midwhorl stage		July 5 (35) late whorl stage		July 15 (45) tasseling stage	
	mono-culture	bean inter-cropping	mono-culture	bean inter-cropping	mono-culture	bean inter-cropping
Total collected (100)	69	72	34	39	28	36
Reared to pupae[1]	38	49	19	14	18	15
Parasites and pathogens	31(45)	23(32)	15(44)	25(64)	10(36)	21(58)
Pathogens	4	3	0	2	2	4
Hexamermis sp.	1	3	0	1	0	2
Insect parasites	26(38)	17(24)	15(44)	22(56)	8(29)	15(42)
Braconidae: *R. laphygmae*	19	+[2] 6	1	1	3	2
Tachinidae: *L. archippivora*	7	11	14	21	5	•[2] 13
Average larval instar	4.8		5.7		5.5	

[1] From the larvae collected at June 20 and July 5 pupal parasites were not collected and on July 15 they were absent.
[2] Significant difference between cropping systems: $^{+} = P \leqslant .10$.
$^{\bullet} = P \leqslant .05$.

TABLE 25. Maize: bean intercropped (P_0, P_1) and as monoculture (P_2). Natural mortality of *D. lineolata* in maize by parasites and pathogens, at St. Lucia, Dept. of Boaco. (Exp. B I)

A. Larvae collected at harvest and reared in the laboratory.

Number of larvae of *D. lineolata* (percentages between brackets)	Maize cultivar (sampling date)				
	X-105-A (Sept. 1)	Tuza Morada (Sept. 24)			
	P_0, P_1, P_2	P_0, P_1, P_2	P_0	P_1	P_2
Total collected (100)	62	114	37	38	39
Reared to adult	26	47	20	13	14
In diapause	2	16	6	5	5
Mortality by					
Unknown causes	3	6	0	4	2
Parasites and pathogens	31(50)	45(40)	11	16	18
Pathogens	17	29	7[1]	9	13
Insect parasites	14(23)	16(14)	4	7	5
A. diatraeae	8	8	1	3	4
P. claripalpis	6	8	3	4	1
			centimetre		
Length of collected larvae: average	1.9	2.2	2.1	2.3	2.1
range	1.1–3.0	1.5–3.0	1.5–3.0	1.5–3.0	1.5–2.6

[1]One larva was infested by nematodes of the family Rhabditidae, a secondary parasite, which probably entered the cadaver to feed on bacteria (W. R. NICKLE, 1977, pers. communic.).

B. Number of larval parasites encountered at harvest, when dissecting stalks

Cropping system	Hybrid X-105-A (C_1)[1,2] Sampling: Sept. 6										Variety Tuza Morada (C_0)[3] Sampling: Sept. 24									
	A. diatraeae				*P. claripalpis*[1]				Relative number of perforations ($P_0 = 1$)	Number of larvae (× 100)	*A. diatraeae*				*P. claripalpis*				Relative number of perforations ($P_0 = 1$)	Number of larvae (× 100)
	R_1^4	R_2	R_3	Tot	R_1	R_2	R_3	Tot			R_1	R_2	R_3	Tot	R_1	R_2	R_3	Tot		
P_0	2	2	3	7	2	0	1	3	1	1.7	1	1	3	5	1	1	1	3	1	1.7
P_1	1	3	1	5	0	0	0	0	1.1	1.7	1	0	1	2	0	0	2	2	1.4	1.9
P_2	0	4	0	4	0	0	1	1	1.1	2.0	1	2	1	4	2	1	0	3	1.9	2.5

[1]Two hymenopterous hyperparasites were reared from the pupae: *Rozanoviella* sp. (Signophoridae) and *Trichopria* sp. (Diapriidae).
[2]Per treatment 480 stalks dissected.
[3]Per treatment 240 stalks dissected.
[4]Replicate.

3.2.5. *Summary and conclusions*

Intercropping of beans in maize is a common practice in Nicaragua and has several agronomic and socio-economic advantages for the small farmer. Intercropping two and three rows of beans in maize was compared for yields and pests with a monoculture of maize. The best yields and returns were obtained by intercropping with two rows of beans. Yields of maize and of beans were considerably higher when the maize hybrid X-105-A was used instead of the tall inland maize variety Tuza Morada.

Bean intercropping reduced the number of maize plants infested by *S. frugiperda* by 20 to 30 per cent. Also the degree of whorl injury was lower. The possible causes of the reduced infestation, oviposition, dispersal of first instar larvae and the natural mortality by parasites and predators were investigated.

The very consistent difference between planting systems in the infestation of maize by *S. frugiperda* led to the assumption that one or more factors were a continuous influence, e.g. oviposition by the moth or dispersal by first instar larvae.

In the field experiments oviposition was lower (non-significantly) with bean intercropping. The space between the maize rows which increases with bean intercropping did not effect oviposition. In a field cage experiment 'beans only' reduced oviposition on maize, but not significantly. These results indicate a lower oviposition as a result of bean intercropping but conclusive evidence was not obtained.

It was proved that plants could be infested by wind dispersed first instar larvae of *S. frugiperda*, hatched from egg masses on neighbouring plants. Bean intercropping reduced this dispersal, probably by the bean plants trapping the airborne larvae. At fixed plant densities and row spacing there were less infested plants after dispersal when one instead of two plants per hole were sown.

Bean intercropping increased the incidence of both the earwig *Doru taeniatum* and spiders on maize, but only for spiders significantly. The earwig whose populations were highest in the second growing period preyed on eggs and larvae of *S. frugiperda* and several unidentified spider species, only on the larvae (chapter 3.4.). However the effect of these predators is difficult to quantify.

Bean intercropping seems to reduce parasitism on *S. frugiperda* by braconids and to increase that of tachinids. Only the braconids are able to reduce the whorl injury as they kill the host at an early larval stage. Tachinids however effect the extent of maize injury only in the following generations. It is unlikely that parasitism was responsable for the lower *S. frugiperda* infestation in maize when bean intercropped.

Bean intercropping reduced the incidence of and injury by *D. lineolata* in the inland maize variety Tuza Morada, but this was not the case when the hybrid X-105-A was used. Wider maize row spacing (field experiment) as well as the presence of beans (cage experiment) decreased the number of egg masses that were deposited, although not significantly. The egg mass size was however significantly smaller. Parasitization of *D. lineolata* larvae was low and not higher with bean intercropping.

ALTIERI et al. (1978) reported a lower pest incidence in beans, when intercropped with maize. We showed that the incidence of *S. frugiperda* and *D. lineolata* in maize may also be considerably reduced. The possible causes for this reduction have been indicated. It would be worthwhile to investigate further how these innate pest control properties can be fully exploited. Cropping systems that increase these control properties should be designed in cooperation with other research disciplines, because socio-economic and agronomic factors may prevail (NORTON, 1975). As cultural control methods seem very appropriate to the small farmer's conditions the research interest should not be directed primarily at the insect, but at the cropping system, which may affect the pest because of colonization of the crop, larval development and survival.

3.3. ABUNDANCE OF INSECT PESTS IN MAIZE-WEED POLYCULTURES

3.3.1. *Introduction*

In the Interior of Nicaragua a high number of *S. frugiperda* larvae was often observed on the weeds in maize fields. A similar occurrence is described by CHERIAN and KYLASAM (1938) (cited by VAN EMDEN, 1977), who reported an infestation of *Spodoptera exigua* (Hübner) in tobacco beds, adjacent to *Eleusine* sp., planted to reduce soil erosion in India. Migration of larvae into the tobacco occurred from *Eleusine* sp., which sometimes contained 8 to 15 times as many larvae as were present in the tobacco beds. In Nicaragua weeds are often present in the small farmer's maize field. This may be partly due to lack of incentives in terms of profit (BARRACLOUGH, 1978) and to a temporary lack of a labour force during the growing periods, as was observed at St. Lucia. Therefore the impact of weeds on maize and maize pests was studied, although it was already known that a delay of one month in weeding maize may cause a 25 per cent reduction in yield (NIETO et al., 1968).

For a literature review on pest management in polycultures reference is made to chapter 3.2.. The experimental site at St. Lucia has been described in the same chapter. The effect of intercropping weeds in maize was studied on the incidence of *S. frugiperda* in both maize (injury and egg masses) and weeds (larvae and egg masses); the relation between *S. frugiperda* larvae in maize and in weeds, the mortality of *S. frugiperda* larvae in maize and weeds by predators and parasites, the stalk injury by *D. lineolata*, and the incidence of some other maize pests was also studied.

3.3.2. *Material and methods*

An overview of the two experiments C I and C II at St. Lucia is given in table A.

3.3.2.1. Experiment C I

In the first growing period of 1978, the maize hybrid X-105-A was sown on May 18 at St. Lucia, Dept. of Boaco. Germination was completed by May 24, 1978. At sowing NPK fertilizer (10-30-10) and urea were applied at a rate of 130 and 65 kg ha^{-1}. Maize was sown with a plantstick, 1 metre

Table A.

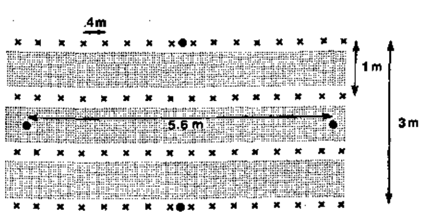
Experi-ment (code)	Growing period (1978)	Material and methods	Results	
			Subject investigated (chapter)	Tables (Tb) and Figures (Fg) (Exp. code)
C I	1st	3.3.2.1. (diagram 5)	Yield and plant development (3.3.3.1.)	Ta: 26(C I,C II)
C II	2nd	3.3.2.2.	Incidence of pests (3.3.3.2.,3.3.3.3.)	Ta: 27,28,29(C I) Fg: 20 (C I), 21 (C II)
			Incidence of predators (3.3.3.5.)	Ta: 31(C I) Fg: 20 (C I), 21 (C II)
			Incidence of parasites (3.3.3.5.)	Ta: 32 (C I, C II)
			Oviposition (3.3.3.4.)	Ta: 30 (C II)

between rows, .4 m apart and 2 plants per plant hole (diagram 5). No weeds were present at sowing (the end of the dry season).

The experiment was laid out in a randomized block design with 3 treatments and 4 replicates. Plot size was 20 × 20 m. The treatments consisted of S_2: the elimination of all weeds by hoeing at two-weekly intervals; S_0 and S_1: weeding in a strip of .17 and .33 m respectively on both sides of the maize row. In this way a band of weeds of .67 m in S_0 and of .33 m in S_1, was left in the middle of the maize rows.

In each quarter of a plot 20 consecutive maize plants in a row were sampled. Whorl injury by *S. frugiperda* was scored according to the index in chapter 3.2.3.3.. All insects encountered (mainly *S. frugiperda* egg masses, spiders and earwigs) were noted. In each plot a wooden frame (open inner surface .33 × .33 m) was put at random at 3 places on the soil surface in between the maize rows, which in S_0 and S_1 plots were weed-covered. Inside the frame wild plant species were identified by descriptions and illustrations of Central American weeds by GARCIA et al. (1975). At the same time the number of larvae and egg masses of *S. frugiperda* were counted. In one replicate 4 pitfall traps were placed in the middle of each plot (diagram 5).

Yield was determined at harvest of a pair of adjacent maize rows 5 m long, randomly taken in each plot (grain weight was adjusted to 15% moisture). From the same plants (about 40 per plot) the smallest stalk diameter at the base of the plant was measured and stalks were dissected for injury by *D. lineolata*; injured internodes, perforations, exit holes, larvae, pupae and pupal skins of the stalk borer were counted.



× two maize plants per plant hole

• pitfalltraps in between and within maize rows

▒ weeds

DIAGRAM 5. Layout of the planting system of a weed intercropped maize plot (S_0) and allocation of pitfall traps. (Exp. C I)

3.3.2.2. Experiment C II

In the second growing period of 1978 a similar experiment with the hybrid X-105-A was sown on October 6 in the same field. Germination was completed by October 11. Fertilizer applications were the same as in the foregoing experiment.

The trial was laid out in a randomized block design with 2 treatments and 3 replicates. Plot size was 28 × 26 m. The planting system of maize was the same as that in Experiment C I. The treatments consisted of S_2: weeding at two-weekly intervals; S_0: maize sown in cleared strips of .5 m wide in a field with natural weeds, afterwards strips of .25 m on both sides of the maize row were weeded, so that a .5 m band of weeds was left in the middle of each row.

The sampling of maize and weeds was carried out as described for Experiment C I, however the number of sampling sites per plot was increased to 6 and 4 respectively. The maize was also sampled for egg masses of *S. frugiperda* on the 17 and 21 days after plant emergence, the number of egg masses per plot counted within half an hour was scored. The weeds were sampled 19 days after plant emergence for egg masses of *S. frugiperda*. Larvae of *S. frugiperda* were collected from maize and weeds in the first growing period and from maize only in the second growing period, they were reared to get an assessment of parasitism.

3.3.3. *Results and discussion*

3.3.3.1. Yield and plant development

In the first growing period (Exp. C I) yield per ha decreased by 23% and stalk diameter by 6% when maize was intercropped with weeds, indicating that weeds constituted a significant competition factor for the maize plants (table 26). Plant height however was not significantly affected in both experiments C I and C II (fig. 20F and 21H; table 26).

3.3.3.2. Maize insects

S. frugiperda

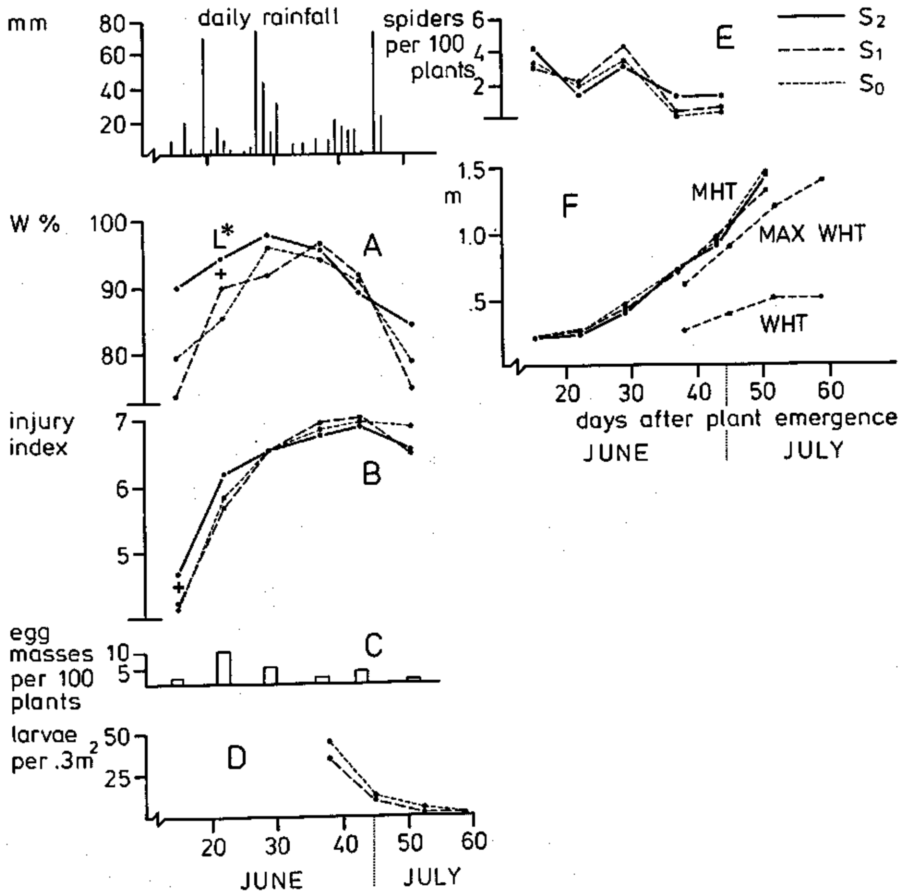
In both experiments C I and C II weed intercropping did not significantly

TABLE 26. Maize: weed intercropped (S_0, S_1) and as monoculture (S_2). The effect on yield and plant development of maize (hybrid X-105-A) in the first and second growing period of 1978 (Exp. C I and C II).

Cropping system		Growing period			
		First (Exp. C I)			Second (Exp. C II)
		Yield per ha (kg)	Plant height[1] (cm)	Stalk diameter (cm)	Plant height[2] (cm)
Weed intercropping	: S_0	3697	120	1.93	51
	S_1	3876	114	1.98	
Monoculture	: S_2	4890$^+$	119	2.09*	48

$^+$ – $P \leq .10$ S_2 versus S_0, S_1.
* – $P \leq .05$

[1]Average of 43 and 51 days after plant emergence.
[2]Average of 34 and 38 days after plant emergence.



Note: for significancies of effects, see figure 16.

FIG. 20. Maize: weed intercropped (S_0, S_1) and as monoculture (S_2). The effect on injury by *S. frugiperda*, the incidence of predators, and on the plant height of maize and weeds. (Exp. C I)
A. Percentage of whorls injured (W) by *S. frugiperda*.
B. Average injury score of whorls injured by *S. frugiperda*.
C. Oviposition by *S. frugiperda* (S_0, S_1 and S_2 combined).
D. Average number of *S. frugiperda* larvae in weeds.
E. Average number of spiders (Araneae).
F. Average plant height of maize (MHT). The average (WHT) and the maximum (MAX WHT) height of weeds (S_0 + S_1 combined).

influence whorl injury by *S. frugiperda* (fig. 20A, 20B and 21A, 21B). The higher percentage of injured whorls and the higher injury scores during early plant development in the weeded plots S_2 were not significant and of short duration.

D. lineolata

There were no significant effects of weed intercropping on *D. lineolata* (Exp. C I, table 27). However the number of injured internodes, perforations and larvae

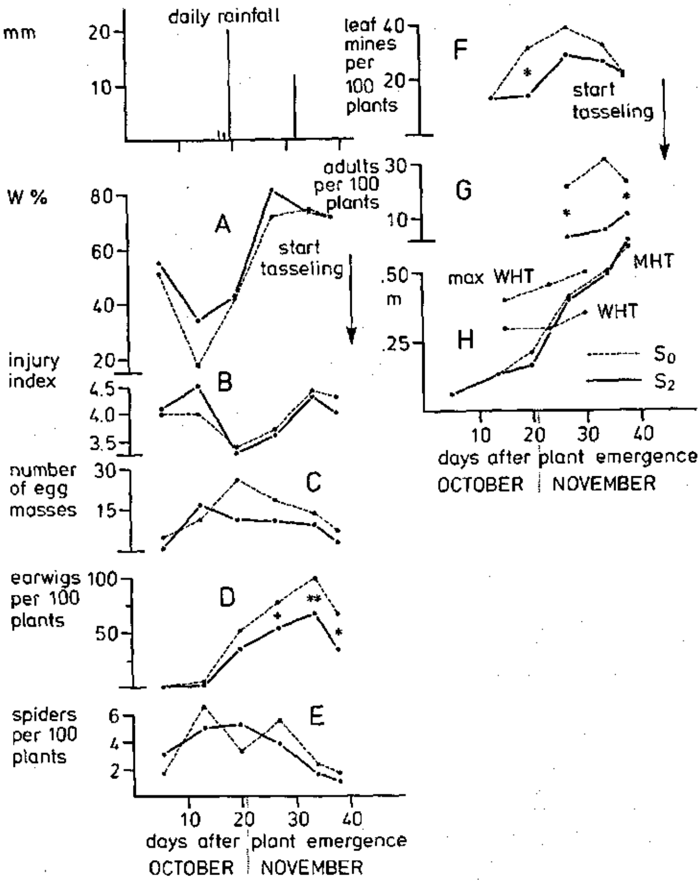


FIG. 21. Maize: weed intercropped (S_0) and as monoculture (S_2). The effect on injury by *S. frugiperda*, the incidence of predators, and on the plant height of maize and weeds. (Exp. C II)
A. Percentage of whorls injured (W) by *S. frugiperda*.
B. Average injury score of whorls injured by *S. frugiperda*.
C. Oviposition by *S. frugiperda* (on 360 plants).
D. Average number of earwigs (*Doru taeniatum*).
E. Average number of spiders (Araneae).
F. Average number of leaf mines by *Liriomyza sorosis*.
G. Average number of adults of *Chauliognathus* sp.
H. Average plant height of maize (MHT); the average (WHT) and the maximum (MAX WHT) height of weeds (only S_0).

were higher in the monoculture. Probably the moths preferred oviposition on the most vigorous plants (see chapter 3.1.). Weed intercropping affected the maize plant by competition (a lower grain yield and a smaller stalk diameter, table 26).

Other maize insects

Collaria oleosa (Distant) (Hemiptera: Miridae) in the second growing period

TABLE 27. Maize: weed intercropped (S_0, S_1) and as monoculture (S_2). The effect on the incidence of and injury by, *D. lineolata* in maize. (Exp. C I)

Cropping system		Number per plant[1]			
		Injured internodes	Perforations	Exit holes	Larvae
Weed intercropping	: S_0	$1.5 \pm .5$	$2.2 \pm .7$	$.5 \pm .1$	$.4 \pm .1$
	S_1	$1.6 \pm .3$	$2.1 \pm .5$	$.3 \pm .2$	$.7 \pm .2$
Monoculture	: S_2	$2.2 \pm .7$	3.3 ± 1.7	$.5 \pm .2$	$.9 \pm .6$

[1]Means ± SD; means are not significantly different (P > .10).

(Exp. C II) caused a white streaking on leaves of graminaceous weeds and on the lower leaves of maize. Weed intercropping in maize significantly increased the number of injured plants from 4 to 37 per cent. This injury probably does not cause loss of yield. BRITTON (1923) mentioned *Collaria* sp. on *Calamagrostis canadensis* and other Gramineae in Connecticut. BRUNER et al.(1975) mentioned *Collaria* sp. on *Digitaria* sp. in Cuba. RYDER et al. (1968) also reported *C. oleosa* as a pest of sorghum in Cuba, injuring the sorghum flowers.

Injury by the leaf miner *Liriomyza sorosis* (Williston) in the second growing period was significantly more in weed intercropped maize (fig. 21F). (We found the same leaf miner in 1977 on *Sorghum vulgare*.)

3.3.3.3. *S. frugiperda* in weeds

In the first growing period (Exp. C I), 38 days after plant emergence a large number of *S. frugiperda* larvae were present in the weeds (table 28, fig. 20D). It is estimated that one million larvae per ha occurred in the planting system S_0 and .4 million per ha in S_1. With a maize plant density of 50,000 plants per ha this means that there were 20 and 8 larvae in the weeds per maize plant in S_0 and S_1 respectively. The number of larvae per unit weed area increased with the width of

TABLE 28. Maize: weed intercropped (S_0, S_1) and as monoculture (S_2). The effect on the incidence of *S. frugiperda* larvae in weeds in the first growing period of 1978. (Exp. C I)

Cropping system		Average number of larvae[1] in weeds per .3 m² sampling date (days after plant emergence)				10 larvae per .3 m² (equivalent per ha)
		June 30 (38)	July 7 (45)	July 14 (52)	July 21 (59)	
Weed intercropping	: S_0	45.0 ± 23.3	12.0 ± 1.4	5.5 ± 4.9	1.3 ± 1.5	$.22 \times 10^6$
	S_1	34.3 ± 25.5	8.8 ± 1.7	2.3 ± 1.7	$.5 \pm 1.0$	$.11 \times 10^6$
Monoculture	: S_2	1.3 ± 2.5	$.0 \pm .0$	$.0 \pm .0$	$.0 \pm .0$	.0
Average larval instar		3.8	4.3	3.0	3.8	

[1]Means ± SD; means of S_0 and S_1 are not significantly different (P > .10).

the weed strip (from S_0 to S_1), but the difference was not significant (table 28). Between 38 and 45 days after plant emergence the larval population decreased by 73% in S_0 and by 74% in the S_1 plots and thereafter remained at a low level. Parasites and possibly predators were responsable for this rapid population decrease; this will be discussed in chapter 3.3.3.5..

FIGUEROA (1976) mentioned four of the twenty weeds identified by us as host plants for *Spodoptera* spp.: *Amaranthus* sp. for *S. sunia* (Guenée) and *S. ornithogalli* (Guenée), *Desmodium* sp. for *S. ornithogalli*, *Digitaria* sp. for *S. frugiperda* and *Portulacca oleracea* L. for *S. eridiana*. About 60% of the soil was covered by the Gramineae *Digitaria* sp. and *Eleusine indica* (L.) Of the larvae counted on weeds, most were found on *Digitaria* sp. and some on *E. indica*, even more were however found on the soil surface. The disturbance while sampling probably caused the larvae to drop from the weeds.

Do the larvae in the weeds migrate towards maize? Because of the similar levels of infestation (observed in fig. 20A, 20B and 21A, 21B) for maize plots with and without weeds it seems improbable that larvae have migrated from weeds to the maize. Maize farmers several times reported an increase in *S. frugiperda* infestations a few days after weeding. The question was firstly whether the larvae encountered in weeds were indeed *S. frugiperda*, and secondly if they were conditioned to weeds.

The colour of the larvae from maize and weeds differed considerably. Larvae from maize plants were light brownish, those from weeds greenish and striped. An identification of adults, reared from larvae of weeds could not be obtained. However using LEVY and HABECK's (1976) keys, the larvae were definitely identified as *S. frugiperda*. During the second growing period of 1978, a very heavy attack of *S. frugiperda* in a weed-free maize field near Managua occurred. A high number of larvae per plant (up to 10) was observed. Feeding was not restricted to the whorl, all maize plants were defoliated leaving only the midribs. These larvae were of the same colour as the larvae in the weeds. OGURA et al. (1971) reported a darkening of the larvae of *Leucania separata* (Walker) under crowded conditions. The same was observed by YAGI (1980) for *Spodoptera exempta* in Kenya. We however did not observe a darkening, but a change from brownish to greenish.

To study the food conditioning of the larvae, larvae were collected from maize and weeds and reared individually in glass jars in the laboratory. They were either offered maize leaves only, *Digitaria* leaves only or a mixture of both. From the faeces it was determined which plant species had been consumed. Larvae originating from maize or *Digitaria* when forced to, fed on both these plants (table 29). When given a choice, there seemed to be a slight preference for maize. As a result conditioning can certainly not be held responsible for the non-occurrence of migration from weeds to maize (it was not determined whether larval development and survival on maize and *Digitaria* sp. are the same).

In the second growing period of 1977 an experiment was carried out to study the effect of weeds on maize pests at La Calera, Managua (MARTINEZ, 1977). Of four treatments one consisted of clean weeding (control), in two further treatments

TABLE 29. Feeding of *S. frugiperda* larvae – field collected from maize and *Digitaria* sp. – on leaves of either one of the plant species or on both. (Food was offered to single larvae in a glass jar.)

Larvae collected from	Number of larvae	Leaves offered from	D[1] = 35 % larvae feeding[2] on				D = 49 % larvae feeding on			
			M	D	M+D	None	M	D	M+D	None
Maize (M)	10	M	++++	X	X	–	++++	X	X	–
	10	D	X	++++	X	–	X	++++	X	–
	10	M+D	++	++	++	–	+++	+	+	–
Digitaria sp. (D)	10	M	++++	X	X	–	++++	X	X	–
	10	D	X	++++	X	–	X	++++	X	–
	10	M+D	+++	–	++	+	+++	++	+	–

[1] D = days after emergence of the maize plants.
[2] – : 0% ++ : 25–50% ++++ : 75–100%.
+ : 0–25% +++ : 50–75% X : does not apply.

strips of 17 and 33 cm on both sides of the maize row were weeded leaving bands of 33 and 67 cm respectively in the middle of the rows, the fourth treatment was not weeded at all. In this latter treatment maize plants suffered greatly from competition and the height was reduced to half that in the other treatments. Larvae of *S. frugiperda* were found in the weeds of all plots. In the unweeded plots many larvae ate all the maize leaves, leaving only the midribs. The high number of larvae per plant and this type of feeding on maize was not observed in the other treatments. When weed leaves intermingle with maize leaves, larvae of *S. frugiperda* easily migrated from the weeds to the maize and vice versa (via leaf contact). In this case weeding should be such that leaf contact does not occur.

Weeding may force the larvae to search for alternative hosts and thus probably increase maize injury as reported by the farmers. Due to the absence of larvae in the weeds in the second growing period of 1978 this could not be confirmed. After weeding increased monitoring for *S. frugiperda* infestations in maize seems advisable. With large numbers of *S. frugiperda* larvae present in the weeds it is recommended that strips on both sides of the maize row are weeded, leaving a band of weeds in the middle of the row to function as feeding site for the larvae, to prevent them searching for the alternative host, maize. This needs further investigation.

In the second growing period no larvae were found in the weeds in spite of the high oviposition (Exp. C II).

3.3.3.4. Oviposition by *S. frugiperda*

In the first growing period (Exp. C I) oviposition on maize was low. Seven of the 25 egg masses were found in the monoculture (S_2) and respectively 11 and 7 in the weed intercropping systems S_0 and S_1. Most egg masses were found 22 days after plant emergence (fig. 20C). No egg masses were found on the weeds.

In the second growing period (Exp. C II) the number of egg masses found was about five times higher. Oviposition on maize increased significantly when intercropped with weeds (table 30, fig. 21C). Only three egg masses were found on weeds (two on *Digitaria* sp. and one on *Eleusine indica)* during regular sampling and when a special search was made for egg masses in the weeds.

The large number of larvae in the weeds in the first growing period (as found in Exp. C I) was probably caused by the weeds, trapping first instar larvae which were dispersed by the wind from the maize plants. The higher chance of survival of larvae hatched from egg masses, which are deposited on maize with interjacent weeds, may be a cause of the higher oviposition on maize (as found in the second growing period; Exp. C II). The average height of the weed vegetation during both growing periods, Exp. C I and Exp. C II, is shown in fig. 20F and 21H, respectively. The possible trapping of dispersing first instar larvae by the weeds in the second growing period (Exp. C II) did not result in a lower infestation of maize plants, when intercropped with weeds, probably because of the higher oviposition on maize with interjacent weeds.

TABLE 30. Weed intercropping in maize and its effect on oviposition by *S. frugiperda*. Analysis of variance: F-values, significancies and means. (Exp. C II)

A. Number of egg masses found within half an hour searching per plot 17 and 21 days after plant emergence.
B. Number of egg masses found during the regular samplings 20, 27, 34 and 38 days after plant emergence.
C. A + B, except the sample of B 20 days after plant emergence.

Source of variation	df	Number x of egg masses (lnx)		
		A	B	C
			F-values	
Block	2	1.50	2.56	.38
Treatment	1	14.7+	7.69	33.9*
Error: V.C.	2	6.75	15.5	5.32
Total	5			
			means	
Grand mean		3.45	2.90	3.74
monoculture		3.25	1.21	3.50
weed intercropping		3.65	1.81	3.98
Standard error		.07	.15	.06
Number of egg masses involved		194	119	268

3.3.3.5. Predators and parasites

Predators

The pitfall traps, which were placed in the three planting systems (S_0, S_1, S_2) in the first growing period in 1978 (Exp. C I, diagram 5) captured several predatory insect species, only two occurred in reasonably high numbers i.e. larvae and adults of a carabid, *Galerita* sp. and adults of the gelastocorid *Nerthra fuscipes*[1]. The first preys readily on *S. frugiperda* larvae in the laboratory, the second might predate the larvae on the soil surface. The predators were more abundant in the weed intercropped plots (table 31). The pitfall traps that were placed within the maize row (no weeds) captured more predators than those between the rows (S_0 and S_1: within the weeds). This may – among other possibilities – merely be a reflection of the mobility of the predators, as weeds may act as a physical barrier.

In the second growing period (Exp. C II) hardly any predatory insects were captured in the pitfall traps, which may indicate the absence of prey (larvae of *S. frugiperda* in weeds).

[1] Identified by R. H. Cobben.

TABLE 31. Maize, weed intercropped (S_0, S_1) and as monoculture (S_2). The capture in pitfall traps of the Larvae (L) and Adults (A) of Carabidae and Gelastocoridae in the first growing period of 1978 (see diagram 5). (Exp. C I)

Date July	Days after plant emergence	Traps in maize rows						Traps between maize rows						Total					
		Weed intercropping				Mono-culture		Weed intercropping				Mono-culture		Weed intercropping				Mono-culture	
		S_0		S_1		S_2		S_0		S_1		S_2		S_0		S_1		S_2	
		A	L	A	L	A	L	A	L	A	L	A	L	A	L	A	L	A	L
		Galerita sp.[1] (Coleoptera: Carabidae)																	
6	44	–	–	–	–	–	–	–	–	–	–	–	–	9	2	7	7	3	0
14	52	4	3	9	7	1	1	1	5	3	3	1	0	5	8	12	10	2	1
20	58	3	0	15	2	5	1	1	0	5	5	4	0	4	0	20	7	9	1
26	64	5	1	3	0	3	0	0	0	3	1	1	0	5	1	6	1	4	0
	Total	12	4	27	9	9	2	2	5	11	9	6	0	23	11	45	25	18	2
		Nerthra fuscipes (Guér.-Mén.) (Hemiptera: Gelastocoridae) (only adults)																	
6	44	–		–		–		–		–		–		1		10		3	
14	52	3		2		0		1		0		0		4		2		0	
20	58	2		3		3		0		2		0		2		5		3	
26	64	2		0		0		0		1		1		2		1		1	
	Total	7		5		3		1		3		1		9		18		7	

[1] Most larvae of neotropical carabid species are not described, but these are probably the same species as the adult (D. M. ANDERSON, pers. communic., 1978).

Spiders were found in low numbers in both the 1978 growing periods (Exp. C I and C II), there was no difference between the planting systems (fig. 20E and 21E).

The earwig *Doru taeniatum* was virtually absent in the first growing period of 1978 (Exp. C I) (a seasonal average of less than one per 200 plants). In the second growing period of 1978 (Exp. C II) however they occurred in high numbers on the maize plants (fig. 21D), 34 days after plant emergence the average number of earwigs was about 2 per 3 plants in S_2 and about one per plant in S_0. Frequently individual plants contained up to 8 earwigs. The number of earwigs was significantly higher in maize plots, when these were intercropped with weeds. One of the reasons for this increase may be the availability of more food (egg masses and young larval instars of *S. frugiperda*).

The adults of *Chauliognathus* sp.[1] (Coleoptera: Cantharidae) (the larvae are predaceous) were observed in maize whorls in the second growing period (Exp. C II). They were more abundant in the weedy plots (fig. 21G). The effect they have on maize pests is however unknown.

Parasites of S. frugiperda

In the first growing period (Exp. C I) larvae of *S. frugiperda* were collected from all plots 35, 42, 48 and 58 days after plant emergence. The first two larvae collections were from both maize and weeds. In the second growing period (Exp. C II) larvae were collected from all plots 22 and 33 days after plant emergence, but only from maize, as there were no larvae in the weeds. The number of larvae reared and the mortality caused by natural biological control agents, such as insect parasites, nematodes and pathogens have been presented for both growing periods in table 32. For materials and methods see chapter 3.4..

In the first growing period (Exp. C I), 35 and 42 days after plant emergence, parasitism by the tachinid *Lespesia archippivora* on larvae from weeds was 10 to 20% higher than on larvae from maize; at 42 days 54% of the maize larvae and 75% of the weed larvae were parasitized by *L. archippivora;* larvae collected from weeds in the S_0 plots were all attacked by this parasite. The decrease of the number of larvae in weeds from 38 to 45 days (fig. 20D) can be largely attributed to the activity of this parasite. Thus weeds may provide an important reservoir of *L. archippivora*. The parasitism by *L. archippivora* on larvae, collected from maize at 48 and 58 days remained at a high level (about 50%). The absence of *L. archippivora* on *S. frugiperda* larvae in maize in the second growing period may perhaps be partly explained by the absence of *S. frugiperda* larvae in weeds.

Intercropping maize with weeds did not influence the parasitism on *S. frugiperda* larvae in maize by *L. archippivora* (first growing period, table 32). However as *L. archippivora* is a mobile insect, it may have been due to the plot size.

In the first growing period (Exp. C I) collecting and rearing of larvae was started too late to evaluate the effect of the hymenopterous parasites. The total

[1] Identified by R. D. Gordon.

TABLE 32. Maize: weed intercropped (S_0,S_1) and as monoculture (S_2). The natural mortality of *S. frugiperda* in maize and weeds by parasites and pathogens in 1978, at St. Lucia, Dept. of Boaco. Larvae were field collected and reared (to adult) in the laboratory. (Exp. C I and C II)

Collection date (1978) (days after plant emergence)	Weed intercropping system	Host plant	Number of larvae collected	Average larval instar (range)	Number of larvae killed by (percentages between brackets)					
					Parasites and pathogens (total)	Pathogens	*Hexamermis* sp.	Insect parasites		
								Total	*L. archippivora*	Others
				first growing period (Exp. C I)						
June 27[5] (35 days)	S_0	Maize	12	4.5(4–5)	6	3	2[1]	2	1	1 *Eiphosoma* sp.
		Weeds	12	4.7(4–5)	8	2	0	6	4	1 *Rogas vaughani* 1 *Zele* sp.
	S_1	Maize	12	4.8(4–6)	3	0	0	3	3	
		Weeds	12	4.5(4–5)	3	1	0	2	2	
	S_2	Maize	12	4.8(4–6)	5	2	0	3	2	1 *Ophion* sp.
	All	Maize	36	4.8(4–6)	14(39)	5(14)	2(5.6)	8(22)	6(17)	2 (5.6)
		Weeds	24	4.6(4–5)	11(46)	3(13)	0(.0)	8(33)	6(25)	2 (8.3)
July 4[5] (42 days)	S_0	Maize	12	5.0(4–6)	8	2	0	6	6	
		Weeds	12	4.5(3–5)	12	0	0	12	12	
	S_1	Maize	11	5.0(4–6)	7	2[2]	0	6	6	
		Weeds	12	4.8(4–6)	9	3	0	6	6	
	S_2	Maize	12	5.2(4–6)	9	2	0	7	7	
	All	Maize	35	5.0(4–6)	24(68)	6(17)	0(.0)	19(54)	19(54)	
		Weeds	24	4.6(3–6)	21(88)	3(13)	0(.0)	18(75)	18(75)	

July 10[6] (48 days)	S_0	Maize	20	(5–6)	13	0	1	13[2]	13[2]	
	S_1		19	(5–6)	11	2	2	10[3,4]	10[3,4]	
	S_2		20	(5–6)	11	0	1	10	10	
	All		59	(5–6)	35(59)	2(3.4)	4(6.8)	33(56)	33(56)	
July 20[6] (58 days)	S_0	Maize	20	(5–6)	11	1	0	10	10	
	S_1		20	(5–6)	10	0	0	10	10	
	S_2		20	(5–6)	7	0	0	7	7	
	All		60	(5–6)	28(47)	1(1.7)	0(.0)	27(45)	27(45)	
second growing period (Exp. C II)										
Nov. 9[7] (22 days)	S_0	Maize	56	4.5(3–6)	19	7	2	10	0	5 *Chelonus* sp. 4. *Rogas* sp. 1 *Zele* sp.
	S_1		53	4.4(3–6)	20	8	4	8	0	4 *Chelonus* sp. 2 *Archytus marmoratus* 1 *Ophion* sp. 1 *Eiphosoma* sp.
	All		109	4.5(3–6)	39(36)	15(14)	6(5.5)	18(17)	0(.0)	18 (17)
Nov. 20[8] (33 days)	S_0	Maize	90	(5–6)	23	21	2	0	0	
	S_1		91	(5–6)	20	18	1	1	0	1 *Ophion* sp.
	All		181	(5–6)	43(24)	39(22)	3(1.7)	1(.6)	0(.0)	1(.6)

[1] 1 larva: *Hexamermis* sp. + entomopathogen.
[2] 1 larva: *Hexamermis* sp. + *L. archippivora*.
[3] 2 larvae: *L. archippivora* + *Hexamermis* sp.
[4] 1 larva: *L. archippivora* + entomopathogen.
[5] 3 larvae collected per plot.
[6] 5 larvae collected per plot.
[7] 10 larvae collected per plot.
[8] 15 larvae collected per plot.

amount of observed parasitism would probably have been higher, had collections commenced earlier. In the second growing period several hymenopterous parasites were reared 22 days after plant emergence. In this growing period the incidence of entomopathogens became increasingly important, while insect parasitism decreased. This is discussed in chapter 3.4..

In both growing periods apparent parasitism on *S. frugiperda* larvae in maize was not influenced by weed intercropping.

3.3.4. *Summary and conclusions*

In two growing periods maize grown in a field of weeds with only cleaned strips on both sides of the maize row, showed an infestation pattern by *S. frugiperda*, that is similar to maize grown in a monoculture. In the first growing period a very high number of *S. frugiperda* larvae were found on several weed species, mainly the Gramineae *Digitaria* sp. and *Eleusine indica*. These larvae were more greenish and striped than the larvae in the maize whorls.

The relations between *S. frugiperda* larvae on maize and weeds was investigated. The larvae from the weeds did not show conditioning to *Digitaria* sp. in laboratory trials, but had a slight preference for maize. Therefore potentially the larvae on the weeds may attack maize. Several times farmers reported an increased *S. frugiperda* attack on maize after weeding. This could not be investigated but if it occurs sampling the maize crop will be necessary after weeding to ascertain possible increased *S. frugiperda* infestations.

In plots without weeding at all, many larvae were found on both the maize and weed leaves. However in other plots with clean strips on both sides of the maize row they were only found on the weed leaves (MARTINEZ, 1977). If leaf contact between maize and weed leaves is necessary for the larvae to migrate from weeds to maize, weeding of strips on both sides of the maize row is advisable, leaving a band of weeds in between the rows as a food scource for the larvae.

Very few egg masses were counted on the weeds. Therefore the larvae in the weeds probably originated from the egg masses deposited on the maize. The first instar larvae when they are dispersed by the wind from the maize are probably trapped by the weeds. Weeds in between the maize rows enhanced oviposition by *S. frugiperda* on maize.

The carabid *Galerita* sp. and the gelastocorid *Nerthra fuscipes*, both potential predators on *S. frugiperda* larvae, occurred in large numbers in the maize plots, when intercropped with weeds. The earwig *Doru taeniatum*, a predator of egg masses and first larval instars of *S. frugiperda* occurred in significantly higher numbers on maize with weeds than on monocultured maize in the second growing period; up to one earwig per plant was sampled in several plots. Larvae of *S. frugiperda* collected in weeds were very heavily parasitized by the tachinid *Lespesia archippivora*. So weeds provide an important reservoir of this parasite. Apparently parasitism of *S. frugiperda* in maize was not influenced by weed intercropping, however this may have been caused by the small plot size as the most important parasite *L. archippivora* is a mobile insect.

The incidence of and the injury by *D. lineolata* in maize was not significantly influenced by weed intercropping. Its lower incidence on maize with weeds is probably caused by lower oviposition on these plants, which suffered from competition by weeds (see chapter 3.1.).

Weed intercropping increased the injury by two unimportant maize insects, namely the mirid *Collaria oleosa* and the leaf miner *Liriomyza sorosis*.

Limited weeding within a maize crop caused considerable yield reduction because of competition, while pest incidence was not reduced. As however weeds frequently occur in the maize fields of the small farmer, weed management is important as a large number of potential maize feeders (*S. frugiperda* larvae) may occur on the non-crop vegetation.

3.4. NATURAL MORTALITY OF *S. FRUGIPERDA* AND *D. LINEOLATA* IN MAIZE

3.4.1. *Parasites*

3.4.1.1. Introduction[1]

S. frugiperda

VAUGHAN (1962) studied parasitism of *S. frugiperda* in 1957 and 1958 at the experimental station La Calera, Managua. He reported the ichneumonids *Pristomerus* sp. (*P. spinator* (F.)[2], *Ophion* sp., the braconids *Chelonus insularis* Cresson (both *C. insularis* and *C. cautus* Cresson[2]), *Rogas laphygmae* Vier., *R. vaughani* Mues., the tachinids *Lespesia archippivora* (Riley), *Archytus* sp., and an unidentified mermithid. The most important were *P. spinator* (8%), *C. insularis* (4%), *L. archippivora* (3%) and the *Rogas* spp. (2%). During the first growing period total parasitism of *S. frugiperda* increased from 2% in June to 46% in July. From August to October parasitism averaged 20%. SAENZ and SEQUEIRA (1972) studied parasitism of *S. frugiperda* near Managua, Rivas, Masaya, Chinandega, Esteli, Matagalpa and Juigalpa in July and August 1971. *Lespesia* sp. was found to be the most important, parasitism ranging from 13 to 38%, followed by *C. insularis* ranging from 5 to 30%; *R. laphygmae* and *Archytas* sp. only occurred at low levels. LACAYO (1977) investigated parasitism of *S. frugiperda* from June to November 1975 at La Calera, Managua. *L. archippivora* parasitized 15 to 17% of the larvae in July and August, *Rogas* sp. 13 and 2% of the larvae in June and July respectively, *Chelonus* sp. 13, 8 and 7% of the larvae in June, July and August respectively. *Archytas marmoratus* (Tns.), *Apanteles* sp., *Pristomerus* sp. and the eulophids *Euplectrus* spp. were present in small numbers. The fungi *Nomuraea rileyi* (Farlow) and *Aspergillus flavus* were the most important pathogens of *S. frugiperda* in Nicaragua (LACAYO, 1977). Mean percentages of larvae attacked by these fungi were 8 and 7 respectively with

[1] Unless stated otherwise the literature reviewed concerns the maize crop.
[2] Original material was checked and again identified in 1978.

a peak of 50% for *N. rileyi* and 25% for *A. flavus* in September.

In Venezuela (Maracay) *L. archippivora* was the most common parasite of *S. frugiperda* while another tachinid parasite *A. marmoratus* was found to be uncommon (NOTZ, 1972). In Mexico (Quintana Roo) ALVARADO (1977a) reported that *Archytas* sp. together with *Sarcophaga* sp. (Diptera: Sarcophagidae) were the most important parasites of *S. frugiperda* parasitizing on 11 to 68% of the collected larvae. In Cuba *Lespesia* sp. was recorded by RYDER and PULGAR (1969). In Arizona (USA) BUTLER (1958a) studied parasites of lepidopterous larvae. He mentioned also *L. archippivora* as the most important tachinid fly and host records included *S. frugiperda*, *S. exigua*, *Trichoplusia ni*, *Heliothis* spp. and *Estigmene acrea*. The records were from the following crops: alfalfa, cotton, maize, sorghum and weeds. He reported *A. marmoratus* from *S. frugiperda*. MILLER (1971) also recorded *A. marmoratus* from *Heliothis zea* in Georgia (USA).

In Venezuela (Maracay) NOTZ (1972) found that of the braconid parasites of *S. frugiperda*, *C. insularis* was more important than *A. marginiventris*. Of the braconids found by BUTLER (1958b) in Arizona (USA) *C. insularis* was very common in crop areas and had the widest host range, namely *S. frugiperda*, *S. exigua*, *S. ornithogalli* and *Heliothis* sp.. *A. marginiventris* was reared only once by him from *S. exigua*. TINGLE et al. (1978) reared *A. marginiventris*, *C. insularis* and *Ophion* sp. from *S. exigua* on the weed *Amaranthus hybridus* in field corn.

Larval mortality by hymenopterous parasites of *S. frugiperda* occurs at the 4 to 6th larval instar, by dipterous parasites it occurs at the 6th larval instar, the praepupae and the pupae. Therefore RYDER and PULGAR (1969) suggested that the application of insecticides should be delayed until the 8th leaf stage of maize in order not to eliminate the braconids and to increase the survival of parasitized *S. frugiperda* larvae. In Peru JAVIER and PERALTA (1975a, b) studied the effect of insecticide applications in maize on the ratio prey (Noctuidae) - predator (Anthocoridae, Nabidae). The ratio was highest when applications were made indiscriminately; when it rose to 3.5 the economic injury level was reached. This level was never reached in maize fields with limited or no insecticide applications.

D. lineolata

The specialized *Diatraea* parasite *Apanteles diatraeae* Mues. (Braconidae) attacks numerous *Diatraea* species in the Greater Antilles, Southern USA and Central America, it was abundant in Mexico and the USA only occasionally (ALAM et al., 1971). LACAYO (1977) reported a parasitism by this insect of 19 to 20% of the larvae of *D. lineolata* in the months November and December 1976 in Nicaragua (La Calera, Managua), however in the rest of this growing period parasitism was only 0–3%. The tachinid *Paratheresia claripalpis* (Wulp) was also reported by her as a parasite of *D. lineolata*. BENNETT (1969) listed several countries from Mexico to Argentina, showing the extensive natural distribution of *P. claripalpis* which attacks a large number of sugar cane moth borer species most of them *Diatraea* spp., including *D. lineolata*. He concluded that the parasite is adapted to a wide range of ecological conditions. LACAYO (1977) listed three entomopathogenous fungi attacking *D. lineolata*: *Aspergillus flavus*, *Fusarium* sp. and *Entomophthora* sp., of which *Entomophthora* sp. was found most frequently.

VAUGHAN (1962) and LACAYO (1977), reviewed above, sampled larvae of *S. frugiperda* in maize near Managua, predominant cotton area. Here aerial applications of insecticides are intensive from September until December. Most maize production however takes place in the Interior of the country, where the use of insecticides is limited (table 6) and high levels of parasitism were reported by SAENZ and SEQUEIRA (1972). Therefore the timing and the method of applying insecticides, should be such that the beneficial fauna is largely preserved. QUEZADA (1973) reported disruption of pupal parasitism of *Rothschildia aroma* Schaus populations on *Spondias* spp. trees in areas with intense and continuous insecticide applications in El Salvador. He states that 'everywhere there are cryptic cases of natural biological control, whose existence is ignored, and whose importance becomes evident only when man-induced disruptions produce upsets of previously innocuous species'. He suggests that in Central America insecticides should be used judiciously to preserve the beneficial insects. Therefore an assessment of parasitism on *S. frugiperda* and *D. lineolata* was made in different parts of the Interior regions and at St. Lucia, a community on the border of the Interior South and Interior Central region (fig. 2). Also from a knowledge of the existing parasites the introduction of others can be considered.

3.4.1.2. Material and methods

From 1974 to 1979 larvae of *S. frugiperda* and *D. lineolata* were collected at random in maize and sorghum fields in different parts of Nicaragua and reared at the experimental station La Calera, Managua. At St. Lucia, Dept. of Boaco, large and frequent collections of *S. frugiperda* larvae were made in 1977 and 1978 and of *D. lineolata* in 1977. The larvae were placed individually in glass jars of .12 m long and .06 m diameter tapped with fine copper gauze at an improvised laboratory in situ. Provisions were taken to exclude predation by ants (*Solenopsis* sp.). Every second or third day, the food for *S. frugiperda* consisting of fresh maize leaves was renewed and changes in larval stage or causes of mortality were noted. *D. lineolata* larvae were collected at the end of the first growing period in 1977 (Exp. B I, chapter 3.2.) at St. Lucia and reared in similar glass jars on pieces of maize stem, which were renewed every week. Larvae or pupae that died from unknown causes, were dissected and eventually studied microscopically for pathogens. Unkown parasites were sent for identification.

3.4.1.3. Results and discussion

Sixteen species of parasites and 3 species of entomopathogens were found for *S. frugiperda* and 4 of each for *D. lineolata* during 1974–1979 (table 33). The results of samples of *S. frugiperda* larvae from St. Lucia during 1977 are presented in table 34 and of those during 1978 in table 24 and 32. The results for *D. lineolata* are presented in table 25. The effect, of bean intercropping in maize, on parasitism of *S. frugiperda* and *D. lineolata* is discussed in chapter 3.2. and the effect of maize-weed intercropping in chapter 3.3..

S. frugiperda

Rogas laphygmae and *Chelonus insularis* were the most important of the braconids encountered (table 33). In 1977 at St. Lucia, *R. laphygmae* was

TABLE 33. Identified parasites and pathogens of *Spodoptera frugiperda* and *Diatraea lineolata* in different parts of Nicaragua (1974–1979)[1,2]

Spodoptera frugiperda (J. E. Smith)	A	B	C	D	E
Parasites					
Hymenoptera					
Braconidae					
Rogas laphygmae Vier.	En	S	L	++	Mg, SL
Rogas vaughani Mues.	En	S	L	+	SL
Zele sp. prob. mellea (Cresson)	En	S	L	0	SL
Chelonus cautus Cresson	En	S	EL	+	Mg, Ms, Ja
Chelonus insularis Cresson	En	S	EL	++	Mg, Ms, SL, Ja
Apanteles prob. *marginiventris* Cresson	En	S	L	0	Ca
Eulophidae					
Euplectrus close to *insularis* How	Ec	G	L	0	Mg
Euplectrus spp.	Ec	G	L	0	Mg
Ichneumonidae					
Campoletis flavicincta (Ashm.)	En	S	L	0	Ja
Ophion sp.	En	S	L	++	Mg, SL, Ca, Ja
Pristomerus spinator (F.)	En	S	L	+	Mg, SL
Eiphosoma vitticolle Cresson	En	S	L	0	SL
Trichogrammatidae					
Trichogramma sp.	En	G	E	+	Mg, Se
Diptera					
Tachinidae					
Archytas marmoratus (Tns.)[3]	En	S	LP	++	Mg, SL, Ja
Lespesia archippivora (Riley)	En	G	L	+++	Mg, Ms, SL, Ca
Hyperparasite of *L. archippivora*:					
Perilampus sp. (Hymenoptera: Perilampidae)	En	S	L	0	SL
Nematoda					
Mermithidae					
Hexamermis sp. or spp.	En	G	L	+++	SL, Ca, Mt, Ja
Pathogens					
Fungi					
Aspergillus flavus			L	+++	
Entomophthora sp.			L	+	
Nomuraea (= *Spicaria*) *rileyi* (Farlow)			L	+++	

Diatraea lineolata (Wlk.)	A	B	C	D	E
Parasites					
Hymenoptera					
Braconidae					
Iphiaulax sp.	En	G	L	++	Mg, SL

	En	G	L	++	Mg, SL
Apanteles diatraeae Mues.	En	G	L	+++	Mg, Mt, SL
Trichogrammatidae					
Trichogramma pretiosum Riley	En	G	E	+++	Mg, SL, Se, Es
Diptera					
Tachinidae					
Paratheresia claripalpis (Wulp)	En	S	LP	++	ALL
Hyperparasites of *P. claripalpis:*					
Trichopria sp. (Hymenoptera: Diapriidae)	En	G	LP	0	SL
Rozanoviella sp. (Hymenoptera: Signiphoridae)	En	G	LP	0	SL
Pathogens					
Fungi					
Aspergillus flavus			L	+	
Entomophthora sp.			L	++	
Hirsutella sp.			L	0	
Fusarium sp.			L	+	

A	B	C			D		E	
Kind of parasitism	Number of parasites per host		Parasite		Occurrence		Locality[4]	
			oviposits in	emerges from				
En – endoparasite	S – solitarious	E	egg	egg	0	rare	Interior North	Ja – Jalapa
Ec – ectoparasite	G – gregarious	EL	egg	larva	+	not common	Interior Central	Es – Esteli
		L	larva	larva	++	common		Mt – Matagalpa
		LP	larva	pupa	+++	very common		Se – Sebaco
							Interior South	Ca – Camoapa
								SL – Santa Lucia
							Pacific Central	Mg – Managua
								Ms – Masaya

[1] Identifications

Taxa	Families	Identified by
Insecta	Braconidae	P. M. Marsh
	Diapriidae	P. M. Marsh
	Eulophidae	G. Gordh, E. E. Grissell
	Ichneumonidae	R. W. Carlson
	Perilampidae	G. Gordh
	Signiphoridae	G. Gordh
	Tachinidae	C. W. Sabrosky
	Trichogrammatidae	E. R. Oatman
Nematoda	Mermithidae	W. R. Nickle
Fungi		G. M. Thomas

[2] For the collection of these data the assistance of my colleagues C. Y. Schotman, L. Lacayo and M. J. Sommeyer is gratefully acknowledged.
[3] Also found in *Heliothis zea* Boddie.
[4] See figure 2.

TABLE 34. Natural mortality of *S. frugiperda* in maize by parasites and pathogens during two growing periods in 1977 at St. Lucia, Dept. of Boaco.

Sampling date (1977)		Cropping system[1]	Number of larvae collected	Length of larvae (cm)		Larvae reared to adult (%)		
				average	range		Unknown causes	Parasites and pathogens (total)
June	21	BI	99	2.4	1.1–3.6	55	20	25
	28	BI	101	2.8	2.0–3.7	69	4.0	27
July	6	BI/MC	48	2.9	1.6–4.1	33	6.3	60
	13	BI/MC	64	2.8	1.5–3.7	61	.0	39
	21	MC	111	2.1	1.0–3.2	45	12	43
August	5	MC	80	2.3	1.0–3.3	31	8.6	60
Sept.	1	MC	63	2.2	1.0–3.5	43	3.2	54
Nov.	7	MC	62	2.2	1.8–3.6	55	8.1	37
	28	MC	93	2.3	1.2–3.0	56	10	34

[1] BI – bean intercropped maize.
MC – monoculture of maize.
[2] 3 larvae: *L. archippivora* and *Hexamermis* sp.
[3] 1 larva: *L. archippivora* and *Hexamermis* sp.
[4] 2 larvae hyperparasitized by *Perilampis* sp. (probably *L. archippivora*).

practically absent (table 34), while in 1978 up to 28% of the larvae were parasitized by this species (table 24). The 1977 sample however, consisted mainly of large larvae and the braconids were missed, because they kill the host during the fourth larval instar. The 1978 data (table 24) and those of LACAYO (1977) indicate that during early plant growth, when usually the highest population of young *S. frugiperda* larvae can be expected, braconids and other hymenopterous parasites are numerous. The larvae are killed by these parasites before they cause much damage. For this reason insecticide applications during early plant growth should be avoided, as was concluded by RYDER and PULGAR (1969).

Eulophids and Trichogrammatids were of little importance. Of the egg masses studied (collected for purposes of artificial infestations and for rearing of the introduced exotic egg parasite *Telenomus remus* (Nixon) only few were parasitized by *Trichogramma* sp.. Only *Ophion* sp. of the ichneumonids was regularly present (table 33).

The most commonly found tachinid at St. Lucia was *Lespesia archippivora* (table 24, 32, 34). This parasite was never found in the Interior North (C. Y. SCHOTMAN, 1978, unpublished data). Parasitism by *L. archippivora* at St. Lucia increased with plant development and reached 40 to 60% at tasseling (table 24, 32, 34). This is because the level of parasitism increases with the age of the

		Percentage mortality by					
Pathogens	*Hexamermis* sp.	Insect parasites					
		Total	Tachinidae		Hymenoptera		
			L. archippivora	*A. marmoratus*	*C. insularis*	*Ophion* sp.	Others
1.0	22	2.0	.0	.0	2.0	.0	
2.0	11	14	1.0	13	.0	.0	
2.1	27[2]	33	19[2]	8.3	4.2	2.1	
.0	14	25	17	3.1	1.6	3.1	
.9	12[3]	31	26[3]	1.8	1.8	1.8	
.0	4.3[3]	57	50[3]	.0	5.7	1.4	
33	3.2	18	3.2[4]	7.9	3.2	3.2	
31	.0	6.4	.0	.0	1.6	1.6	1.6 *R. laphygmae* 1.6 *Pristomerus* sp.
23	.0	11	.0	11	.0	.0	

collected larvae (*L. archippivora* parasitizes also in the late larval instars of the host; BRYAN et al., 1968). The larvae are possibly also more exposed to parasitism when the tassel emerges and the whorl disappears. As this parasite causes mortality of *S. frugiperda* during the last larval instar, its effect on the injury caused to maize will be negligable. However the next generation of *S. frugiperda* will be reduced. *Perilampus* sp., a hyperparasite reared from *L. archippivora* has also been reported in Venezuela (NOTZ, 1972). *Archytas marmoratus*, the other tachinid parasite of *S. frugiperda* was frequently found at St. Lucia in 1977 in both the first and second growing period. (The adult of this species emerges from the pupae). It was more frequently found in the Interior North, were *L. archippivora* is absent (or nearly). This parasite was also reared from *Heliothis zea*; this host has also been recorded by MILLER (1971).

The mermithid nematode *Hexamermis* sp. is a very common parasite of *S. frugiperda* in the Interior North and Interior South of Nicaragua, but very rare in the Pacific plain. In certain regions of the Interior South it was found in more than 50% of the larvae in both growing periods of 1977 (SCHOTMAN, 1978, unpublished data). At St. Lucia *Hexamermis* sp.[1] was frequently present in the larvae of *S. frugiperda* in 1977 (table 34), however in 1978 its incidence was low (table 24 and 32). The mermithids kill the larvae, when they emerge. As the

[1] A species of *Hexamermis* was also found in very high percentages in the slug *Vaginulus plebeius* Fisher, a serious bean pest. The parasitized slugs were not killed by the emerging nematodes. According to W.R. NICKLE (1979, pers. communic.) the nematodes from the slug were different to those reared from *S. frugiperda*.

nematode usually leaves the larvae at a late larval instar, its impact on maize injury and on subsequent generations of *S. frugiperda* will be the same as discussed for the tachinids. Carbofuran, a systemic insecticide and nematicide was promoted in 1978 to control white grub (*Phyllophaga* spp.) in beans. This pesticide may annihilate the mermithids.

Serious problems with *S. frugiperda* may arise if the parasitism by braconids, tachinids and mermithids is disrupted by the indiscriminate use of insecticides. Probably for this reason maize crops in the Pacific North region of Nicaragua (major cotton producing area) were seriously affected by *S. frugiperda*; the adjacent cotton fields were sprayed about 20 times per season.

The entomopathogens found in *S. frugiperda* larvae are listed in table 33. The fungus *Nomuraea rileyi* was the most frequently found pathogen, that caused the highest natural mortality in the second growing period of 1978 at La Calera, Managua (SCHOTMAN, 1978, unpublished data). The number of insect parasites dropped sharply in the second growing periods of 1977 and 1978 at St. Lucia, but the incidence of entomopathogens increased (table 32 and 34). The same phenomenon has been observed in cotton (FALCON and SMITH, 1973), also in isolated areas where insecticides had not been used. One theory is that the entomopathogens eliminate parasitized hosts and hosts for parasitism. Another theory suggests that the adult parasites are affected by the entomopathogens (FALCON and DAXL, 1973). Further investigations will be necessary to fully explain this reduction in the prevalence of insect parasites.

The percentage parasitism was higher than that found from one single sample, because the larvae are taken away from the field and protected against further parasitism. If subsequent samples are taken until the life cycle is completed, a better impression will be obtained of the total effect of parasitism. At a certain stage of one generation we may find 50% of the larvae parasitized by tachinids. If at the moment of collection 90% of the original population had already been eliminated by previous parasitism, predation and other mortality factors, the real mortality by tachinids of the original population would be only 5%. Suppose previous parasitism was 30%, then total parasitism would be 35%. In the case of *S. frugiperda* however this way of computing for one generation separately would be extremely difficult as in the tropics the generations overlap (see also exclusion technique, described by SOUTHWOOD, 1966).

D. lineolata

Of the larvae of *D. lineolata* collected at St. Lucia, 14 to 23% were parasitized by the parasites *Apanteles diatraeae* and *Paratheresia claripalpis* (table 25). The parasite *Iphiaulax* sp. was found late in the growing season. LACAYO (1977) reported 19–20% larval and larval-pupal parasitism (mainly *A. diatraeae*) in November/December at La Calera, Managua. The hyperparasite *Trichopria* sp., which was only once found as a pupal parasite of *P. claripalpis* is also recorded for a number of other countries (BENNETT, 1969).

Trichogramma pretiosum is a very common egg parasite of *D. lineolata* in Nicaragua. FLANDERS (1968) mentioned *T. pretiosum* as the most commonly

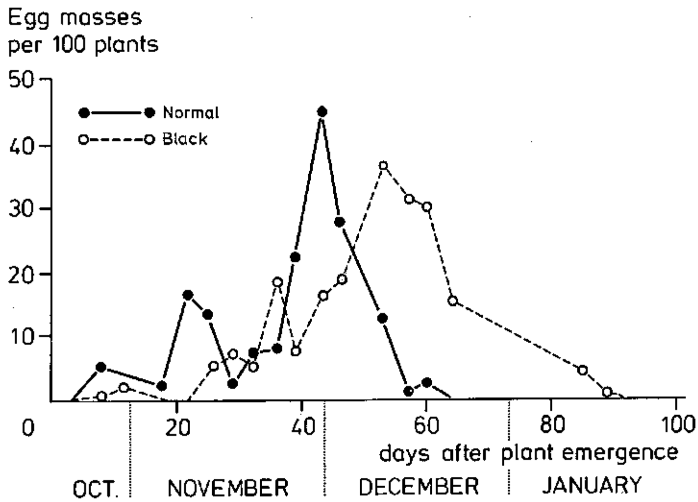


FIG. 22. The average number of black (parasitized by *Trichogramma pretiosum*) and normal egg masses of *D. lineolata* counted on field maize during plant development in the second growing period (variety Salco sown October 10, 1976 at Campos Azules, Dept. of Jinotepe; 10 consecutive plants in a row were sampled twice a week from 10 random sites).

found *Trichogramma* in the USA. OATMAN et al. (1970) reported *T. pretiosum* as a common parasite of *Heliothis zea* eggs, in maize, tomato and other vegetable and field crop plants in Southern California; on cotton and maize in Northwestern Mexico; and on maize in the Central and Southern areas of Mexico. The parasite is also known from Costa Rica and Guatemala (E. R. OATMAN, 1980, pers. communic.).

In the field the eggs turned black in about 3.2 days after being parasitized and the adult parasite eclosed 6 to 7 days later. The development of *T. pretiosum* from egg to adult took about 10 days under field conditions. The empty black chorion remained on an average 1.5 days (range 0 to 3) on the leaf before dropping. A non-parasitized egg eclosed in about five days. This empty chorion, in contrast to the black chorion, is hardly visible, because of its transparency and drops from the leaf within a day after eclosion. The black eggs are therefore visible on the leaf about one week longer than the non-parasitized ones. In figure 22 the curve of black eggs lags behind the curve of eggs that appear normal. (It is not known, why in later sampling dates normal eggs were no longer found.) Here the data on black and non-black eggs of one sample gives no true indication of parasitism. A 144 cream coloured eggs were collected from a maize field (variety Salco) at midwhorl stage in June 1976 and reared in the laboratory, 49% of them were parasitized.

At St. Lucia the entomopathogens were a more important mortality factor than the larval and larval-pupal parasites in the first growing period of 1977 (table 25).

TABLE 35. List of predators with observed (field or laboratory) or presumed predation of egg masses (E) and larvae (L) of *Spodoptera frugiperda*.

Predators	Stage of prey
Araneae (several unidentified species)	L
Carabidae	
Calosoma sp.	L
Galerita sp[1]	L
Chrysopidae	
Chrysopa sp. prob. *externa* Hag.[2]	E, L
Dermaptera[3]	
Doru taeniatum (Dohrn) (= lineare)	E, L
Labidura riparia (Pallas)	E, L
Formicidae[4]	
Ectatomma ruidum Rogar	L
Lygaeidae	
Geocoris sp.	E
Nabidae	
Nabis sp.	E, L
Pentatomidae	
Euschistus sp.	L
Euthyrhynchus sp.	L
Podisus sp.	L
Proxis spp.	L
Reduviidae	
Apiomerus pictipes H.S.	L
Castolus plagiaticollis Stål	L
Pithocoris sp.	L
Rhiginia cruciata	L
Sinea sp.	L
Zelus grassans Stål	L
Zelus sp.	L
Others	L
Vespidae	
Polistes canadensis (L.)	L
P. mayor Beauv.	L
Polistes sp.	L
Polybia occidentalis Oliv.	L
Stelopolybia areata Say	L

[1] Identified by D. M. Anderson.
[2] Identified by O. S. Flint.
[3] Identified by A. Brindle.
[4] Identified by D. R. Smith.
Note: remainders were identified by comparison with identified species of the collection of insect species at the Department of Parasitology, INTA, La Calera, Managua, Nicaragua.

3.4.2. *Predators*

3.4.2.1. General

Arthropod predators that according to field and laboratory observations could possibly be important are listed in table 35, with the stage of prey on which they feed. Predators in maize when intercropped with beans are discussed in chapter 3.2., and when grown with interjacent weeds in chapter 3.3.. Earwigs as predators of *S. frugiperda* are treated in chapter 3.4.2.2..

Preying by pentatomids, reduviids, nabids and predatory wasps on *S. frugiperda* larvae was frequently observed in the field, but these predators are so mobile that population estimates are difficult to make. Several unidentified species of spiders preyed on the early larval instars of *S. frugiperda*. In the field experiment B I significantly more spiders were found on the tall maize variety Tuza Morada compared to the hybrid X-105-A (fig. 18C). *Chrysopa* larvae regularly preyed on egg masses of *S. frugiperda*. The larvae of *S. frugiperda* are probably more exposed to predation at tasseling, when shelter from the whorl disappears.

Polistes sp., *Polybia* sp. and related wasps belong to the most frequently observed predators, especially in the Interior South. VAN DINTHER (1955) also mentioned Vespidae (*Polistes* spp., *Polybia* spp. and others) as an important group of predators of *Spodoptera* spp.. To increase the effectiveness of *Polistes* spp. the following practice merits further investigation. Artificial nesting sites (wooden boxes of .15 × .15 × .15 m fixed at about 1 m above soil surface on a pole with the open site downwards) are placed in natural vegetation until occupied, and transferred to maize fields (see LAWSON et al., 1961).

Predation on *S. frugiperda* larvae by birds is reported by CORTES (1977) in alfalfa, by GENUNG et al. (1976) in pastures and by VAN DINTHER (1955), who did not specify a crop. Larvae killed by insecticides stick to a growing whorl leaf, which carries it out of the whorl, they are then exposed to predation by birds, as was found in Nicaragua. It is unlikely that birds will prey on larvae in the maize whorl.

The ant *Solenopsis globularia*[1] (F. Smith) preys on larvae of *D. lineolata* diapausing in the maize stubble, to what extent is not known. Burning of maize and sorghum stubble at the end of the dry season does not kill all diapausing larvae (especially those in the base of the maize stalk below the soil surface). Burning however seemed to make it possible for external control agents to have easier access when the stalk is burned off at ground level (VAN HUIS, 1975).

3.4.2.2. Earwigs as predators of *S. frugiperda*

The earwig *Doru taeniatum* (Dohrn)[2] was found regularly in the Interior of Nicaragua. They have also been reported as being very common in the Northern part of Nicaragua (ESTRADA, 1960) and in Guatemala (PAINTER, 1955). Both

[1] Identified by D. R. SMITH.
[2] Identified by A. BRINDLE, Manchester Museum, University of Manchester, England.

authors used the species name *Doru lineare*, but according to BRINDLE (1971) and GURNEY (1972) all records from Central and North America refer to *taeniatum*. *Labidura riparia* (Pallas) was found in great numbers in weeds in maize fields in the Pacific plain. Because *D. taeniatum* is so common on maize plants in Nicaragua its role as a predator of *S. frugiperda* was investigated at St. Lucia, Dept. of Boaco.

3.4.2.2.1. Literature

BUSCHMAN et al. (1977) mentions *D. taeniatum* and *L. riparia* as egg predators of *Anticarsia gemmatalis* Hübner in soybeans in Florida. GUAGLIUMI (1969) reported *Doru* spp. preying on *Mahanarva posticata* (Homoptera: Cercopidae) in sugarcane, while ACOSTA (1964) listed *Doru lineare* (= *D. taeniatum)* as a predator of larvae and adults of *Delphax maidis* (Ashmead) (Homoptera: Delphacidae) in maize. THOMPSON and SIMMONDS (1965) listed *Doru taeniatum* as a predator of *Aphis maidis* and *Diatraea saccharalis* in Cuba.

ORPHANIDES et al. (1971) mentioned *L. riparia* as a predator of all exposed stages of *Pectinophora gossypiella* (Saunders) in cotton: egg, last instar larva, cocoon and pupa. The preferred food of *L. riparia* consisted primarily of litter or soil inhabiting insects, including the larvae and pupae of various Lepidoptera common in most agricultural fields (SCHLINGER et al., 1959). They found that earwigs readily climbed alfalfa stems in the laboratory to prey on aphids which lead them to suggest that the earwigs may resort to this type of feeding during the night. *L. riparia* occurred in larger numbers on soybean foliage during the night (BUSCHMAN et al., 1977). AFIFY and FARGHALY (1970) and AMMAR and FARRAG (1974) reported *L. riparia* as a predator of a large numbers of eggs and young larvae of *Spodoptera littoralis* (Boisd.) in the laboratory and observed them climbing cotton plants. WADDILL (1978) observed them preying on *Diabrotica balteata* in the laboratory.

3.4.2.2.2. Material and methods (Exp. D)

Eggs and larvae of *S. frugiperda* were offered on a piece of maize leaf in a petridish to each of 6 adults and 2 larvae of *D. taeniatum* in the laboratory.

Predation was also investigated under field conditions in 3 nylon screen field cages (3.6 × 1.8 × 1.8 m) placed over 2 rows of maize plants (hybrid X-105-A). Three days before starting the trials the caged maize plants were sprayed with methomyl (Lannate 90% a.i. SP, .25 kg ha^{-1}) to kill all arthropods.

Seventeen days after plant emergence (Oct. 28, 1978) one adult earwig was placed on each maize whorl in the cage). Every day from Oct. 29 to Nov. 2, egg masses were attached to the underside of a random leaf in a varying number per cage. The next day the same leaves were checked for egg masses.

A pair of adjacent half-rows (16 plants) of one cage were infested at 26 days with 2 first instar larvae of *S. frugiperda* per plant and the other cage-half (15 plants) was infested with 4 first instar larvae per plant (controls: ND = 2–, 4–). The cage halves were separated by plastic. In the other 2 cages, one *D. taeniatum* adult (D+) per plant was introduced. One of these cages (27 plants) was infested with 2 and the other cage (32 plants) with 4 first instar larvae of *S. frugiperda* per plant whorl (Treatments: ND = 2+, 4+). During the next 6 days whorl injury of all the plants was scored according to the injury index of chapter 3.2.3.3..

Larvae of *S. frugiperda* were obtained from reared egg masses. Egg masses of *S. frugiperda* and *D. taeniatum* were collected from the surrounding maize crop.

3.4.2.2.3. Results and discussion

Eggs and the first three larval instars of *S. frugiperda* were accepted by *Doru taeniatum*, when offered in a petri-dish. Later larval instars were rejected. The earwig did not react, until its antennae touched the prey. This seems to be in accordance with the conclusions of VAN HEERDT (1946), who found that for the location of food, visual and olfactory stimuli are not very important to the earwig *Forficula auricularia* L..

When egg masses (average size 109 eggs) were offered between one and 13 egg masses per field cage, *D. taeniatum* (one adult per plant) consumed 50 per cent or more in almost all cases (table 36). An egg mass was either left untouched or completely eaten, suggesting that when an egg mass is found by *D. taeniatum* it will be entirely consumed. The fact that *D. taeniatum* was able to find the egg masses indicates that the adult is mobile and searches widely.

In field cages *D. taeniatum* (one adult per plant) reduced the percentage of injured whorls (infested with 2 and 4 first instar larvae of *S. frugiperda*) by half within six days of the infestation (fig. 23A). The average injury level per injured whorl was also reduced (fig. 23B). Judging from the similar patterns of the percentage of injured whorls for the two larval densities (2 and 4 larvae per plant) (fig. 23A), it seems that when the earwig finds an infested plant, all the larvae present will be consumed.

The earwigs during the day were found on the largest plants. In the field experiment B I significantly more earwigs were found on the taller maize variety Tuza Morada (C_0) as compared to the hybrid X-105-A (C_1) (fig. 18B), and more on fertilized plants, which grew taller than on unfertilized plants (fig. 18D). It is not known why the earwigs were found during the day in the whorls or behind the collar sheaths of the *tallest* plants.

Eggs of *D. taeniatum* were found several times behind the collar sheath of maize plants and once in a *D. lineolata* tunnel.

The maximum numbers of *D. taeniatum* found per 100 maize plants in the first and second growing period at St. Lucia, Dept. of Boaco were 6 and 100 respectively (fig. 15B, 16C, 17C, 21D). *D. taeniatum* probably is an important natural enemy of *S. frugiperda* in maize, especially in the Interior of Nicaragua with the high densities of the earwig in the second growing period.

TABLE 36. Predation by the earwig *Doru taeniatum* on *S. frugiperda* egg masses offered in varying numbers. (Egg masses distributed at random on maize plants 18 to 22 days after emergence in a field cage; one earwig per plant.) (Exp. D)

Egg masses per cage (± 30 plants)	Number of replicates	Predated egg masses (%)	Egg masses per cage (± 30 plants)	Number of replicates	Predated egg masses (%)
1	2	50	7	1	86
2	1	50	8	1	50
3	2	67	9	1	44
4	1	25	11	2	50
5	1	60	13	1	83

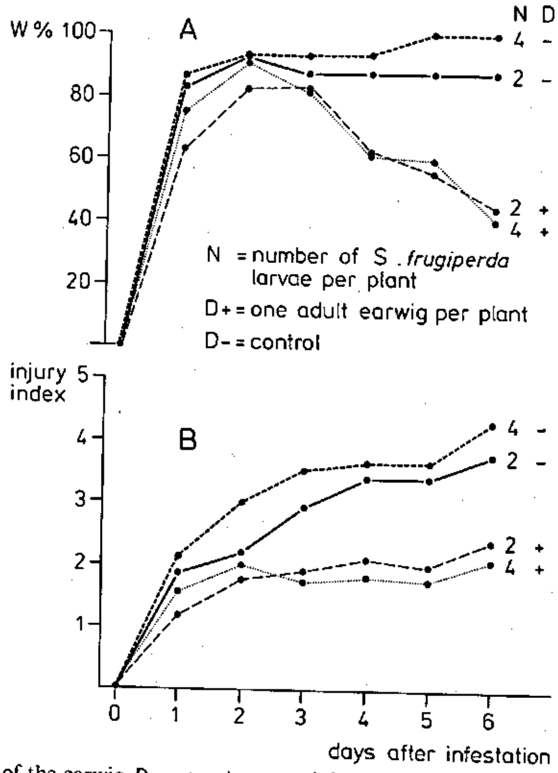


FIG. 23. The effect of the earwig *Doru taeniatum* on injury to the maize by *S. frugiperda*. (Maize whorls were artificially infested 26 days after plant emergence under different infestation treatments: ND = 4+, 2+, 4–, 2–, as specified in the figure). (Exp. D)
A. Percentage of injured whorls (W).
B. Average injury score of injured whorls.

Further investigations on the ecology and feeding habits of this predator will be necessary to explore its optimal use in the control of *S. frugiperda* in maize and sorghum.

3.4.3. *Rainfall and larval mortality of S. frugiperda*

3.4.3.1. Introduction

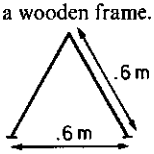
In a survey when maize farmers were questioned about the effect of heavy rain showers on maize pests several answered that larvae of *S. frugiperda* would be knocked down from the plant by rain and be drowned. Figure 15A seems to indicate larval mortality caused by rain. This is shown by the decrease in the percentage of infestation several days after heavy rain. The rain may have prevented a population build-up. However after 37 days, with less rain, the population increased.

HARCOURT (1966) reported that rainfall is an important cause of mortality of the first two larval instars of *Pieris rapae* L. on cabbage. SANDHU et al. (1975) found that the effect of rain on the population of the mite *Oligonychus indicus* (Hirst) varied for different cultivars of maize.

In two trials the effect of rain on whorl injury by *S. frugiperda* was investigated by sheltering some of the maize plants.

3.4.3.2. Material and methods (Exp. E)

In the second growing period of 1978 the hybrid X-105-A was sown in a plot of 20 × 10 m on October 14 at St. Lucia, Dept. of Boaco. The distance between rows was 1 m, in the row 2 plants per plant hole were. 18 m apart. In the 5 inner rows 8 plots were selected. The length of the row was 2 m. In 4 of these plots plants were sheltered by placing a transparent plastic roof about .3 m above the top of the plants. The roof was supported by a wooden frame. Its height was adjustable. Slanting rain



could not reach the plant whorl, but the soil underneath the shelter received sufficient rain to permit normal plant growth. Wind velocity during the trials was rather constant (average 2.5 m s^{-1}) and sufficiently strong to prevent a high temperature under the roof. The roof was placed above the plots only during the two trials (from Oct. 27 to Nov. 3 and from Nov. 6 to 14) to reduce effects other than rainfall such as light intensity. The other 4 plots were not sheltered from rain.

Four days before the artificial infestation of the first instar larvae, methomyl (Lannate 90% a.i. SP, .25 kg ha^{-1}) was applied with a knapsack sprayer so that the whorls would be free of *S. frugiperda* larvae. Thereafter, egg masses deposited on plants, frame and roof, were removed every day. Artificial infestation consisted of 3 first instar larvae per plant, reared from egg masses collected in the field.

In the first trial plants were infested 8 days after plant emergence (average plant height .11 m) and in the second trial the plants were infested 18 days after plant emergence (average plant height .23 m). On the third day of the second trial when it had not rained for 10 days the whorls of the unsheltered plants were given an artificial shower with a watering can. The amount was such that the whorl ran over with water. Screened plants received the same amount of water at the base. Rainfall was registered with an automatic rain-gauge. After the infestation whorl injury was scored daily according to the injury index of chapter 3.2.3.3.. Larval counts were not carried out as the required examination destroys the plant. The rather refined injury index gave sufficient indication of larval presence. The design permitted a one-way analysis of variance.

3.4.3.3. Results and discussion

For both trials the injury during the first days after infestation is the same for screened and unscreened plants (fig. 24). Larval establishment and feeding activity apparently were not influenced by the screening. After rainfall and artificial showering the first significant differences were obtained first in the injury score and next in the percentage of injured whorls (fig. 24). Before discussing these results, it should be taken into account that after larval death the injury gradually grew out of the whorl and from previous experience it was known that three to four days after a control activity the whorl would be scored as healthy. Therefore the effect of rain on larval mortality in the percentage of injured whorls is evident three to four days after the rain has fallen. The injury score may also indicate a lower number of larvae per infested plant, but this may only be ascertained after the three to four day period.

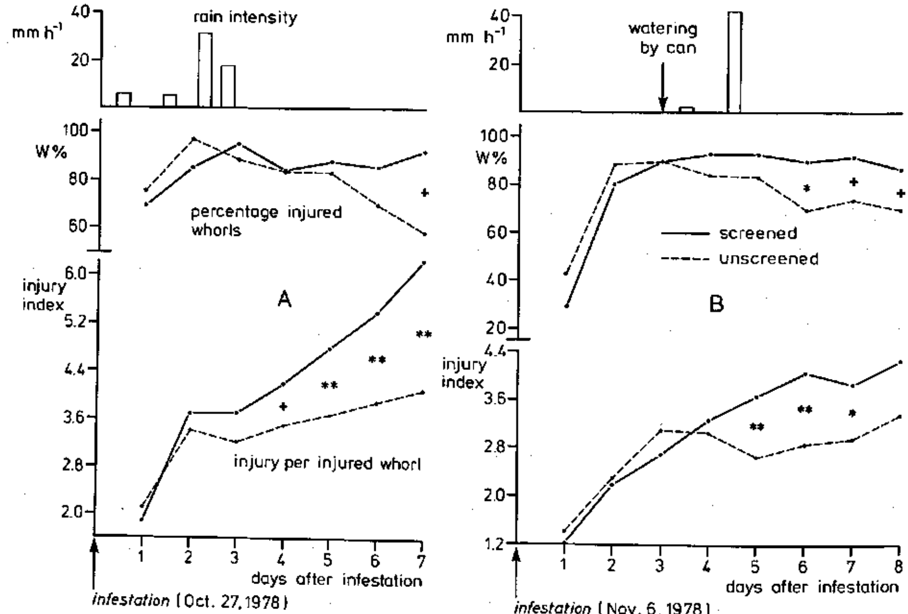


FIG. 24. Screening maize plants from rain. The effect on the percentage of whorls injured (W) by *S. frugiperda* and on the average injury score of injured whorls after artificial infestation with first instar larvae (Exp. E) on:

A. eight days after plant emergence.

B. eighteen days after plant emergence.

The low rain intensities of the first two days after infestation in the first trial did not cause mortality of *S. frugiperda* larvae (fig. 24A). The effect however of the heavy rainfall before the third observation day showed itself the next day in the injury score and four to five days later in the percentage of injured whorls. On the last day of this trial the number of injured whorls in the unscreened treatments was 36 per cent lower than in the screened treatments. At this date the injury score per injured whorl was significantly lower when not screened, indicating a lower number of larvae.

The artificial showering in the second trial possibly caused some larval mortality (fig. 24B). A shower however with water jets differs greatly from natural rainfall, the drops of the latter reach the plant at high velocities. Heavy rainfall is also normally accompanied by gusts of wind. The significant differences were caused by the artifical shower on the third day as well as by the natural rainfall on the fourth day after infestation. In plants that were not screened the percentage of injured whorls was 20 per cent lower. The significant lower injury score three days after the last rainfall indicates a lower number of larvae per injured whorl.

Heavy rainfall fills the whorl with water, which then overflows. This process was simulated by watering recently infested whorls. When the whorl filled with water, the first instar larvae floated on the water surface and subsequently were washed from the plant. It seems unlikely that these small larvae are able to regain the plant. Light rainfall does not cause the whorl to overflow, but the water filters slowly down between the leaves. In other observations rainfall only caused mortality of the first three larval instars of *S. frugiperda*. When larvae hatch from an egg mass, they remain together at the same spot (a 'larvae mass') for the first hours and when they start dispersing, they will probably be washed away from the plant by heavy rainfall; particularly when this larvae mass occurs on the upper side of the leaf (chapter 3.1.).

Rainfall during the early infestations of *S. frugiperda* in maize decreased the percentage of infested plants and also reduced the number of larvae per infested plant, it is therefore an important control factor of the early instars of *S. frugiperda* larvae.

3.4.4. *Summary and conclusions*

In Nicaragua 15 insect parasite species, one species of a nematode parasite, three entomopathogen species and a large number of predator species have been found on *S. frugiperda* in maize. Important parasites are the braconids (up to 30% parasitism of the collected larvae, mainly *Rogas laphygmae* and *Chelonus insularis)*, the tachinids (up to 60% parasitism in maize and up to 100% in weeds, mainly *Lespesia archippivora)* and mermithids (up to 30% parasitism, *Hexamermis* sp.). In the first growing period when most of the maize is grown these are the most important, while in the second growing period the entomopathogens (up to 30%) prevail. The braconids attack the eggs *(Chelonus* spp.) or the early larval instars *(Rogas* spp.) and kill the host at about the fourth larval instar, before the pest is able to cause much leaf injury. The tachinids and the mermithid kill the host in the last larval instar or even later, while not restricting damage. They reduce the size of the next generation of *S. frugiperda*.

A large number of predator species of *S. frugiperda* was observed. Important groups are *Polistes* wasps, pentatomids, reduviids, nabids, chrysopids, spiders and earwigs. Two earwig species occur in Nicaragua. *Labidura riparia* was found in the Pacific plain. Its predacious habits are described in the literature. A special study was conducted on *Doru taeniatum*, which occurs in the Interior of Nicaragua. This earwig preyed on the eggs and the first three larval instars of *S. frugiperda*. In cage studies a population density of one earwig per plant reduced the percentage of infested plants by a half. Populations of this density have been observed during the second growing period.

Rainfall a few days after artificial infestation reduced *S. frugiperda* infestations by 20 to 30 per cent. Field observations also indicated that rainfall is probably an important mortality factor of *S. frugiperda* larvae. Its effect is restricted to the first larval instars.

It may be concluded that during early infestations there are three powerful natural mortality factors of *S. frugiperda* namely the braconids, *D. taeniatum* and rainfall. Early use of insecticides can disrupt the first two control actions and should therefore be avoided. During later infestations mermithids and tachinids cause a high mortality of *S. frugiperda* larvae. An indiscriminate use of chemicals may also disrupt this parasitism thereby increasing infestations and necessitating further applications of insecticides. Misuse of insecticides in the small farmer's maize field may create more problems than it solves.

Trichogramma pretiosum reduced the egg populations of *D. lineolata* by at least a half. *Apanteles diatraeae* and *Paratheresia claripalpis* were the most important of the larval and larval-pupal parasites, but levels of parasitism were low. Therefore the introduction of other larval parasites should be considered (see chapter 5.2.).

4. ASPECTS OF CROP LOSS ASSESSMENT IN MAIZE FOR *S. FRUGIPERDA* AND *D. LINEOLATA*

4.1. *S.FRUGIPERDA* AND *D.LINEOLATA*: DAMAGE TO MAIZE USING DIFFERENT FERTILIZER LEVELS AND PLANT DENSITIES

4.1.1. *Introduction*

In the general introduction it was mentioned that of the foodgrain farmers in Nicaragua only 8 per cent use fertilizers and 8 per cent insecticides. Extension services strongly recommend the use of new varieties, fertilizers and insecticides for the cultivation of maize. These inputs in the peasant agriculture bring about agroecological, socio-economical and health risks (chapter 1.1.4.). Therefore it is of great importance to know the eventual effect of these inputs both individually and combined with each other. In traditional foodgrain agriculture, plant densities are generally rather low, because the low yielding inland varieties need to be spaced widely.

The introduction of new varieties means that plant densities are increased. *S. frugiperda* defoliates the plant, diminishing the photosynthetic surface. This may impair root development, which results in less competition between plants. In this field experiment it was investigated whether increased plant density with and without fertilization compensates for the damage by *S. frugiperda*.

Plant density, soil fertility and fertilizer influence the physiological condition and the phenotype of the plant. A physiological change in the plant (its nutritional quality) may affect the development of the insect and a change in phenotype may cause the insect to behave differently (e.g. oviposition). In this way agronomic practices can alter the pest status of insects that attack crops. The effect of fertilizer, plant density and the level of *S. frugiperda* injury, either alone or in combination, on the yield and the development of the maize plant was investigated. The effect of fertilizer and plant density on injury by *S. frugiperda* and by *D. lineolata* was also considered. Little effort has been made sofar to investigate these relationships (LEUCK et al., 1974; BRADER, 1976). Multidisciplinary research teams, which include entomologists, agronomists, plant physiologists and soil chemists should undertake these important investigations, because the scope of this type of research exceeds the bounderies of their specific disciplines.

4.1.2. *Literature*

S. frugiperda

No results are available of research dealing with the effect of *S. frugiperda* injury on the maize plant, sown at different plant densities. HANWAY (1969) found that a reduction in grain yield due to defoliation at the 10-leaf stage was not influenced by plant density.

LEUCK et al. (1974) discussed the importance of the genetic ability of a plant species or variety, to take up soil nutrients and to use this characteristic in breeding for resistance. A difference in this ability influences the physiology of the plant. As dietary hosts for insects the physiologically different plant will most probably have a different effect on insect populations. The increased genetic ability to absorb and utilize a nutrient element which contributes to resistance, may be used as a criterion for varietal selection.

LEUCK et al. (1974) studied the effect of foliar nutrient sprays on Coastal Bermudagrass, Antigua maize and sorghum, on the feeding preferences of the first instar larvae of *S. frugiperda*. All compounds sprayed on the foliage deterred larval feeding when compared with the unfertilized check. Based on former experience, LEUCK et al. (1974) linked non-preference with mortality and concluded that the sprayed compounds are potentially important insect control chemicals.

LEUCK (1972) mentioned that larvae of *S. frugiperda* fed on foliage of NP and NPK fertilized plants of pearl millet (*Pennisetum typhoidus* (Burm.)) showed faster weight gains, lower mortality and had a shorter development period, a higher pupal weight and a shorter life cycle from oviposition to adult emergence. When the first instar larvae of *S. frugiperda* were exposed to excised foliage of maize which had received various fertilizer treatments, during the whorl stage of the plant, the leaves of the fertilized plants were preferred (WISEMAN et al., 1973). Larval and pupal weight after eight days of forced feeding on the foliage of NPK fertilized plants were significantly higher, and the time to pupation shorter than for the unfertilized control. Larval mortality however was not influenced. Except for larval mortality these results agree with the findings of LEUCK (1972).

Maize stalk borers

Fertilization and damage

SCOTT et al. (1965) found that in field maize, artificially infested with egg masses of *O. nubilalis*, there was a greater reduction in yield in fertilized plots when compared to non-fertilized plots. PARISI et al. (1973) investigated the injury by *D. saccharalis* to maize in relation to plant density and fertilizer in three localities in Argentina. Only in one heavily infested maize field did the injury per plant increase slightly with the N-treatment.

Plant density and damage

In the latter maize field these authors observed a small but significant decrease of injured internodes per plant with increased plant density. FICHT (1932) reported that the number of eggs and larvae of *O. nubilalis* increased with plant density when measured per unit area, and decreased when measured per plant. HARDING et al. (1971) mentioned that neither the establishment nor the control of the first and second generation *O. nubilalis* were significantly influenced by row spacing of maize plants. ZEPP and KEASTER (1977) reported that the percentage of plants infested by the second generation *D. grandiosella* was not influenced by densities between 16,500 and 91,500 plants per ha in rows spaced at .97 m.

Fertilizer, plant density and larval development

Fertilizer and plant density effect phenotype and physiology of the maize plant.

The maize borer may react to phenotypical changes in the plant by modifying its oviposition behaviour. Oviposition was found to be positively related to leaf area and/or plant height for *O. nubilalis* (FICHT, 1932; PATCH, 1929 and 1942), for *D. grandiosella* (TURNER and BEARD, 1950; STEWART and WALTON, 1964) and for *D. lineolata* (Exp. A I).

Several authors mentioned physiological changes in the maize plant because of increased plant density. Dense plant populations of maize reduced the content of nitrate reductase in the plant, causing a lower rate of conversion into protein (HAGEMAN et al., 1961). The complex effect of mutual shading at higher plant densities on carbohydrate storage is discussed by DAYNARD et al. (1969) and ZEPP and KEASTER (1977). Fertilizing also changes the physiological condition of the plant, e.g. nitrogen is necessary for protein synthesis.

The physiologically different plants will probably exert an effect on the development of the larvae. Larvae of *O. nubilalis*, which are fed on maize leaves containing a relatively high level of protein and little sugar, had a high survival rate and a low weight. However when grown on stem internodes, which are low in protein and relatively high in sugar, the survival rate was low (BOTTGER, 1951). Combining the results of HAGEMAN et al. (1961) and BOTTGER (1951) one is tempted to conclude that survival of *O. nubilalis* larvae would be lower at higher plant densities. However, FICHT (1932) reported increased larval survival when there was a higher plant density. It demonstrates that one has to be very careful in concluding that simultaneously occurring changes in the plant and the insect are causally related.

The maximum loss of yield in maize by *O. nubilalis* when the plant densities were high was mentioned by SCOTT et al. (1965) and was attributed to one of the following effects: increased larval survival at denser stands and a greater infestation effect on yield when maize is grown under competition stress. The authors also found some evidence that N-fertilizer increased larval survival. CANNON and ORTEGA (1966) reported that nitrogen and phosphorous had a positive effect on the survival of *O. nubilalis* larvae. TAYLOR et al. (1952) mentioned the higher survival of this borer on vigorous plants than on small plants of the same age deficient in nutrients. PATCH (1947) also reported that fertilizer increased survival of this borer.

4.1.3. *Material and methods (Exp. F)*

June 15, 1978, the hybrid X-105-A was bulk sown at the experimental station La Calera, Managua. Six days after emergence the plants were thinned to densities of 50,000, 70,000, 90,000 and 110,000 plants per ha. The fertilizer treatment consisted of 1. no fertilizer application and 2. application of NPK fertilizer (10-30-10) and urea at sowing at the rate of 130 and 65 kg ha^{-1}. The urea treatment was repeated after 4 weeks. To obtain 3 levels of *S. frugiperda* injury the following treatments were given:

1. weekly application of 6 kg ha^{-1} of granular phoxim (Volaton 2.5%), a non-systemic organophosphorous insecticide with brief persistance;
2. artificial infestation with first and second instar larvae (5 per plant) (reared from field collected egg masses) one week after plant emergence;
3. natural infestation.

In the separate analysis of both naturally and artificially infested plants there was no difference between the two ways of infestation for all the variables studied. Results are therefore presented without making a distinction between the two ways of infestation.

A split-plot design was chosen with 4 replicates, the 2 fertilizer treatments in the main plots and for each main plot 12 combinations of 4 plant densities and 3 *S. frugiperda* injury levels in the subplots, giving a total of 96 subplots. The fertilizer treatments were applied by main plots because the study of the fertilizer effect was considered less important than its possible interactions with the other factors. This means that only a very pronounced fertilizer effect will be significant. Each subplot consisted of 4 rows, .9 m apart, 5 m long. Subplots were spaced 1.8 m from each other. Data were collected from the 2 inner rows.

On 14, 22, 29 and 36 days after plant emergence, the number of plants with healthy and injured whorls was counted and the height of 6 consecutive plants was measured in each subplot. On 17 and 42 days after plant emergence the dry weight of the roots was determined from 2 plants per subplot. At harvest the following data per subplot were collected: the number of plants, the number of ears, the number of plants with 2 ears, and the number of lodged and broken (below cob) plants. Cobs without grains were disregarded. The grain yield was adjusted to 15% moisture. From 20 ears taken at random per subplot, length and diameter were determined. To evaluate stalk injury by *D. lineolata* at harvest, on each of 20 plants per subplot (10 consecutive plants in each inner row) the number of injured internodes and the number of perforations were counted. The smallest diameter of the lowest internode was measured.

In the analysis of variance the percentage of plants (100x) with whorls injured by *S. frugiperda* was transformed by the arcsin $\sqrt{x}$ transformation. Only when the insecticide treatment was included in the analysis the number of injured internodes and the number of perforations were transformed by lnx. In the analysis of the influence of fertilizer and plant density on *S. frugiperda* and *D. lineolata* injury, the insecticide treatment was excluded. For equal treatment combinations in the subplots a clear linear soil fertility gradient orthogonal to replicates and fertilizer treatment was apparent. This soil fertility gradient was dealt with as a covariable concurrent with the main effects. The F-value of the covariable was determined with all the main effects and interactions present. The sign of the regression coefficient of the covariable is indicated. The gradient was not only used as a correction factor, but also as an explanatory variable. Means and interaction means have all been adjusted for the covariable. The analysis of variance was done by means of the computer program SPSS.

4.1.4. *Results and discussion*

The results are presented in two tables of analysis of variance. Table 37 presents the effects of the treatments on yield, plant development and injury by *S. frugiperda* and *D. lineolata*. Table 38 shows the effects of fertilizer and plant density on the injury by both insects in an analysis in which the protected subplots were not included.

When evaluating the effect of whorl protection on maize one has to consider that the damage by both *S. frugiperda* and *D. lineolata* cannot be separated. Other experiments however (chapter 4.4. and 5.1.) indicate that the injury by *S. frugiperda* can be held responsible for the major variation in the investigated maize plant characteristics.

4.1.4.1. Whorl protection and insect injury

The whorl protection treatment was effective (table 37). In the protected subplots the percentage of whorls injured by *S. frugiperda* were 41, 65, 57 and 19 lower than in the unprotected subplots on the successive sampling dates (14, 22, 29, 36 days after plant emergence, respectively). Whorl protection also considerably reduced stalk injury by *D. lineolata*: the number of injured internodes was reduced by 75% and the number of perforations by 83%.

At the early whorl stage, fourteen days after plant emergence, the percentage of injured whorls showed a significant three-way interaction (table 37, fig. 25A): without whorl protection the percentage of injured whorls remained almost the same for the increasing plant densities, fertilized subplots (P-F+) only having a 4% higher injury level than the unfertilized subplots (P-F-). In the whorl protected and not fertilized subplots (P+F-) control of *S. frugiperda* tended to be somewhat more efficient with decreasing plant density. This may have been the cause of a better application of the granulated insecticide at lower plant densities. With fertilizer (P+F+) however the percentage of injured whorls decreased from 50 at the lowest plant density to 30 at the highest. Thus the insecticide was

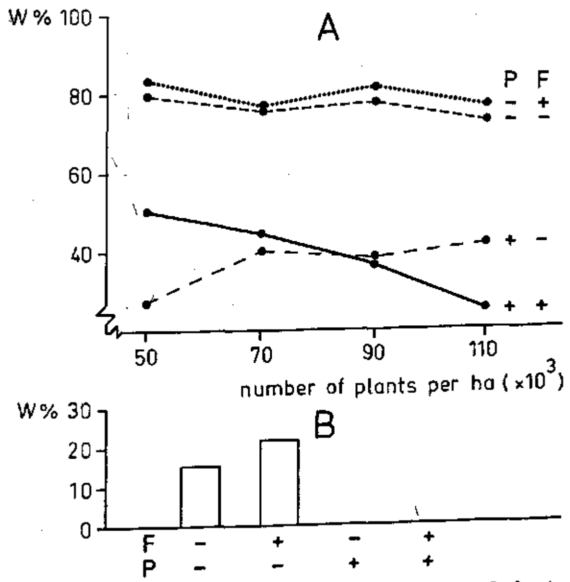


FIG. 25. Treatment effects on the percentage of whorls injured (W) by *S. frugiperda*. (Exp. F)
A. The effect of plant density (D), whorl protection (P) and fertilizer (F) 14 days after plant emergence (significant three-way interaction D × P × F, table 37).
B. The effect of whorl protection and fertilizer 36 days after plant emergence (weakly significant two-way interaction P × F, table 37).

Treatment	Without	With
Whorl protection (P)	–	+
Fertilizer (F)	–	+

TABLE 37. Whorl protection, plant densities and fertilizer. The effects on yield and plant development of maize and on the injury by *S. frugiperda* and *D. lineolata*. Analysis of variance: F-values, significancies and means. (Exp. F)

Source of variation	df	Grain yield per plot	Grain yield per plant	Number of plants: Total	Number of plants: Broken and lodged	Number of plants: Lost	Number of plants: With two ears	Number of ears
				F-values[3]				
Main effects								
Blocks	3	4.07	8.67^{+}	.85	4.48	1.11	.67	1.65
Fertilizer (F)	1	6.57^{+}	5.86^{+}	.17	.04	.30	5.92^{+}	14.7*
Error (a)	3	2.60^{+}	.90	1.90	.32	5.81**	1.67	1.51
Plant density (D)	3	1.13	20.8**	70.1**	9.91**	17.7**	10.4**	11.2**
Protection (P)	1	98.6**	36.8**	8.03**	10.5**	1.85	9.39**	31.4**
Soil fertility: cov.	1	94.8**	41.3**	10.9**	2.55	.03	13.8**	6.20*
sign[4]		+	+	+	–	–	–	+
Two-way interactions								
F × D	3	2.17^{+}	1.40	.97	1.71	2.46^{+}	.41	.04
F × P	1	13.4**	8.41**	.19	.01	.91	.15	.16
D × P	3	2.88*	1.97	.80	.76	.11	.40	.84
Three-way interactions								
F × D × P	3	.83	.64	.54	.52	.42	.75	.85
Error (b): V.C.	73	16.0	21.2	10.7	55.6	57.5	41.6	11.7
Total	95							
				means				
		kg ha^{-1}	gram	number per ha ($\times 10^3$)				
Grand mean		3651	54.3	69.1	5.52	11.0	7.20	62.6
							percentage deviation from	
Fertilizer								
unfertilized		–7	–5	–1	1	–8	–14	–6
fertilized		7	5	1	–1	8	14	6
Plant density (plants ha^{-1})								
50.000		–1	.22	–21	–35	–54	31	–10
70.000		1	8	–9	–16	–25	13	–3
90.000		4	–6	9	4	23	–11	7
110.000		–4	–24	20	47	56	–33	6
Whorl protection								
unprotected[5]		–11	–9	–2	13	6	–10	–5
protected		22	18	4	–26	–12	20	10

[1] Average over samplings 29 and 36 days after plant emergence.
[2] Date = days after plant emergence.
[3] Blocks and fertilizer against error (a); the rest, including error (a), against error (b).
[4] Sign of regression coefficient on increasing soil fertility (covariable).
[5] Control is double.
[6] Backtransformed.
[7] Percentage deviations of backtransformed values do not add up to zero.

Ear size: Length	Ear size: Diameter	Plant height[1]	Stalk diameter	Dry root weight at date[2]: 17	Dry root weight at date[2]: 42	*S. frugiperda* Percentage (100 x) injured whorls (arcsin $\sqrt{x}$) at date[2]: 14	22	29	36	*D. lineolata* Stalk injury x per plant (ln 10 x): injured internodes	perforations
					F-values[3]						
1.47	2.68	24.0*	41.3**	2.13	6.70^{+}	1.04	.30	.84	.64	.06	.23
1.47	.76	128.**	135.**	2.52	13.2*	.79	1.85	5.02	3.13	.88	1.38
32.2**	1.15	1.24	.81	3.32*	.80	2.34^{+}	2.57^{+}	1.74	2.50^{+}	11.5**	5.33**
20.4**	2.92*	8.04**	16.2**	1.31	2.67^{+}	1.53	1.84	1.98	5.40**	1.25	1.66
.25	14.9**	78.4**	3.91^{+}	24.1**	.25	322.**	946.**	636.**	591.**	122.**	117.**
3015**	32.8**	28.1**	4.53*	4.73*	.35	2.32	4.13*	1.40	.33	.20	.33
+	+	+	–	+	–	+	–	+	+	+	+
.31	.94	4.11**	2.71^{+}	.54	.13	1.81	.50	.41	1.22	.49	.29
.82	.30	3.41^{+}	.29	.81	.65	.08	.58	1.66	3.70^{+}	.42	1.13
8.23**	1.35	1.32	.15	.25	.37	.86	.34	.82	1.65	.53	1.11
6.99**	.80	.94	.36	.86	2.36^{+}	3.20*	.10	2.18^{+}	.41	.90	.35
9.51	5.47	7.84	5.14	33.7	31.4	11.6	13.1	21.9	27.8	125.	43.9
					means						
cm			mm	gram per plant		percentage[6]				number per plant[6]	
14.0	3.53	78.9	17.3	.627	9.29	66.0	54.6	34.5	8.7	1.32	2.52
grand mean										deviation from grand mean (%)[7]	
–2	–0	–10	–5	–10	–12	65	52	31	7	–11	–10
2	0	10	5	10	12	67	57	38	10	12	12
5	3	–5	5	12	16	68	58	38	11	11	16
3	0	–2	2	0	0	66	56	38	10	0	0
5	–1	3	–3	–6	–10	67	53	32	7	–8	–9
–13	–2	4	–4	–6	–6	62	51	31	6	0	–4
0	–1	–5	–1	–12	1	79	77	59	19	33	36
–0	3	10	2	24	–2	38	12	2	0	–42	–47

less effective at lower plant densities in fertilized plots. Fertilizers were applied per unit area, resulting in a higher fertilizer-plant ratio at lower plant densities. A possible explanation for a less efficient control at lower plant densities could be that young larvae were less sensitive to the insecticide, when grown on plants which had more fertilizer at its disposal. This interaction was not significant at later sampling dates. However it should be taken into account that the sampling at fourteen days was five days after the first insecticide application. This application was responsible for a high mortality of young larvae, which had not previously been exposed to insecticides. This in contrast to the later samplings (table 37).

A weakly significant interaction between whorl protection and fertilizer was present in the percentage of whorls injured by *S. frugiperda* 36 days after plant emergence (table 37, fig. 25B). With no whorl protection, fertilizer increased the percentage of injured whorls (P-F+ versus P-F-). When the whorls were protected there were hardly any injured whorls left in both fertilized (P+F+) and non-fertilized (P+F-) plots. The positive effect of fertilizer on the percentage of injured whorls will be discussed in greater detail later.

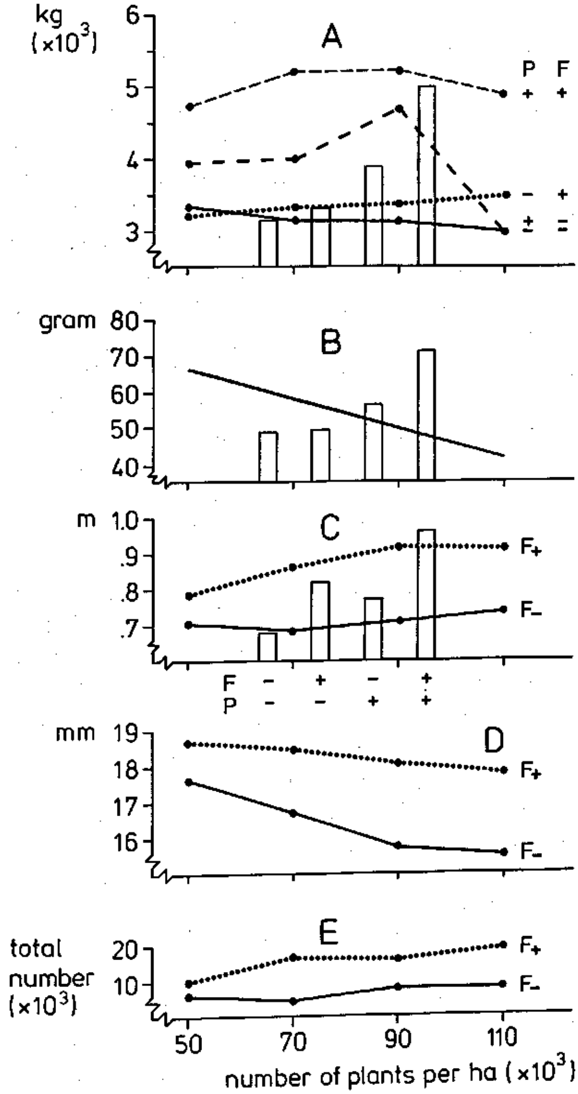
4.1.4.2. Yield and plant development

Yield

In grain yield per plot and per plant, whorl protection interacted significantly with the fertilizer treatment (table 37, fig. 26A, 26B). Whorl protection alone (P+F-) increased yield per ha by 24%, combined with fertilizer (P+F+) by 60%. For yield per plant these percentages are 16 and 47 respectively. Fertilizer alone (P-F +) increased yield per ha by 6% and yield per plant by 1%. These results indicate, that fertilizers are effective only when combined with whorl protection. A decision to control *S. frugiperda* should precede the decision on the use of fertilizer.

For grain yield per plot a significant interaction was present between whorl protection and plant density and a weak interaction between fertilizer and plant density (table 37). One treatment combination is mainly responsible for these interactions, namely whorl protection without fertilizer (P+F-) (fig. 26A). This treatment combination increased grain yield for densities from 50,000 to 90,000 plants per ha while at the high density of 110,000 plants per ha it declined sharply, suggesting strong competition between plants at the highest plant density. However when whorls protection was combined with fertilizer (P+F+) yield reduction for the highest density of 110,000 plants was negligible. Apparently fertilizer partly neutralized the competition effect brought about by whorl protection at high densities. With no control and no fertilizer (P-F-) yields declined gradually by 10% for densities from 50,000 to 110,000 plants per ha, while with fertilizer (P-F+) there was a gradual increase in yield of 9% in this range. Fertilizer increased yields more at the higher densities where competition effects were stronger.

In the introduction the assumption was made, that a higher plant density



Note: In graphs A, B and C the histograms give the averages of the four densities for each of the four F× P treatments.

FIG. 26. Whorl protection, plant density and fertilizer treatments. The effect on yield and plant development of maize (for significancies of tested effects see table 37). (Exp. F)

A. Grain yield per ha.
B. Grain yield per plant.
C. Plant height (average of 29 and 36 days after plant emergence).
D. Stalk diameter.
E. Number of plants lost.

Treatment	Without	With
Whorl protection (P)	−	+
Fertilizer (F)	−	+

compensates for a lower yield per plant, because of whorl injury by *S. frugiperda*. Reduced photosynthetic leaf surface would cause less root development, resulting in less competition between plants. The assumption that root development is less when whorls are not protected is statistically affirmed by the lower dry root weight (36%) 17 days after plant emergence (table 37). However just before tasseling (42 days after plant emergence) dry root weight was not affected by plant protection (table 37). Because the grain yield per plant diminished linearly with plant density (fig. 26B) the competition effects were already present at the lowest density of 50,000 plants per ha. Therefore the above assumption should have been investigated including in the experiment some lower plant densities.

Sown plant density gave significant differencies in grain yield per plant and the number of plants per ha at harvest (table 37). The linear decrease of grain yield per plant and the linear increase of the number of plants with rising plant density meant that the grain yield per ha did not show a significant density main effect.

Plant development

Whorl protection

In general whorl protection resulted in a more vigorous plant, which is expressed by the following plant characteristics (table 37): higher plants, in particular when fertilized (fig. 26C); larger stalk diameter (3%); increased dry root weight at seventeen days (36%); less broken and lodged plants (39%); higher plant numbers at harvest (6%). A heavier root system and a wider stalk diameter probably caused less broken and lodged plants and less plant loss. Whorl protection also significantly stimulated ear features: number of ears, plants producing two ears and ear diameter. The number of ears was increased by 15%, plants producing two ears by 30%. This was partly because of the higher number of plants and partly because of the increased vigour of the plant, both as a result of whorl protection as explained above. Ear diameter increased by 4%.

Plant density

Apart from the dry root weight (measured at 17 days), the plant density influenced all plant characteristics significantly (table 37). The effect was in most cases detrimental except for the variables 'number of plants' and 'number of ears' (which reflect the plant density treatment), and except for plant height which increased with plant density. Higher plants, smaller stalk diameter and less root development resulted in weaker plants, which lodge, break and die. In fertilized plots the plant height increased more, and the stalk diameter decreased less with higher plant densities as compared to unfertilized plots (a significant and a weakly significant interaction respectively, table 37; fig. 26C, 26D). At higher plant densities fertilizer application caused more plant loss (fig. 26E).

Fertilizer and soil fertility

Plant height, stalk diameter and dry root weight (42 days after plant emergence) were significantly increased by the use of fertilizer. Ear formation was also significantly influenced by fertilizer treatment. The application of fertilizer increased the number of ears by 12% and the number of plants which had two ears by 28% (table 37). The soil fertility gradient, which seemed to be a rather important covariable, showed its strongest effect in ear size. Yield variables, number of plants, number of ears, and plant height were also positively influenced by soil fertility.

Three-way interactions of whorl protection, fertilizer and plant density

Ear length showed a significant three-way interaction and the dry root weight (measured at 42 days after plant emergence) a weakly significant three-way interaction (table 37). The ear length showed a pattern that that was difficult to explain in the three-way interaction. The covariable for ear length had an extremely high F-value. Because means are adjusted for the covariable, small deviations from linearity of the covariable will affect the means considerably. It is therefore not deemed worthwhile to discuss this interaction. Dry root weight 42 days after plant emergence showed only a weak three-way interaction. The interaction will not be discussed because it does not show a clear pattern.

4.1.4.3. Fertilizer, plant density and insect injury

S. frugiperda

Fertilizer

Fertilized plots showed an increased number of whorls injured by *S. frugiperda* 14, 22, 29 and 36 days after plant emergence by 3, 5, 10 and 5% respectively (table 38). The fertilizer effect, however, was not significant. After the midwhorl stage the analysis gave higher F-values for the fertilizer effect than before midwhorl. There may be two factors involved: a higher oviposition, or a better survival of larvae on fertilized plants. In the experiment A II that investigated oviposition preference in nylon screen cages (chapter 3.1.) *S. frugiperda* deposited more egg masses on fertilized than on unfertilized plants, however the difference was not significant. There is some indication that survival by the larvae is higher, when plants are fertilized (LEUCK, 1972). In two experiments the gain in weight of the larvae was highest under these conditions (LEUCK, 1972; WISEMAN et al., 1973). Our experiment did not show whether oviposition and/or larval survival was responsible for the differences.

Plant density

Up till the first three sampling dates (up to 30 days after plant emergence) the number of injured whorls per plot increased significantly with plant density (table 38). It may be that a higher oviposition occurred at a higher plant density or that the colonization of plants by a certain number of young larvae was more efficient (in infesting more plants per unit area). Because in another experiment (B IV) plant density hardly influenced oviposition (table 20), probably dispersal of first instar larvae was more succesful at higher plant densities (see also Exp. B V, chapter 3.2.).

TABLE 38. Plant densities and fertilizer (only unprotected plots). The effect on injury by *S. frugiperda* and *D. lineolata* in maize. Analysis of variance: F-values, significancies and means. (Exp. F)

Source of variation	df	*S. frugiperda*								*D. lineolata* (number of)			
		Percentage (100 x) injured whorls (arcsin $\sqrt{x}$) at date[1]				Number of injured whorls per plot at date[1]				Injured internodes per		Perforations per	
		14	22	29	36	14	22	29	36	plant	plot	plant	plot
		F-values[2]											
Main effects													
Blocks	3	1.92	.45	1.28	.64	3.46[3]	.59	1.24	.91	.38	1.03	.63	1.56
Fertilizer (F)	1	1.45	1.25	4.63	2.66	4.97[3]	2.96	5.79^{+}	4.94	4.66	4.92	5.10	5.33
Error (a)	3	1.28	2.85*	2.10	3.63*	.05	3.20*	2.11	3.81*	3.41*	3.61*	2.53^{+}	3.06*
Density (D)	3	1.51	.50	2.58^{+}	5.82**	43.3**	23.6**	5.50**	.64	1.44	4.61**	1.43	4.22*
Soil fertility: cov	1	1.95	2.50	1.95	.51	7.43**	1.01	3.55^{+}	4.76*	6.00*	12.3**	3.09^{+}	8.97**
sign[4]		+	–	+	+	+	+	+	+	+	+	+	+
Two-way interactions													
F × D	3	.11	.30	.30	1.11	.73	.64	.29	.93	.40	.92	.35	.96
Error (b): C.V.	49	10.0	11.5	16.2	20.6	12.2	16.5	25.5	33.9	24.4	25.7	28.3	26.9
Total	63												

	means											
									number per			
	percentage[5]				number per plot				plant	plot	plant	plot
Grand mean	78.6	77.3	59.1	18.6	55.1	52.2	37.8	11.5	1.83	124.	3.64	246.
Fertilizer					percentage deviation from grand mean							
unfertilized	77	75	54	16	-3	-6	-11	-22	-12	-13	-13	-13
fertilized	80	80	64	21	3	6	11	22	12	13	13	13
Plant density (plants ha^{-1})					number per plot							
50.000	82	79	64	23	43	40	31	12	8	-15	9	-14
70.000	77	79	64	21	49	49	38	12	2	-3	3	-3
90.000	80	76	54	16	62	56	38	10	-9	-2	-12	-4
110.000	75	75	54	14	66	65	45	12	-1	20	0	21

[1] Date = days after emergence.
[2] Blocks and Fertilizer against error (a); the rest, including error (a) against error (b).
[3] Against error (b).
[4] Sign of regression coefficient on increasing soil fertility (covariable).
[5] Backtransformed.

On the subsequent weekly sampling dates the number of injured whorls per plot decreased in time more rapidly at higher plant densities than at lower plant densities (table 38). At the last sampling date the number of injured whorls per plot was the same for all plant densities and the percentage of injured whorls after midwhorl was significantly higher at lower plant densities. An explanation for this is that competition (for light, water and mineral nutrients) is stronger with increasing plant density and the development of the maize plant. Thus the physiological and phenotypical changes occurring in plants under competition stress will become more pronounced in the more advanced whorl stage. When the effect of competition stress (at a high plant density) can be compared with the effect of the absence of fertilizer then a lower larval survival at a higher density would explain the results: strong competition effects between plants after the midwhorl stage would cause a higher mortality at a higher plant density. A shorter larval development at higher plant densities would also be an explanation, however LEUCK (1972) and WISEMAN et al. (1973) found in their experiments a longer larval development on nutrient deficient plants.

Other less likely possibilities can be suggested. Firstly, the young larvae would be more mobile at higher plant densities, the same larva injuring several plants, while later instars would remain on the same plant. My own observations were that larvae and especially young larvae are very much confined to one and the same plant. Secondly plants infested at the whorl stage in higher densities would have a greater chance of dying and with the plant the larvae. However no interactions of any importance (table 37: F-values lower than one) occurred between plant protection and plant density for the variables, 'number of plants', 'number of broken and lodged plants' and 'number of plants lost'.

D. lineolata

Fertilizer and soil fertility

D. lineolata injury per plant was higher in the fertilized plots than in the unfertilized plots. Although differences were considerable they were not significant at the low number of degrees of freedom (table 37 and 38). The effect of soil fertility (the covariable) on *D. lineolata* injury could be tested more accurately and appeared to be significantly positive (table 38).

In cage experiment A II fertilized plants received more eggs than unfertilized plants. In field experiment A I a very close relationship was observed between leaf area and oviposition for plants of different age. Plant height was also highly correlated with oviposition. Between both extremes in soil fertility the difference in plant height was .1 metre. Fertilizer brought about a .2 m difference in plant height (average plant height 36 days after plant emergence: .92 m), there was also a visible difference between the plants in the fertilized plots (dark green leaves) and those in the unfertilized plots (light green leaves). For these reasons it is very likely that oviposition did play an important role in the observed differences.

The application of fertilizer was observed to increase the larval survival of the maize borer *O. nubilalis* (CANNON and ORTEGA, 1966; TAYLOR et al., 1952;

PATCH, 1947) and should be considered as another explanatory factor for the differences in injury by *D. lineolata* as a result of the fertilizer treatment.

Plant density

Increased plant density caused a significantly higher injury per plot, while injury per plant seemed to diminish (table 38). This outcome is in accordance with the results obtained for *D. saccharalis* (PARISI et al., 1973) and for *O. nubilalis* (FICHT, 1932).

At higher plant densities, plant height increased (36 days after plant emergence there was a difference of .1 m between the plants in the lowest and highest plant densities. It is likely that leaf area increased per unit area with plant density, while leaf area per plant diminished because of competition effects. If the amount of available leaf area determined oviposition this would be an explanation for the above results.

FICHT (1932) found evidence and SCOTT et al. (1965) found indirect indications for the increased survival of *O. nubilalis* at higher plant densities. The only indication for increased survival of *D. lineolata* in higher plant densities in this experiment is the reverse trend of decreasing injury per plant at a density of 110,000 plants per ha. At this density strong competition effects were apparent in this experiment.

4.1.5. *Summary and conclusions*

NPK fertilizer was responsible for increased injury by both *S. frugiperda* (a maximum of 10% of infested plants after midwhorl) and *D. lineolata* (24% injured internodes and 26% perforations). Also soil fertility increased the injury by both pests. It could not be determined which of the factors, oviposition or larval survival, was responsible for these effects. The use of fertilizer alone increased yield by merely 6 per cent, which may be partly due to the increased incidence of both pests.

Increased plant density seems to cause a more efficient colonization (probably by dispersal of first instar larvae) of *S. frugiperda*, larval mortality seemed to increase with progressing plant development (possibly because of nutritional factors as competition effects become stronger). Regarding *D. lineolata*, a higher plant density increased the injury per unit area and decreased it per plant. Egg deposits in proportion to the available green leaf area probably explains these results.

Increasing plant density did not compensate for *S. frugiperda* damage. In this experiment however, plant densities were probably too high, so that all treatments with fertilizer and whorl protection resulted in increasing competition between plants. Yield per unit area was rather stable with increasing plant densities, except for the treatment, in which the whorl was protected but not fertilized; at the sown density of 110,000 plants per ha the effect of protection was nullified by competition. The rather stable yield per unit area at all plant densities was achieved by the balancing effect of a decreasing yield per plant with an increasing plant density.

The most important result of this experiment is the synergistic effect of whorl protection and the use of NPK fertilizer on grain yield. Whorl protection alone increased yield by 24 per cent and fertilizer alone by 6 per cent. In combination however they increased yield by 60 cent. Thus the decision to control *S. frugiperda* should be preceded by the decision on fertilizer use. Yield increase by whorl protection will be greatly enhanced by using fertilizer. This is a well known phenomenon from the green revolution. These factors should be taken into account when promoting agrochemicals for the small farmer who is in a delicate socio-economic position.

4.2. *S. FRUGIPERDA:* SIMULATED LEAF INJURY AND PLANT SENSITIVITY AT VARIOUS WHORL STAGES

4.2.1. *Introduction*

Defoliation studies in maize have been undertaken for: simulation of hail damage in relation to policies for crop hail insurance (HICKS et al., 1977; CROOKSTON and HICKS, 1978), synchronization of flowering of inbreds by clipping young maize plants of early flowering lines to delay development (DUNGAN and GAUSMAN, 1951; CLONINGER et al., 1974), competition studies between plants when defoliation is caused by hail or insect injury (HANWAY, 1969; ALLISON et al., 1975), and simulation of insect injury only (CONDE, 1976).

Early plant stages were able to withstand considerable injury without seriously affecting the yield (HICKS et al., 1977; BROWN and MOHAMED, 1972) and maize characteristics, such as the number of cobs, the cob weight and the plant height (BROWN and MOHAMED, 1972). Occasionally maize cultivars respond by yielding more following defoliation at a very early stage of growth (CLONINGER et al., 1974; CROOKSTON and HICKS, 1978).

Vegetative pruning at floral initiation possibly results in timely stimulation of embryonic ear growth (CROOKSTON and HICKS, 1978). Slowing vegetative growth in the period from floral initiation until pollination favours the development of a high number of seeds in many cereals (EASTIN and SULLIVAN, 1974).

CONDE (1976) observed in Guatemala that when all the leaves were removed from .25 to .60 m high maize plants, the grain yield was not reduced and he concluded that injury by *S. frugiperda* during this phase of plant development would neither reduce grain yields. BROWN and MOHAMED (1972) assessed yield losses by simulating the injury caused by *Spodoptera exempta* in maize and sorghum in Kenya. In these experiments the plant was defoliated at one phase during plant development and was not representative for a sustained attack by a whorl defoliating insect. *S. exempta* is characterized by spectacular population fluctuations; large populations may quickly demolish a maize field and move to another field, a 'typical' armyworm behaviour (BROWN, 1972). Injury by *S. frugiperda* (USA: 'fall armyworm') in Nicaragua is generally limited to the whorl. Last larval instars eat away most of the whorl. Populations were occasionally so numerous that external leaf feeding and stem tunneling occurred, this was observed several times late in the second growing period in the Pacific plain, especially in fields with an abundance of graminaceous weeds (chapter 3.3.). This type of injury was also reported from Kansas, USA by BURKHARDT (1952). It was however not considered in this experiment.

In Central America the extension services recommend the use of an economic threshold of 20 per cent of whorls injured by *S. frugiperda* in maize. This injury level is indicated for all whorl stages. An experiment was set up to investigate the effect of whorl injury (simulating a *S. frugiperda* attack) at different stages of plant growth on the yield and plant development of maize.

4.2.2. *Material and methods (Exp. G)*

The experiment was sown June 13, 1978 at the research station La Calera, Managua. NPK fertilizer (10-30-10) and urea were applied at sowing at a rate of 130 and 65 kg ha^{-1}. The urea treatment was repeated after 4 weeks. During the whole period of plant development, the field was treated each week with chlorpyrifos (Lorsban 480E) at a rate of .6 litre ha^{-1}.

The whorl stages of long, intermediate and short-season maize cultivars (C_1-C_4, hybrids and open pollinating varieties) were divided into four equitemporal periods (T_1-T_4) (table 39). On each day of a period the plants were subjected to artificial whorl defoliation, to simulate a sustained attack of this maize pest. In preliminary studies it was found, that whorl injury by *S. frugiperda* starts about 3 cm above the last fully developed leaf. The most severe whorl injury brought about by *S. frugiperda* implies that the part of the whorl above this height is completely eaten away. The artificial injury therefore consisted in cutting the whorl with scissors at 3 cm above the last fully extended leaf. The whorl was cut every day in the period indicated.

The experiment was laid out according to a split-plot design with 4 replicates containing 4 cultivars in the main plots and 4 defoliation treatments plus a control in the subplots within each main plot. The subplots consisted of 4 rows, 5 m long and .9 m apart. Within rows plants were spaced at .15 m. The 2 inner rows were the sampling unit. A space of 1.8 m was left open between the subplots.

At the end of a cultivar's defoliation treatment the dry weight was determined from all the green leaves, including the whorl, of 2 representative plants per subplot both in the treatment and the control. The sample taken from the last defoliation period of Synt-Nic-2 (C_4) is missing. At the start of tasseling the number of plants with emerging tassels was counted. The following data were taken at harvest: number of plants, number of lodged and broken (below the cob) plants, plant height, ear length and diameter, grain weight (adjusted to 15% moisture). Ears from broken and lodged plants were marked in the field and weighed separately.

TABLE 39. Specification of treatments in Experiment G: artificial defoliation of the whorl in four equitemporal periods (T_1–T_4) with four maize cultivars (C_1–C_4).

Maize cultivars		Crop cycle duration (days from plant emergence to harvest)	Defoliation treatment (days after plant emergence) T_1	T_2	T_3	T_4
Hybrids						
B-666	(C_1)	115	5–16	17–28	29–40	41–52
X-105-A	(C_2)	105	5–14	15–24	25–34	35–44
Open pollinating varieties						
NB-2	(C_3)	105	5–14	15–24	25–34	35–44
Synt-Nic-2	(C_4)	90	5–12	13–20	21–28	29–36

When analyzing the data it appeared more appropriate to make an analysis of variance for each variety separately. The results from the different cultivars were compared or combined. For each variable analyzed, the error mean squares of the 4 cultivars were tested for heterogeneity (PEARSON and HARTLEY, 1954). As no significance occurred the pooled error mean square was used for calculating the F-values. For defoliation treatments various contrasts were made among treatments and between treatments and the control; the treatment sum of squares was partitioned into linear, quadratic and cubic components with the purpose of detecting possible simple trends.

4.2.3. *Results and discussion*

The analysis of variance of the effect of whorl defoliation during different plant growth stages on yield and plant development of maize is presented in Appendix 1. Results in terms of treatment means are illustrated by figure 27.

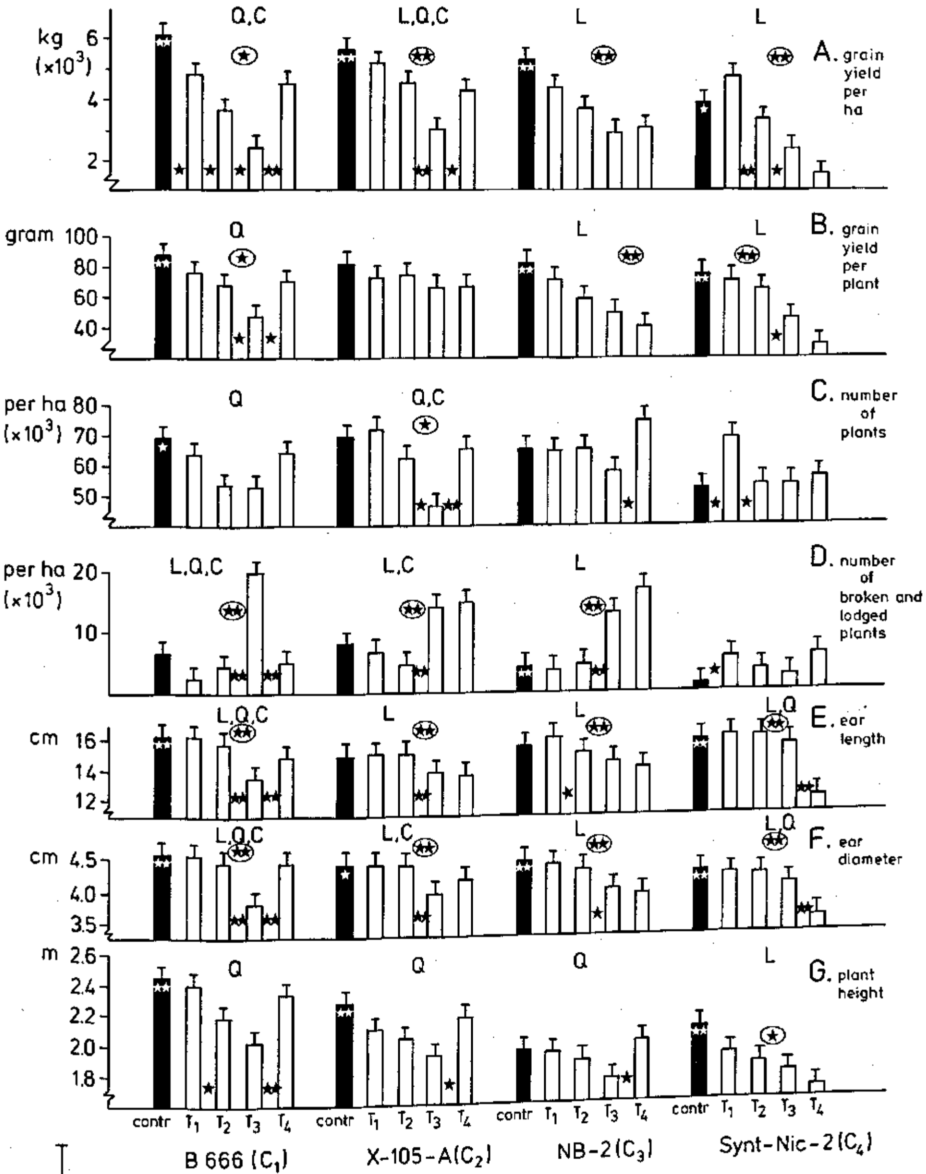
Yield. for each cultivar, grain yield per ha of the control was significantly higher than the combined defoliation treatments (fig. 27A). The four cultivars also shared another significant effect: defoliations after midwhorl stage lowered the yield per plot (T_3, T_4) more than before midwhorl (T_1, T_2). In the open pollinating varieties (C_3, C_4) yield decreased linearly with defoliations T_1 to T_4. For the hybrids (C_1, C_2) however defoliation T_4 in the fourth period affected the plant less and resulted in higher yields than the defoliation T_3 (significant quadratic effects). Only in the long-season hybrid B-666 (C_1) the defoliation T_1 resulted in a significantly lower yield than the control.

The same effects were obtained for grain yield per plant (fig. 27B) as for grain yield per plot, except that for X-105-A (C_2) there were no significant differences between treatments.

Number of plants (fig. 27C). Defoliation around midwhorl (T_2, T_3) caused the greatest plant loss in the long-season hybrid B-666 (C_1) (significant quadratic effect). DefoliationT_3 in the period just after midwhorl caused the greatest plant loss in the two intermediate-season cultivars (C_2, C_3), especially X-105-A (C_2). The number of plants for the short-season variety C_4 was not influenced by defoliation; the high number of plants for the defoliation T_1 must have been due to random effects.

Lodged and broken plants (fig. 27D). The defoliation T_3 in the period after the midwhorl stage caused most breaking and lodging of plants in the long-season hybrid C_1. The defoliation treatments T_3 and T_4 caused breaking and lodging of a high number of plants in both intermediate-season varieties C_2 and C_3. The lodged and broken plants from defoliation T_3 and T_4 produced ears with reduced grain weight (table 40). This indicates an overall reduced plant vigour, which resulted in the lower average grain yield per plant for the cultivars B-666 (C_1), NB-2 (C_3) and which may also include the hybrid X-105-A (C_2) (fig. 27D and 27B).

Ear size. The effect of defoliation on ear length and diameter (fig. 27E and 27F) were similar to those on yield (fig. 27A and 27B). Defoliation after midwhorl (T_3, T_4) reduced ear size significantly when compared with earlier defoliations (T_1, T_2) (also expressed by the significant linear component). Although ear size shows almost the same tendency as grain yield per plant there were some differences. Firstly Synt-Nic-2 (C_4) showed apart from the linear



CULTIVARS

standard error

significantly different from the defoliation treatments

Control

adjacent treatments are significantly different

significant differencies between defoliations before and after midwhorl (T_1, T_2 versus T_3, T_4)

Components of trend through the periods of defoliation (T_1 to T_4): L – Linear, Q – Quadratic, C – Cubic; letters L, Q, C in the figure indicate significant components ($P \leqslant .05$).

FIG. 27. Artificial whorl defoliation during four equitemporal periods (T_1 to T_4) compared with a control in four maize cultivars (C_1 to C_4). The effect on yield and plant development. (Exp. G)

TABLE 40. Lodged and broken plants after midwhorl stage for the defoliation treatments T_3 and T_4 of four maize cultivars (C_1 to C_4). (Exp. G)
A. The percentage of broken and lodged plants.
B. Grain yield per plant from broken and lodged plants as a percentage of grain yield of erect plants.

Cultivar		T_3		T_4	
		A[1]	B[1]	A	B
B-666	(C_1)	38	96	8	71
X-105-A	(C_2)	31	38	22	67
NB-2	(C_3)	23	62	23	70
SN-2	(C_4)	5	38	11	89

[1]Figures A may be computed from Appendix 1, for figures B one needs more detailed results.

decrease, a sharp decrease as a result of the last defoliation (T_4). Secondly for X-105-A (C_2) ear size was significantly lower as a result of the defoliations after midwhorl (T_3, T_4) than before midwhorl (T_1, T_2). The defoliations in the first period (T_1) and to a lesser extent in the second period (T_2) hardly affected the ear size of all cultivars. Ear length was probably even stimulated by the defoliation T_1 at the earliest growth stage, when floral initiation took place. The early defoliation probably enhanced embryonic ear growth, as reported by CROOKSTON and HICKS (1978).

Plant height (fig. 27G). For Synt-Nic-2 (C_4) the successive whorl defoliations linearly decreased plant height. For the other cultivars the successive defoliations in the first three periods also decreased plant height about linearly, but it was hardly affected by defoliation T_4 (significant quadratic effect).

The variable that contributed most to the yield per ha was grain yield per plant for Synt-Nic-2 (C_4) and NB-2 (C_3), number of plants for X-105-A (C_2), and both variables for B-666 (C_1) (fig. 27A, B, C).

Whorl cuttings in the first three periods reduced dry leaf weight by 70 to 90% compared with the control (table 41), but in the last period (T_4) by only 20 to 40%. Although percentage reduction of dry leaf weight was about the same for the first three defoliations, the effect on grain yield per ha was different. The defoliations after midwhorl appeared to be most detrimental and except for B-666 (C_1) the defoliations before midwhorl hardly lowered yields. Injury before midwhorl was probably compensated for by a lengthening of the whorl stage for the four cultivars, expressed by a retardation of tasseling (between 4 to 6 days) (fig. 28), which increased with the duration of the crop cycle of the cultivars. The percentage of dry weight of leaves removed (compared to the control) for the defoliation T_4 (in the last period) was lower than for the other defoliations (table 41). For both hybrids (C_1 and C_2) yield per ha was also less reduced by defoliation T_4 than by defoliation T_3. However for the open pollinating varieties (C_3, C_4) there was no difference in yield per ha between defoliations after midwhorl (T_3, T_4), both T_3 and T_4 decreased yield considerably.

TABLE 41. Dry leaf weight per plant of control and defoliated plants the day after each defoliation treatment (T_1 to T_4). (Exp. G)

A. Dry leaf weight (grams) of untreated control at the day after the corresponding defoliation treatment.

B. Dry leaf weight left on the defoliated plants as a percentage of the dry leaf weight of the untreated control.

Cultivar		T_1		T_2		T_3		T_4	
		A	B	A	B	A	B	A	B
B-666	(C_1)	1.44	14	11.3	13	35.4	30	48.9	81
X-105-A	(C_2)	1.28	18	8.91	15	26.6	23	44.4	64
NB-2	(C_3)	1.08	20	8.07	14	26.9	18	45.9	63
SN-2	(C_4)	.61	30	3.42	23	13.3	26	missing value	

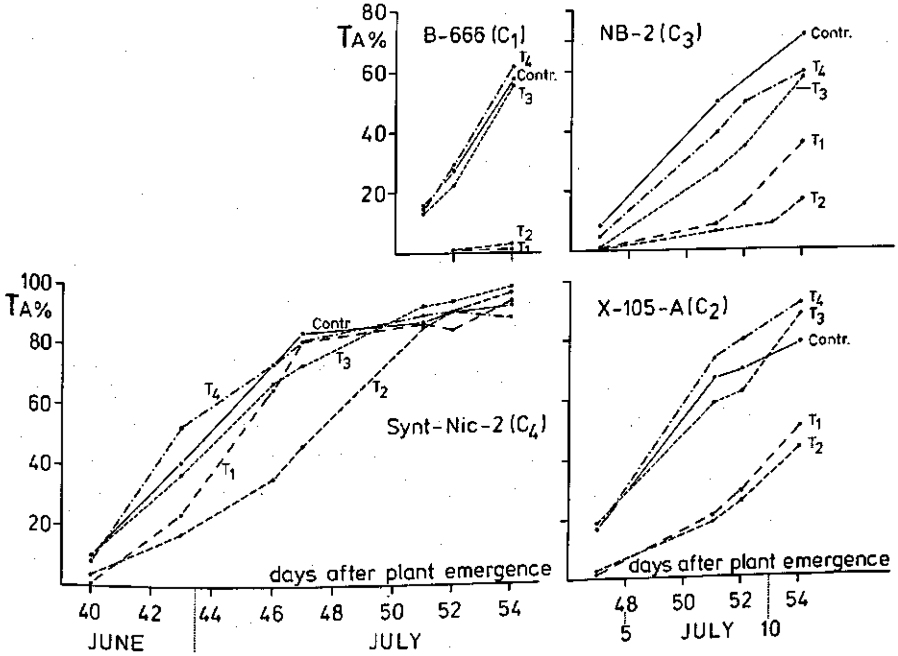


FIG. 28. Whorl defoliation in four equitemporal periods (T_1 to T_4, Contr. = untreated control) in four maize cultivars (C_1 to C_4). The effect on the time of tasseling: percentage of tassels emerging (Ta) with the progressing of the tasseling period. (Exp. G)

4.2.4. *Summary and conclusions*

Four maize cultivars were daily submitted to artificial whorl defoliation, simulating *S. frugiperda* injury, during four equitemporal periods. For a practical interpretation of the results of this experiment, it should be realized firstly that the whorl cutting treatments were inflicted on all plants and secondly that the artificial defoliations simulated the maximum intensity of injury by *S.*

frugiperda. Therefore the simulated injury was 'exaggerated' compared with natural injury, particularly in the early development of the plant, because firstly the small larvae cause limited leaf injury and secondly the number of injured whorls often increases with the plant growth stage.

The severe defoliations before the midwhorl stage in this experiment caused only a moderate loss of yield. The damage at early growth stage was probably compensated for by the tasseling being retarded. Other investigations also indicated that the maize plant at an early stage of growth was able to withstand considerable injury, without serious loss of yield (see introduction). If for this reason chemical control against *S. frugiperda* could be omitted before midwhorl (first three weeks), it would create a number of additional advantages in terms of the overall pest management strategy against *S. frugiperda*. This will be discussed in chapter 6. Attempts however to reduce injury after midwhorl with adequate control measures deserves full attention.

It should be noted that this experiment was not designed to investigate the possible interaction between defoliations in the different whorl stages, as this would require combinations of defoliations as separate treatments.

4.3. *S. FRUGIPERDA*: SENSITIVITY OF MAIZE TO WHORL INJURY AT VARIOUS GROWTH STAGES AND SOIL MOISTURE STRESS

4.3.1. *Introduction*

In the maize producing areas in Nicaragua rainfall during the growing season is an uncertain factor. From 1960 to 1978 there were eight years with an annual rainfall of less than 1000 mm, which can be considered as dry years (fig. 1 and 2). Very few farmers have irrigation facilities at their disposal. Many fields are not suitable for irrigation because of their slope and most soils are too marginal to make irrigation economical. Therefore the effect of whorl injury by *S. frugiperda* on the maize yield was investigated under different soil moisture regimes.

In several Central American countries it was suggested that the whorl injury by *S. frugiperda* would hardly cause any loss of yield if plants were able to grow with sufficient soil moisture (e.g. CONDE, 1976). The vigorous growth of the plant would compensate for much of the injury. However under dry conditions a synergistic effect of drought and whorl injury was expected. The problem was: does whorl protection increase yield independently of moisture stress? This was investigated during the dry season, when *Diatraea lineolata* is in diapause and its damage cannot interact with damage by *S. frugiperda*.

The plant sensitivity, at various whorl stages of four maize cultivars to *S. frugiperda* damage has been investigated by simulating the injury by artificial defoliation (chapter 4.2.). In the experiment to be discussed in this chapter the plant sensitivity to injury at various whorl stages was also the subject to investigation, but in combination with different soil moisture conditions and by using real *S. frugiperda* infestations. Maize whorls were artificially infested with *S. frugiperda* larvae and whorl protection was started at different stages of growth of the plant. That in this experiment moisture stress affected whorl injury (and/or larvae of *S. frugiperda*) was incidentally observed.

4.3.2. *Literature*

When moisture stress occurred prior to silking, grain yield was reduced by 25 per cent, when it occurred at and after silking yield was reduced by 50 and 21 per cent respectively (DENMEAD and SHAW, 1960). When the plant was actively expanding, moisture stress retarded enlargement of plant sections. When the stress was removed the growth rate returned to a normal level after a few days. DENMEAD and SHAW (1960) concluded that moisture stress probably affected grain yield indirectly by reducing the leaf area and hence the assimilatory capacity at the time of the development of the ear. Stress imposed during the first 30 days after sowing did not retard growth sufficiently to influence yield noticeably.

4.3.3. *Material and methods (Exp. H)*

March 9, 1978, the hybrid X-105-A was sown at the experimental station La Calera, Managua. NPK fertilizer (10-30-10) was applied at sowing at the rate of 130 kg ha^{-1}. Urea was applied at a rate of 65 kg ha^{-1}, 19 and 32 days after plant emergence. Eleven days after emergence plants were thinned out to .15 m in the row, leaving a density of 66,667 plants ha^{-1}.

Drought simulation treatments consisted of irrigation at intervals of 7 (M_1), of 11–12 (M_2), and of 14 days (M_3). Every day (except weekends), from 13 days after plant emergence and until tasseling a soil sample was taken from each plot and the percentage of soil moisture was determined. Field capacity and the wilting point were measured from 12 soil samples, one taken from each plot. The 4 protection treatments were as follows: whorls were protected from 7 (P_1), from 15 (P_2) and from 30 days (P_3) after plant emergence, until tasseling (45 days after plant emergence); for comparison an unprotected control (P_0) was added. For the protection treatments granular phoxi.n (Volaton 2.5%) was hand-applied weekly at a rate of 6 kg ha^{-1}. Seven and 20 days after plant emergence each plant in the subplots that had not yet been protected, was manually infested with 5 first-to-second instar larvae, which had been reared from egg masses collected in the field.

The design was a split-plot with 4 replicates, 3 soil humidity levels in the main plots and 4 protection treatments in the subplots within each main plot. There were two reasons for choosing this design. The first and primary interest was the protection treatments and the interactions with soil moisture stress. Secondly this was the most convenient way to implement the irrigation treatment. The whole trial was irrigated by inundation at sowing and germination. From tasseling onwards the maize plants were sprayed with methyl parathion 48% EC at a rate of .7 l ha^{-1}.

Each plot consisted of 8 rows, 10 m long, and 1 m apart. The plots were surrounded by soil ridges of about .25 m high and spaced 5 m apart. An irrigation channel ran through the middle of the field, at each side of the channel lay 6 plots (2 replicates). Each subplot consisted of 4 rows of 5 m, the 2 inner rows being the sample unit.

Twice a week the number of plants and injured whorls were counted and the height of 6 consecutive plants measured. At harvest the following data were recorded: the number of plants, the number of plants with 2 cobs, the number of cobs, the ear length and diameter, grain weight (adjusted to 15% moisture). Birds caused some grain loss; missing grains on the ear were counted, a sample of grains weighed, and grain weight per subplot was adjusted.

Percentage of injured whorls (100x) was transformed with arcsin $\sqrt{x}$. The analysis of variance was carried out by means of the computer program SPSS.

4.3.4. *Results and discussion*

The analysis of variance of the effect of soil moisture stress and whorl

TABLE 42. Whorl protection of maize starting at three different stages of plant development (P_1–P_3) and an untreated control (P_0), with three different soil moisture levels (M_1–M_3). The effects on yield and plant development of maize, and on the injury by *S. frugiperda*. Analysis of variance: F-values, significancies and means. (Exp. H)

Source of variation	df	Grain Yield per		Number of plants			Number of ears	Ear size		Plant height[1]	*S. frugiperda* Percentage (100 x) injured whorls (arcsin $\sqrt{x}$) at date (d)[2]		
		plot	plant	Total	Lost	With two ears		Length	Diameter		$10<d<15$	$15<d<30$	$d>30$
								F-values[3]					
Main effects													
Block	3	1.59	5.82*	2.24	3.96^{+}	.89	.94	.65	4.27^{+4}	2.52	1.69	5.09*	2.13
Soil moisture (M)	2	4.04^{+}	3.93^{+}	1.89	6.03*	3.00	1.39	3.76^{+}	5.51^{*4}	10.9**	1.66	.67	.06
M_1–M_3 (M_L)	1	8.06*	7.43*	3.78^{+}	11.7*	1.54	2.58	3.03	10.8^{*4}	21.3**	3.26	.08	.02
M_2–M_1 M_3	1	.02	.34	.00	.35	4.46^{+}	.19	4.63^{+}	.49^{4}	.38	.05	1.26	.10
Error (a)	6	1.65	.65	1.53	1.71	.90	1.71	.80	.35	4.07**	4.00**	6.44**	1.80
Protection period (P)	3	4.05*	3.43*	1.04	1.19	6.47**	2.49^{+}	3.05*	1.47	1.73	42.7**	201.**	311.**
P_0–$P_1P_2P_3$ (P_I)	1	9.72**	10.1**	.00	.30	13.2**	5.48*	6.97*	3.18^{+}	.16	8.55**	184.**	921.**
P_1–P_2P_3 (P_{II})	1	2.40	.09	3.11^{+}	1.46	.02	1.91	1.50	1.28	1.91	118.**	116.**	.04
P_2–P_3	1	.05	.10	.01	1.81	6.09*	.10	.75	.20	3.11^{+}	1.33	302.**	11.3**
Interactions													
M × P	6	1.08	1.02	1.20	1.53	1.87	2.34^{+}	.38	.91	1.37	.40	1.64	.63
M_L × P_I	1	4.80*	3.46^{+}	.40	.08	.45	4.04^{+}	.24	1.56	5.86*	–	–	–
M_L × P_{II}	1	.02	.15	.17	.99	8.44**	.43	.01	.14	.04	–	–	–
Error (b): V.C.	27	24.6	24.6	15.3	59.2	73.0	14.7	7.04	4.10	11.0	15.2	10.4	12.3
Total	47												

	means											
	kg/ha	gram	number per ha				cm			percentage[5]		
Grand mean	2798	64.7	43.4	8.69	1.39	39.9	14.4	3.97	103.	19.2	39.7	31.0
	percentage deviation from grand mean											
Soil moisture M_1	15	8	6	−43	−1	6	1	2	16	16	37	31
M_2	1	3	−0	−9	−28	−2	2	1	3	19	44	32
M_3	−16	−11	−6	52	29	−4	−3	−3	−19	23	39	31
Standard error	11	12	7	27	33	10	4	2	6	3.4[6]	3.5[6]	3.6[6]
Protection period P_1	15	8	6	−20	21	8	−0	2	3	7	17	15
P_2	3	8	−3	−10	57	−1	4	0	3	24	18	12
P_3	1	4	−3	22	−14	1	1	−0	−5	26	65	20
P_0	−19	−20	0	8	−64	−8	−5	−2	−1	23	63	83
Standard error	6	7	4	15	19	6	2	1	3	2.0[6]	2.0[6]	2.1[6]

[1] Averages over samplings at 36, 39, 42 and 47 days after plant emergence.
[2] Date = days after plant emergence.
[3] Block and soil moisture against error (a); the rest including error (a) against error (b).
[4] Against error (b).
[5] Backtransformed.
[6] Arcsin $\sqrt{x}$.

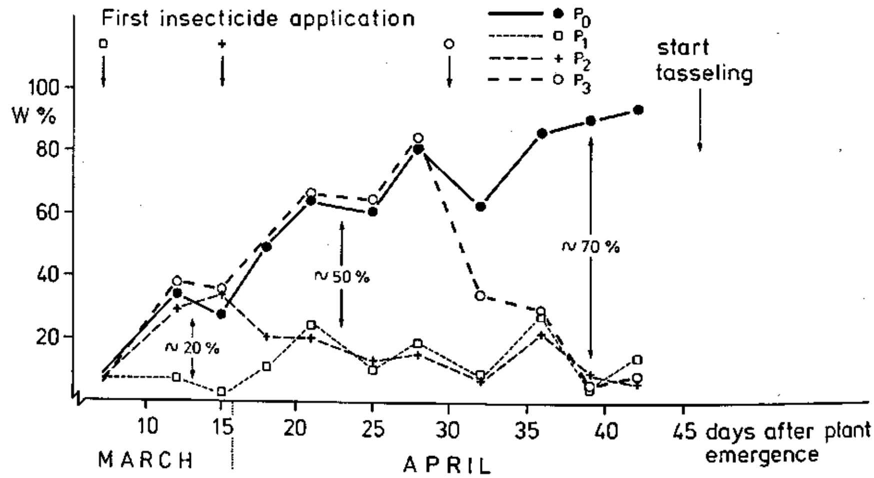


FIG. 29. Percentage of whorls injured (W) by *S. frugiperda* during plant development in maize without whorl protection (P_0) and with whorl protection starting 7 (P_1), 15 (P_2) or 30 days (P_3) after plant emergence. (Exp. H)

protection on maize plant characteristics and on injury by *S. frugiperda* is presented in table 42.

4.3.4.1. Plant sensitivity at various whorl stages

Protection resulted in a lower percentage of whorls injured by *S. frugiperda* compared to the unprotected control P_0 (table 42, fig. 29). There was about a 20% difference in infestation measured in the second week after plant emergence between complete whorl protection (P_1) and whorl protection after 15 days (P_2). Between complete whorl protection (P_1) and whorl protection starting at 30 days (P_3) the difference in the number of injured whorls was about 50% and between the control (P_0) and whorl protection after 30 days of plant emergence (P_3), the difference was about 70%.

For the combined protection treatments (P_1, P_2, P_3), yield per plot and per plant, ear length, the number of ears, and the number of plants with two ears were significantly higher than in the control P_0 (table 42, P_I). Except for the number of plants with two ears, these variables did not show any differences between the whorl protection treatments, although the 50% difference in the number of injured whorls between treatments P_3 and both P_1 and P_2 lasted at least two weeks between 15 and 30 days after plant emergence (fig. 29).

It may be concluded that the maize plant was not very sensitive to whorl injury by *S. frugiperda* before the midwhorl stage. This confirmed the results of experiment G (chapter 4.2.) with artificial defoliation at different whorl stages.

4.3.4.2. The effect of whorl protection under soil moisture stress

The difference in the percentage of moisture available to the maize plant in the different irrigation treatments is presented in figure 31C. The treatment of weekly irrigation (M_1) had a much higher percentage of moisture available to the maize plant than the treatment of fortnightly irrigation (M_3). Significant rainfall occurred 40 days after plant emergence, which was two and four days before the planned irrigation treatments, despite the disturbance the treatment of strongest soil moisture stress (M_3) was visible until five days before tasseling (see fig. 31C).

Grain yield, number of plants harvested, plant height and ear diameter decreased with increasing soil moisture stress (significant linear components M_L, table 42).

The main interest in this experiment was to investigate if different levels of soil moisture affected damage by *S. frugiperda*. Such an effect seemed absent, because there were no significant interactions (M × P) between soil moisture and protection (table 42). However in the combined whorl protection treatments (P_1,

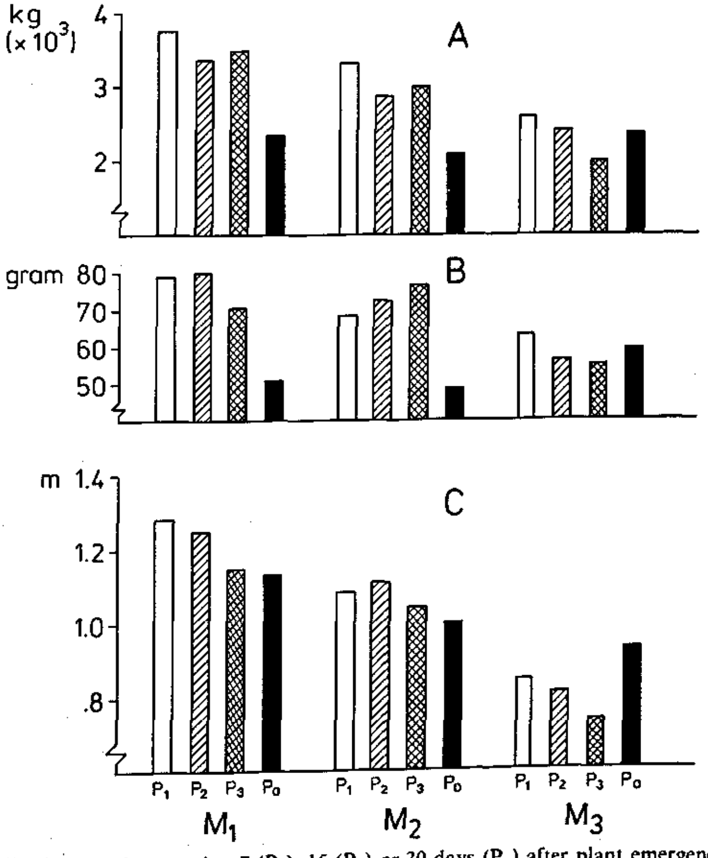


FIG. 30. Whorl protection starting 7 (P_1), 15 (P_2) or 30 days (P_3) after plant emergence and an untreated control (P_0), with three soil moisture levels: irrigation at time intervals of 7 (M_1), 11 to 12 (M_2) and 14 days (M_3). The effect on yield and plant height of maize (table 42). Exp. H
A. Grain yield per ha.
B. Grain yield per plant.
C. Plant height (average of sampling dates 36, 39, 42 and 47 days after plant emergence).

P_2, P_3), yield per area and per plant diminished with increasing soil moisture stress (fig. 30A and 30B), while without whorl protection (P_0) the yields were about the same under all soil moisture conditions: without whorl protection (P_0) the yield decreased by 38% with sufficient soil moisture supply (M_1) and by 9% with severe soil moisture stress (M_3) (both when compared to complete protection P_1). For a better understanding the interaction was split up into several components.

The first interaction component concerned the contrast between the control (P_0) and the combined whorl protection treatments (P_1, P_2, P_3) for the two extremes in soil humidity (M_1 versus M_3). The interaction component ($M_L \times P_I$; see table 42) is characterized by the following vector:

Soil moisture stress		Whorl Protection Treatments			Control
		P_1 1	P_2 1	P_3 1	P_0 -3
M_1	1	1	1	1	-3
M_2	0	0	0	0	0
M_3	-1	-1	-1	-1	3

The vector expresses a reduction (e.g. in yield) by whorl protection with increasing soil moisture stress. The component was significant for the yield per plot and for plant height and weakly significant for yield per plant and the number of ears (table 42). Under soil moisture stress plant height was even higher without whorl protection than with it (fig. 30C), while whorl protection hardly influenced the yield per plot and per plant (fig. 30A and 30B).

This result may have the following reasons. Firstly under soil moisture stress plants were more sensitive to phytotoxic effects of pesticides. Phoxim (Volaton) was well known for this effect on maize. Although in this experiment no visible phytotoxic effects were observed, this does not exclude the possibility of subclinical effects. Secondly *S. frugiperda* reduced the transpiring leaf area by defoliation, removing some of the stress (under soil moisture stress a large transpiring leaf area may be a disadvantage to plant growth).

Protection throughout whorl development (P_1) and protection starting at 15 and 30 days (P_2, P_3) were not significantly different for the maize variables studied (table 42, P_{II}). It was also investigated if this contrast P_{II} between protection treatments would show an interaction with the linear component of soil moisture (M_L). The interaction ($M_L \times P_{II}$, see table 42) expressed by the contrast vector is presented in table 43. This interaction component was not significant for the maize variables, except for the number of plants with two ears. Thus the effect of the whorl protection treatments was not altered by soil moisture conditions for most of the variables.

The number of plants producing two ears which had a sufficient soil moisture supply, diminished when proctection started at a later whorl stage, it was highest under moisture stress when protection started at 15 days (P_2) (table 43).

TABLE 43. Three whorl protection treatments (P_1–P_3) and three soil moisture levels (M_1–M_3). The effect on the average number of plants with two ears at harvest; the interaction contrast[1] $M_L \times P_{II}$ is highly significant[2] (table 42). (Exp. H)

Interaction contrast vector $M_L \times P_{II}$		Contrast vector P_1 (2)	P_2 (−1)	P_3 (−1)	Number of plants with two ears per ha (x 10^3) P_1	P_2	P_3
M_1	(1)	2	−1	−1	2.8	1.7	1.1
M_2	(0)	0	0	0	.6	2.0	.9
M_3	(−1)	−2	1	1	1.7	3.1	1.7

[1] The interaction contrast is the inproduct of the contrast vector and the response vector.
[2] 'Significant' means significantly different from zero.

DAMPTEY and ASPINALL (1976) found an increase in cobs when water deficit was imposed during early plant development, due to stimulation of axillary inflorescences. In Experiment F (chapter 4.1.) dry root weight 17 days after plant emergence was less in plants that had received no whorl protection. Starting the whorl protection 15 days after plant emergence in plants which grew under moisture stress and also had a poorly developed root system (as they were not protected before) may have increased the stress factor causing stimulation of several female inflorescences.

4.3.4.3. The effect of irrigation on whorl infestation

The percentage of injured whorls (of unprotected subplots) was highest for maize that was deprived the longest of irrigation (significant differences of 10 to 25% were found 12, 18 and 21 days after plant emergence, fig. 31A). Probably two processes are involved. Firstly, the percentage of injured whorls increased most in the subplots deprived longest of irrigation. Secondly irrigation of plants suffering from moisture stress stopped the increase or decreased the percentage of injured whorls. It is difficult to point out which effect of irrigation caused the observed differences. A few possible explanations are suggested.

1. Moisture stress reduced plant growth; this made whorl injury by *S. frugiperda* more easily visible. After irrigation normal plant growth would be resumed and whorl injury masked. The growth rate at 12 days (when the percentage of injured whorls differed) was different for the three soil moisture levels (fig. 31B). However, 18 and 21 days after plant emergence (when the percentage of injured whorls also differed) the growth rate was the same for all soil moisture treatments. Irrigation of plants suffering from soil moisture stress could show exuberant growth masking the injury, but figure 31B does not give evidence of an exceptionally high growth rate.
2. Moisture stress favoured the development of the insect, and irrigation of plants under soil moisture stress resulted in larval mortality. Under moisture stress the physiology of the plant changes (MATTAS and PAULI, 1964). It is

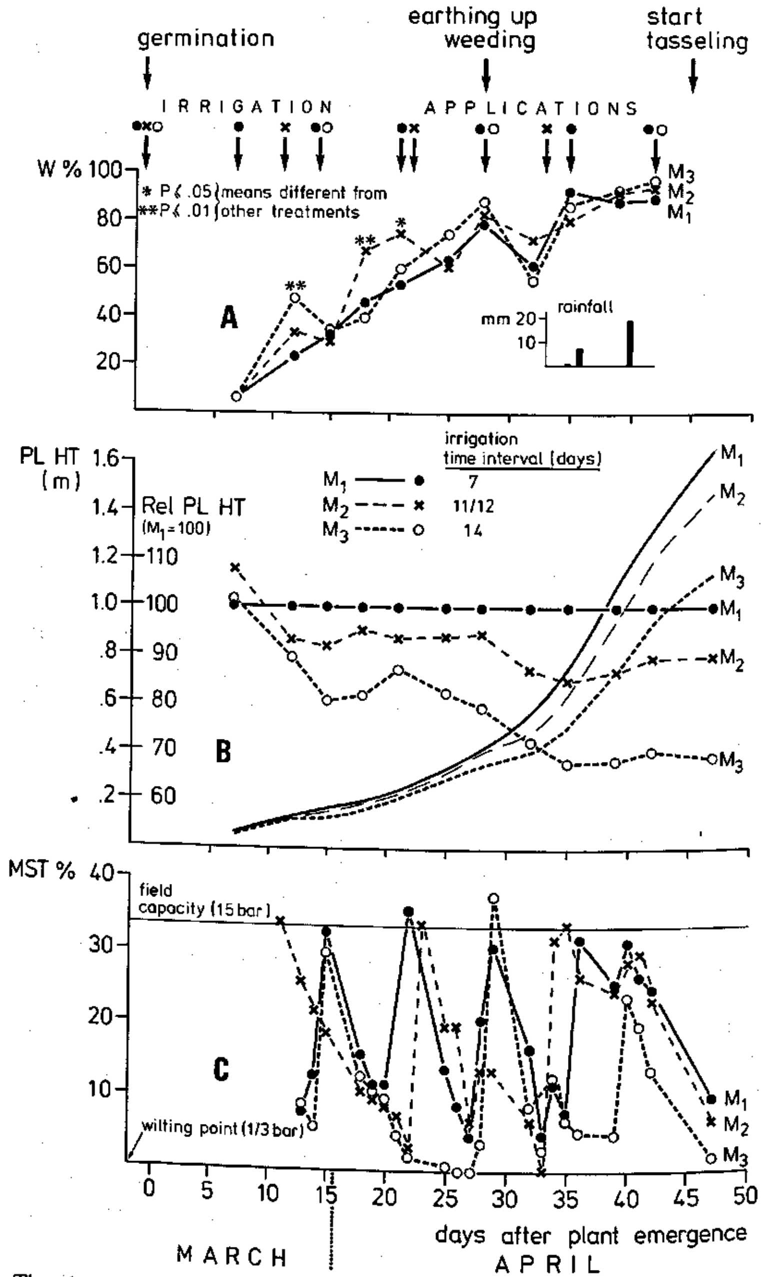


FIG. 31. Three levels of soil moisture (M_1, M_2, M_3) during the development of the maize plant. The effect on injury by *S. frugiperda* and the height of the plant. (Exp. H)
A. Percentage of whorls injured (W) by *S. frugiperda*.
B. Average plant height (PL HT) and relative plant height (Rel PL HT) (M_1 = 100).
C. Percentage of soil moisture (MST) available to the maize plant.

however not known what effect these physiologically different plants could exert on the development or behaviour of the insect. Apart from feeding responses there may have been physical effects. CHIANG (1959) mentioned that larvae of *Ostrinia nubilalis* were found to be drowned in a 'transparent jelly' on the rolled up whorl leaves. This jelly was frequently observed by us when whorls were dissected. However, the influence of soil moisture stress and irrigation on the occurrence of the jelly was not investigated.
3. Effects on larval behaviour. Under soil moisture stress one larva would injure several plants. This was not investigated, but seems unlikely.

Besides these possibilities one could consider the effects of irrigation on oviposition and/or predation. The phenomenon exists and further investigations on the effect of withering plants on the development and behaviour of the pest are necessary.

4.3.5. *Summary and conclusions*

There were no significant differences between grain yields of maize because of whorl protection which started 7, 15 or 30 days after plant emergence. The maize plant withstood considerable whorl injury up to 30 days after plant emergence. The low sensitivity of the maize plant to defoliation at an early growth stage was also demonstrated in experiment G (chapter 4.2.). Without whorl protection yields were about the same for all soil moisture levels. Under sufficient soil moisture, whorl protection increased yields by 50 per cent, but under severe soil moisture stress whorl protection did not increase yields. This is probably because when the whorl is protected there is an enlarged transpiring leaf area, which may be a disadvantage to plant growth under severe soil moisture stress.

The observed whorl infestation by *S. frugiperda* was highest for maize deprived longest of irrigation. It remains to be investigated whether this effect is caused by plant growth (visual) or by changes in larval development or behaviour.

In the tropics maize and sorghum are often grown under heavy soil moisture stress. Investigations of the effect of whorl protection on yield under drought conditions and of the effect of withering plants on larval development and behaviour are of great importance for the development of integrated pest management. The research in tropical countries should undertake these investigations and the irrigation facilities of the experimental stations should not be used as a matter of course.

4.4. *D. LINEOLATA:* YIELD AND PLANT DEVELOPMENT OF ARTIFICIALLY INFESTED MAIZE CULTIVARS. METHODS OF LOSS ASSESSMENT

4.4.1. *Introduction*

In tropical America losses caused by the neotropical corn borer *Diatraea lineolata* have not yet been assessed. Therefore references include other maize borers, viz. the european corn borer, *Ostrinia nubilalis* (Hbn.) and the southwestern corn borer, *Diatraea grandiosella* Dyar.

D. lineolata may cause several types of damage. In the second growing period infestations are usually high and 'dead heart' may occur as a result of the larva feeding on the meristematic tissue of the bud. This type of damage was mentioned by ARBUTHNOT et al. (1958) for *D. grandiosella*. It was observed that stalks tunnelled by *D. lineolata* late in the second growing period broke. Second generation borers of *O. nubilalis* were mainly responsible for stalk breakage and ear drop (CHIANG et al., 1954). CHIANG and HODSON (1950) concluded that stalk breakage usually occurs so late in the season that its effect on ear growth was negligible, this may also be the case in Nicaragua. The rainfall diminishes from November onwards, so the chance of ear putrefication on broken stalks is small. These types of damage may occur, but were not observed in this experiment.

The physiological damage by maize borers is difficult to quantify. It has been tried by investigation to estimate yield loss based on either the borer or its injury. In the United States PATCH et al. (1942) established a standard estimate of '3 per cent yield loss per borer per plant', which became widely accepted. This estimate was only considered valid for univoltine strains of the borer. Working with bivoltine strains, damage is overestimated because the second brood larvae cause less loss of yield (JARVIS et al., 1961; CHIANG et al., 1954). No additional effect of the interaction of first and second brood infestation was observed either for *O. nubilalis* (JARVIS et al., 1961) or for *D. grandiosella* (SCOTT and DAVIS, 1974).

PATCH et al. (1942) found that reduction of yield was proportional to the number of larvae of the first generation of *O. nubilalis* per plant, up to 22 borers per plant. JARVIS et al. (1961) also found a linear decrease of yield per unit of injury within the range of their experimental data. DAVIS et al. (1978) reported that the yield decreased linearly with the increasing number of egg masses of the first brood of *D. grandiosella*.

Environmental conditions seem to affect yield reduction per borer. PATCH et al. (1942) mentioned that at a higher yield, the yield was reduced less by the first generation *O. nubilalis*. He also indicated that at a given yield, loss was promoted by drought. Similar results were found by CHIANG (1964), who suggested that plants under physiological stress were more sensitive to injury by this borer.

Only CHIANG (1964) has investigated the sensitivity of feeding sites of the maize plant. When six fully extended leaves were present, he infested the maize stalk at the second, fourth and sixth internode artificially with egg masses of *O. nubilalis* in pre-drilled tunnels; the infestation near the base of the plant had the greatest adverse effect on plant growth.

The borer as well as different types of injury have been used as a criterion to estimate yield loss. PENNY and DICKE (1959) reported that yield loss by first generation borers of *O. nubilalis* were mainly responsible for stalk breakage and to leaf feeding by the borers, but factors other than leaf feeding resistance appeared to have some influence on damage caused. EVERETT et al. (1958) also demonstrated an inverse relationship between leaf lesions and yield, but the best way to predict the loss of yield was number of cavities or larvae per plant at the end of the first brood infestation. JARVIS et al. (1961) showed that cavities in split or dissected stalks gave a better estimate of plant damage than the number of larvae present. SCOTT and DAVIS (1974) in host resistance studies used leaf feeding ratings and tunnel length to measure the effectiveness of infestations by the first brood of *D. grandiosella*, while for the second brood only tunnel length was used. GUTHRIE et al. (1975) indicated that yield loss by infestation of second brood *O. nubilalis* was primarily due to collar and sheath feeding, causing premature senescence of the tissue. SCOTT et al. (1967) used the number of cavities as a direct measurement to compare the level of resistance for the second brood of *O. nubilalis*. These results show that the borer variable (e.g. larvae, exit holes, cavities, perforations) best suited for indicating yield loss depends on factors such as time of infestation, maize cultivar and environmental conditions.

Between the borer variables, high correlations may be expected. This was reported by GHIDIU et al. (1979) who found a highly significant correlation between entrance holes and stalk cavities by first and second generation *O. nubilalis* in single cross hybrids that were susceptible, intermediate and resistant to maize borer feeding. The regression of stalk cavities on entrance holes was linear. BARRY and ANTONIO (1979) found a high correlation between leaf feeding injury by first generation *D. grandiosella* and the average number of larvae, tunnels and the tunnel length per plant.

Loss of yield by borers may be caused either by reduced ear size (less kernels) or a reduction in kernel size. Infestation of *O. nubilalis* at the pollen shedding stage reduced ear size but most of the yield loss was caused by a reduction in kernel size (GUTHRIE et al., 1975). Both broods of *D. grandiosella* reduced kernel weight, but the major cause of yield loss was a reduction in number of kernels per plant (SCOTT and DAVIS, 1974).

Besides the ear, other plant parts may also be affected. DAVIS et al. (1978) obtained a 12% reduction in plant height when 30 or more first brood eggs of *D. grandiosella* were applied per plant. SCOTT and DAVIS (1974) reported reduced plant height (7%) by the feeding of the first brood larvae of this borer. CHIANG and HOLDAWAY (1959) observed a reduction in leaf size and in internode length because of infestation by first generation larvae of *O. nubilalis*. This happened before physical destruction or obstruction of vascular bundles in the stalk occurred and must have been caused by borer feeding on the leaf blades, perhaps associated with chemical changes in the plant, due to phytotoxic secretion produced by borers or associated micro-organisms.

The growth stage of the host may affect borer development. PATCH (1943) and LUCKMANN and DECKER (1952) found that larval survival of *O. nubilalis* increased rapidly from about 10 days before tasseling. TURNER and BEARD (1950) stated that survival increased with stage of plant growth before tasseling. CHIANG and HOLDAWAY (1960) reported a 60% mortality for first brood larvae of *O. nubilalis* during the first two hours and nearly 80% during the first 24 hours of its life on the plant.

CHIANG (1964) mentioned that larval development may be influenced by the feeding site of *O. nubilalis*. Survival and development rates of larvae were highest for borers established near the ear.

HENSLEY and ARBUTHNOT (1957) concluded that *D. grandiosella* infesting at the whorl stage, preferred to tunnel below the ear zone. Only very few tunnels were found between ear zone and tassel. PATCH (1943) observed that with the increasing stage of development of the plant, borer populations of *O. nubilalis* were found at lower stalk levels. KEVAN (1944) reported that although some larvae of *D. lineolata* tunnelled upwards, they as a rule tunnelled downwards. When tunneling upwards they normally followed the main stem, but they could also end up in the centre of the cob. However he gave no figures for this tunneling behaviour.

Before a decision can be made on the control of *D. lineolata* in tropical America it will be necessary to assess the loss of yield in both growing periods. However before loss of yield can be estimated from injury in the field, loss assessment methods have to be available. Several times an attempt was made to make a rough estimate of the effect of the borer attack on yield per plant by sampling a large number (150) of individual plants from a maize field at harvest. Although the results seemed to indicate yield loss, the large variation between the plants resulted in a not significant relation between injury and yield per plant.

All the loss assessments reviewed above, except that of CHIANG (1964), have been carried out by considering experimental plots, in which differences in borer attack between plots were introduced either by manual infestations of egg masses, young larvae or by different applications of insecticides. This methodology is appropriate when no other maize pests interfere. In Latin America however *Spodoptera frugiperda* infestations are omnipresent. In chapter 5.1. it is shown that applying insecticides against *S. frugiperda* may increase *D. lineolata* infestations. A selective insecticide, which affects *S. frugiperda*, but not *D. lineolata*, is probably not available. Therefore the use of insecticides in an assessment of loss by *D. lineolata* can be excluded. The assessment of loss by the artificial infestation of plants in plots may be a possibility, but it will be complicated firstly by *D. lineolata* infestations that occur naturally and secondly by the interaction of damage by *D. lineolata* and *S. frugiperda*.

To avoid these problems the best way would be to exclude other maize pests, which in this experiment was done by using nylon-screen field cages. A disadvantage of the cages is the artificial environment (shading and reduced wind velocity). In these cages plants were artificially infested with first larval instars of *D. lineolata* at two stages of plant growth. Yield and plant development variables were measured per individual plant. In this way firstly an assessment of loss could be made by considering whole plots (between-plots analysis) and secondly an assessment per plant within each treatment (within-plots analysis). Samples were taken from each internode to investigate the sensitivity of feeding sites.

4.4.2. *Material and methods*

4.4.2.1. Experiments (J)

The hybrid X-105-A was sown in 12 nylon screen cages (3.6 × 1.8 × 1.8 m) June 30, 1978 at the experimental station La Calera, Managua. At sowing NPK fertilizer (10-30-10) and urea were applied at a rate of 130 and 65 kg ha^{-1} respectively. Four weeks after plant emergence the urea treatment was repeated. The crop germinated July 5, 1978. Seventeen days after plant emergence the insecticide methomyl (Lannate 90% a.i. SP, .25 kg ha^{-1}) was applied to control the beginning of an infestation by *S. frugiperda*. Moths of *S. frugiperda* oviposited abundantly on the nylon screen of the cages, and the egg masses were removed with a pencil or treated with a concentrated solution of mefosfolan (Cytrolane 250E). Each cage consisted of 2 rows, .9 m apart and plant spacing was .15 m. The design was intended to be a randomized block design with 3 treatments and 4 replicates. Two treatments, namely an infestation at midwhorl and one at silking stage would be compared with a control. Since the plants grew so tall that the roof of the screen was pushed upwards the intended infestation at tasseling stage was suspended. Cages were removed from the plants just after tasseling. From this moment onwards oviposition by naturally occurring moths could happen on all plants. Thus there remained two treatments, namely those plants receiving both artificial and natural infestation (W + NI) and those plants receiving a natural infestation (NI). In treatment W + NI (4 cages) all whorls were infested with 15 larvae (L_1-L_2, 3 to 5 days after hatching), 5 each at 24, 26 and 28 days after plant emergence (the larvae were reared from eggs, oviposited by adults, obtained from field collected larvae). After tasseling the same plants were exposed to natural oviposition (NI). In treatment NI (8 cages) plants were only exposed to oviposition by moths that occurred naturally. In this treatment 1 cage and 2 cage rows were omitted in the statistical analysis as a number of plants were lost due to cutworm (probably *Agrotis* sp.). All plants were labelled. Plant height was measured 23, 30 and 37 days after plant emergence.

The open-pollinating, short variety Nic-Synt-2 was sown August 25, 1978, close to the X-105-A plots. Four days after sowing the nylon screen cages were placed over the plots. The method of sowing and the amount of fertilizer were the same as in the above experiment. The urea treatment was repeated 13 and 35 days after plant emergence. Since plants in the first experiment suffered from cutworm, granulated phoxim (Volaton 2.5%) was applied at sowing at a rate of 25 kg ha^{-1}. Germination was completed by August 30. Twenty one days after plant emergence methomyl (Lannate 90% a.i. SP, .25 kg ha^{-1}) was applied to control a light spider mite infestation (probably *Oligonychus pratensis*). The design was a randomized block design with 3 treatments and 4 replicates. Treatments W and S were infestations at the whorl and silking stage respectively. An untreated control was added. In treatment W (4 cages) all whorls were infested with 7 larvae (L_1-L_2, 3 to 5 days after hatching), 3, 2 and 2 larvae on 24, 26 and 28 days respectively. In treatments S (4 cages) all plants (leaves in the vicinity of the cob) were infested with a total of 7 larvae (L_1-L_2, 3 to 5 days after hatching), 4 and 3 larvae at 42 and 44 days respectively after plant emergence. The larvae were reared from eggs, deposited by adults, reared from field collected larvae. Maize stalks were checked weekly for the presence of exit holes, which were taped to prevent a second infestation. All plants were labelled. Plant height was measured 24 and 30 days after plant emergence.

After harvest the ears of all plants (from X-105-A and Nic-Synt-2) were labelled and weighed. Ear length and diameter were measured, and at the widest part of the ear (an arbitrarily chosen place) 5 grains were taken, and weighed. Per cage, grain moisture was determined from five samples of grains from all ears. Grain weight of the ear was adjusted to 15 per cent moisture. For each individual plant the smallest diameter of the lowest internode was measured and the number of internodes above and below the cob recorded. Borer presence was measured per internode by the following variables: number of perforations, exit holes, larvae (diapausing, active and dead), pupae and pupal skins. Below the cob tunnel length was measured. If the ear shank showed perforations it was scored as injured.

4.4.2.2. Statistical analysis

The effect of treatments on yield and plant development characteristics was investigated by two types of analyses. In the first, treatment effects were investigated for whole cages by a simple analysis of variance (between-plots analysis). To reduce possible plot (cage) effects the analysis was also done with a covariable representing plant height at the moment of infestation. The between-plots analysis however failed to show significant effects by the low number of degrees of freedom. In the second analysis, the effect of each separate treatment was investigated for individual plants (a within-plots analysis). This could be done as all measurements in a plot had been carried out per plant. The procedure of investigation was a correlation and regression analysis. The within-plots analysis gives information, independent of the between-plots analysis. Both results can be compared.

The statistical analyses were carried out by means of the computer program SPSS. The analyses are summarized as follows:

Between-plots analysis		Chapter		
Cultivar	Treatment	Material and methods	Results	Analysis of variance (tables)
Nic-Synt-2	W, S, Control	4.4.2.1.	4.4.3.2.	44A
X-105-A	NI,W+NI,Control	4.4.2.2.	4.4.3.2.	44B

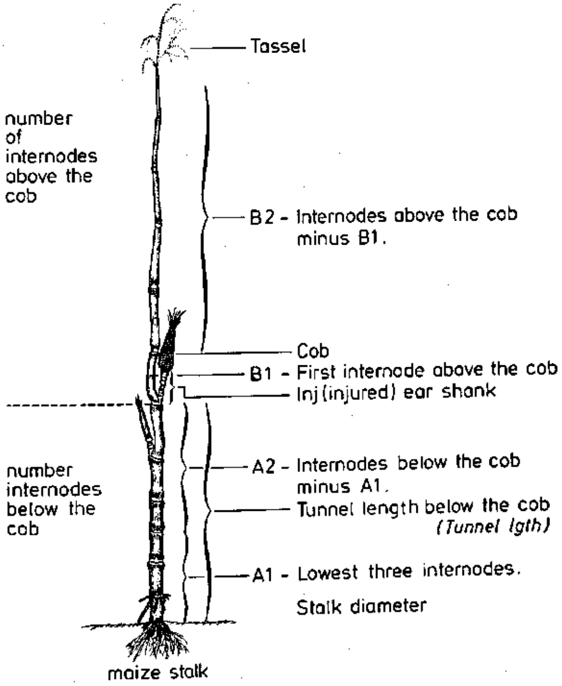
Within-plots analysis		Chapter		Analysis (tables)		
Cultivar	Treatment	Material and methods	Results	Correlation		Multiple regression
				per stem part	per plant	
Nic-Synt-2	W	4.4.2.2.1.	4.4.3.3.1.	45	46A	47
	S	and	4.4.3.3.2.	48	46B	49
X-105-A	NI	4.4.2.2.2.	4.4.3.3.3.			50
	W+NI		4.4.3.3.4.	51		52

4.4.2.2.1. Correlation

To be able to get an impression of how borer variables per stalk part, plant development variables and yield variables (see fig. 32) correlate within these groups of variables, and how these groups are interrelated, a correlation matrix was made. In calculating the correlation matrix the effect of cages and cage rows ('control' variables) has been eliminated from the relationship between all variables. The matrix therefore contains partial correlation coefficients. The matrix has been reordered with a COR program[1], to emphasize a statistical grouping of the variables. With the help of the rearranged

[1] Fortran program of M. Keuls, Dept. of Mathematics, Agricultural University, Wageningen. The procedure of the COR program is as follows: Only the lower triangle is considered of the square symmetrical matrix. As a first step the variables in this lower triangle are rearranged in the order of the sums of squares of correlation coefficients. The sign of a variable is changed (if necessary) to get mainly positive coefficients in the horizontal part of the correlation triangle. Next a grouping (and reordering) of variables is arranged starting from the first, as follows. A new variable showing a high sum of squares of correlations with predecessors in the last group, joins this group if the maximum correlation coefficient in the first half (+1) of this group exceeds a predetermined threshold (Thr); in the other case this variable opens a new group. Thr is lowered with a predefined quantity (Id), however only after a group of at least 5 variables. The correlation triangle is presented with a selected value of Thr and Id, so that the triangle shows clear blocks of high correlations in the diagonal.

Borer variables (independent or predictor variables).
For both infestations several grouping of borer variables were made corresponding to feeding sites. Their relation to the yield variables was studied by correlation analysis. Especially the lowest internodes and the two internodes below and above the cob were considered. Finally the following feeding sites, with corresponding borer variables were selected, these represented clearly the observed effects.



In each feeding site (A1, A2, B1, B2) the following variables representing borer activity were used:

injured internodes (1)	: A11, A21, B11, B21
perforations (2)	: A12, A22, B12, B22
exit holes (3)	: A13, A23, B13, B23
larvae (larvae + pupae + pupal skins) (4)	: A14, A24, B14, B24

With injured ear shank and tunnel length below the cob a total of 18 borer variables were used as potential predictors for the yield variables.

Plant development variables (control variables)

number of internodes below the cob	– intern BC
number of internodes above the cob	– intern AC
plant height at infestation	– plant hght
stalk diameter	– stalk diam

Yield variables (dependent or criterion variables)

grain yield	– grain yld
kernel weight	– kernel wght
ear length	– ear lgth
ear diameter	– ear diam

FIG. 32. Variables used in the multiple correlation and regression analyses (within-plots) of the treatments W and S (data of infestation at the whorl and at the silking stage respectively) of the maize variety Nic-Synt-2. (Exp. J)

correlation triangle an attempt was made to find the causal relationship, by means of logical reasoning and independent knowledge, between the independent (borer) variables, the dependent (yield) variables and the plant development (possibly control) variables. A path diagram presents the relationships.

Elimination of the plant development variables which are not influenced by the borer (plant height during infestation, number of internodes below and above the cob) produced a new correlation matrix of partial correlation coefficients. In a multiple regression analysis with this partial correlation matrix as input, the relation between stalk diameter and borer variables was determined. If the relation was non-significant, stalk diameter was also classed as a control variable. In the ultimate partial correlation triangle the variables have been arranged in the same order as in the triangle uncontrolled for plant development variables which had been produced with the COR program. The triangles are presented together for comparison.

Equivalent results can be obtained in a multiple regression analysis on the original data in which cage rows and other control variables are entered into the equation first before the borer variables. From this run residuals were analyzed from two scattergrams. The first one plotted standardized residuals against predicted values and the second one plotted standardized residuals against the sequence of plants in cage rows. Outliers appeared to be those plants which had a very small (less than 30 gram) grain yield. These plants therefore have been eliminated from all analyses. An analysis of autocorrelation was performed using the last scattergram and using the Durbin-Watson statistic to determine the effect of neighbouring plants. However statistical tables presented for Durbin and Watson tests are limited to $n \leqslant 100$. Because of the partial correlation procedure it can be expected that such autocorrelation was lessened or eliminated. Autocorrelation seems absent, but the number of degrees of freedom used in our analyses may be overestimated. In this computer run the percentage of variation explained in the yield variables ($R^2 \times 100$) by first cage rows, then plant development variables (covariables) and finally borer variables were determined.

4.4.2.2.2. Regression

The last correlation matrix, combined with the means and standard deviations of the variables, is used as an input for the multiple regression analysis to predict yield from the borer variables. The borer variables were entered into the equation by a *hierarchical* procedure. At each step a variable entered the regression equation that explained most of the remaining variation, not accounted for by the variables entered up till now. The final set of predictor (borer) variables was chosen with F-values higher than one (1) for each. No more than two per cent explained variation was lost in this selection procedure. The selection of these borer variables does not necessarily mean that some variables could not have been replaced by others without loss of explained variation. However in general the selected and presented group of borer variables are good predictors. The F-values for each borer variable selected are presented which show how significant this variable explains the part of the variation, still unaccounted for by all other selected borer variables.

The multiple regression analysis gives two types of regression coefficients, the nonstandardized b_{yx} and the standardized β_{yx} or beta weight. The nonstandardized regression coefficient is the slope of the regression line and indicates the expected change in Y with a change of one unit in only one of the X variables. When both Y and X are standardized they are rescaled to unit variance ($S_x = S_y = 1$; S_x, S_y = standard deviations of X and Y respectively). The relationship between beta weights and unstandardized regression coefficients is $\beta_{yx} = b_{yx}S_x/S_y$.

The squared multiple correlation coefficient (R^2) multiplied by 100 gives the total amount of variation explained by the borer variables. R^2 may be computed as the vector product ($\beta \times r$) of β and the partial correlation coefficients r (COOLEY and LOHNES, 1971). For the different groups of borer variables, representing stalk parts, their 'symmetrical' contribution to R^2 could be calculated in this way. Because of the collinearity between the borer variables, presentation of the regression coefficients does not make much sense: they depend on the chosen set of variables in the equation. For this reason regression factor structure coefficients (RFSC) r/R are presented, where r is the partial correlation coefficient and R is the multiple correlation coeffient (COOLEY and LOHNES, 1971).

In order to get an indication of the loss in yield by borer injury, the experimental means ($\bar{a}_j$) of the selected borer variables are multiplied with their unstandardized regression coefficients(b_j). By using this procedure for a number of borer variables (j) in each group – representing a stalk part – the contribution of a group to loss in the criterion variable is suggested by $\sum_{1}^{j} \bar{a}_j b_j$.

The constant represents the value of the criterion variable, which would have been obtained without infestation. The selection of the borer variables into the regression equation means that the unstandardized regression coefficients have some independance, however only to a certain extent, as between the selected borer variables there is still much correlation. The loss in criterion variables per feeding site and per plant, as indicated by this procedure, can therefore only be considered as a rough estimate.

4.4.3. *Results and discussion*

4.4.3.1. Physiological damage and anatomy of the plant

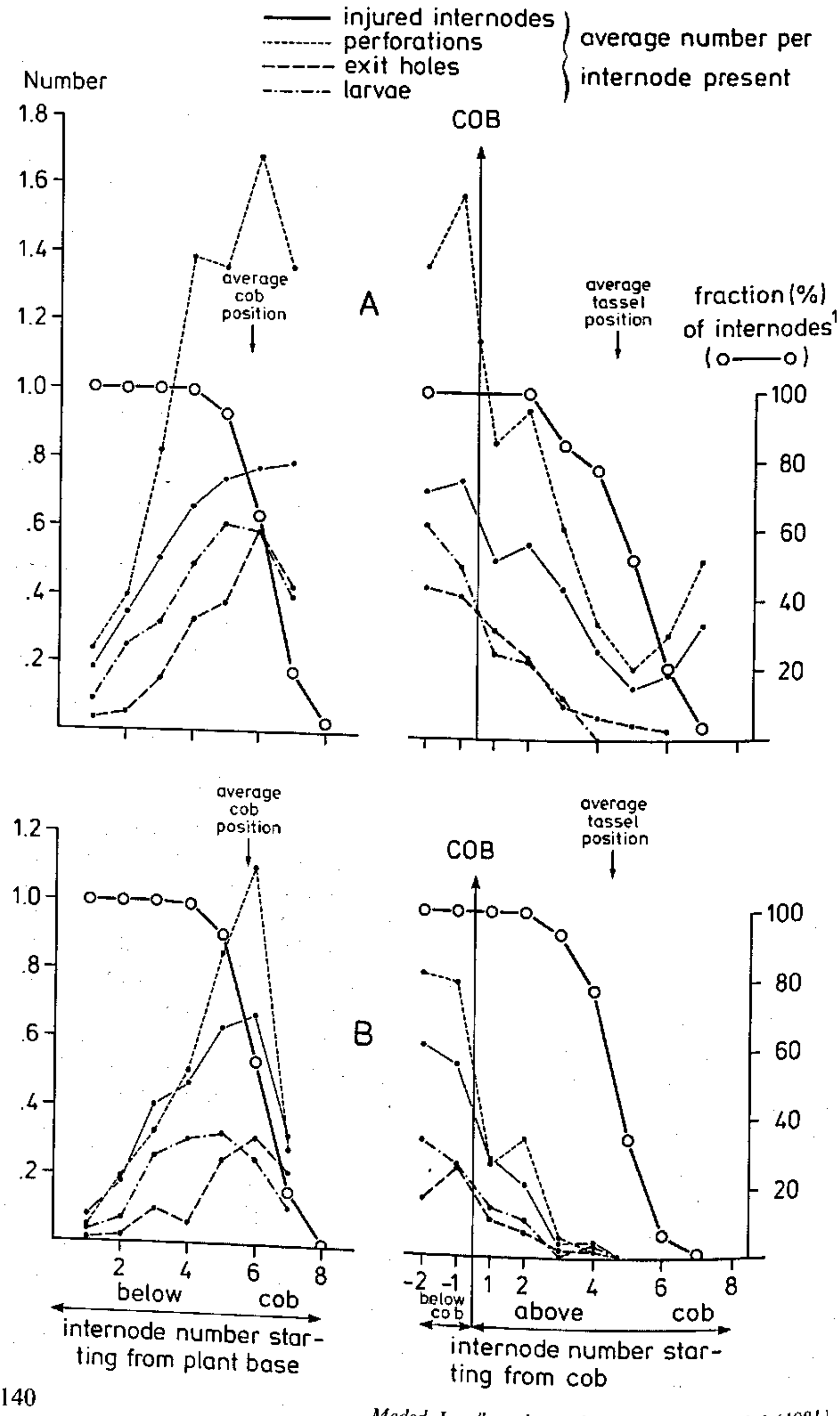
The injury by borers in the stalk consists – among others – of the destruction of vascular bundles through which the translocation of water, minerals and assimilates takes place. The upward stream in a plant is of water and minerals and the downward stream of assimilates. Assimilates are largely used by the cob to support grain development, and the roots where they provide energy for the uptake of minerals.

Anatomical studie[1] on transsections of the maize cultivar Black Mexican Sweet showed a scattered distribution of vascular bundles throughout the section with smaller bundles densely arranged near the periphery and larger bundles more widely spaced in the centre. The vascular bundles are collateral, each enclosed in a sheath of parenchyma. The peripheral bundles are surrounded with more sclerenchymatic tissue than those in the centre. ESAU (1965) also discusses *Zea* in this way.

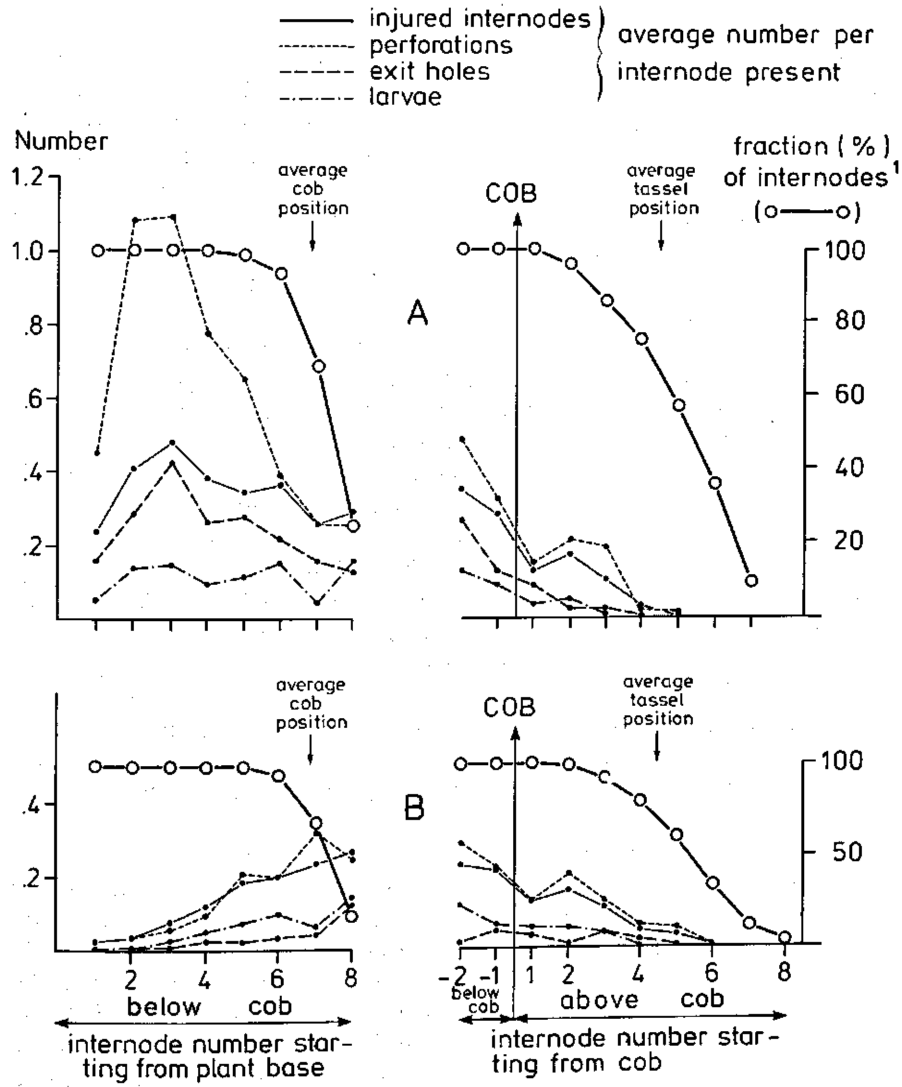
KUMAZAWA (1961) mentioned two systems of vascular bundles for *Zea mays*, one inside the other but independent and not directly connected with each other. The outer system is represented by the outermost peripheral bundles and the inner system by the compound bundles situated at the sub-peripheral region of the stem. KUMAZAWA (1961) observed that large leaf trace strands enter the medullary region of the stem and the smaller ones do not become medullary; both however derive from the same leaf and constitute two independent vascular systems (the inner and the outer respectively). As the borer normally does not tunnel at the periphery of the stem, it may be expected that at least the outer most peripheral vascular bundles remain intact and that the translocation of water, minerals and assimilates will only partly be obstructed. The injury of these vascular systems of the maize plant by stem borers is a subject that should be studied further.

Figure 33A and 33B show the vertical distribution of borer variables over the maize stalk (variety Nic-Synt-2) as a result of an infestation at whorl (W) and silking stage (S) respectively. The distributions are rather symmetrical and uni-

[1] Sections provided by A. A. M. VAN LAMMEREN, Laboratory of Plant Cytology and Morphology, Agricultural University at Wageningen.



injured internodes
perforations
exit holes
larvae
average number per internode present
Number
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
COB
average cob position
A
average tassel position
fraction (%) of internodes[1] (o——o)
100
80
60
40
20
1.2
1.0
.8
.6
.4
.2
average cob position
B
COB
average tassel position
100
80
60
40
20
2
4
6
8
below
cob
internode number starting from plant base
-2
-1
below cob
1
2
4
6
8
above
cob
internode number starting from cob



[1]Distribution of internodes over the internode ranks (rank = position number of the internode counted from the base or from the cob).

FIG. 34. Borer variables per internode of maize plants at harvest (hybrid X-105-A) infested by *D. lineolata*. (Exp. J)

A. Artificial infestation with larvae of plants at midwhorl stage, plus B (treatment W + NI) (137 plants).

B. Natural oviposition on plants after tasseling stage (treatment NI) (227 plants).

---

[1]Distribution of internodes over the internode ranks (rank = position number of the internode counted from the base or from the cob).

FIG. 33. Borer variables per internode of maize plants at harvest (variety Nic-Synt-2) artificially infested with *D. lineolata* larvae. (Exp. J)

A. Infested at whorl stage (treatment W) (168 plants).

B. Infested at silking stage (treatment S) (169 plants).

modal with a peak just below the cob. The graphs on the right represent the borer injury and presence per internode of the two internodes just below the cob and of the internodes above the cob. An irregularity exists in the distribution around the cob: borer injury decreases sharply from the internode below the cob to the internode above the cob. In both treatments W and S the average number of injured ear shanks was about .25 (see table 47 and 49, respectively). When this figure is compared to the difference in injured internodes between the internode below and that above the cob in figure 33A and 33B, the tunneling of the larvae towards the ear shank seems responsible for the observed irregularity (the same phenomena can be observed for the natural infestation after tasseling (treatment NI) of the maize hybrid X-105-A in figure 34B). Correlation analysis (as will be dealt with later) shows that weak relations exist between borer variables below (A) and above the cob (B) (see table 45 and 48).

Several assumptions may be put forward, two seem to be the most plausible. Firstly the ear shank attracts larvae and prevents tunneling from the internode below the cob to the internode above the cob and vice versa. Secondly the nodal plate, above which the ear is attached to the stalk by the ear shank, is strengthened by sclerenchymatic tissue that supports the ear, so that the plate becomes a mechanical barrier for the larvae to penetrate, this assumption was studied using the maize variety Black Mexican Sweet.

A horizontal network of vascular bundles at the nodal plates was observed coming from the leaves. However the nodal plate above which the ear shank is attached was anatomically not different from the other nodal plates of the stalk. KUMAZAWA (1961), when discussing the nodal plates, also did not mention such a difference.

It seems therefore more plausible that the ear shank attracted borer larvae. CHIPPENDALE and REDDY (1974) mentioned a feeding response of *D. grandiosella* to glucose, fructose, sucrose and dextrins. As assimilates are transported by the vascular bundles below and above the cob to the ear via the ear shank, orientation of *D. lineolata* larvae towards the ear shank because of the quality of the food is possible. CHIANG (1964) observed a higher survival of *O. nubilalis* larvae near the cob. In our experiment a higher survival near the cob may also be the cause of the observed symmetrical and unimodal distribution of the borer over the stalk in figure 33A and 34B (in fig. 33B larvae had been placed in the vicinity of the cob). It may also be the reason that the same vertical distribution pattern was observed for eggs deposited by the moth in the field experiment A I (see fig. 8).

4.4.3.2. Between-plots analysis

The analysis of whole plots is presented in table 44. Infestation treatments reduced the value of the yield and plant development variables. Differences however were not significant (a possible variation between cages, not caused by the borer was reduced by introducing a covariable, representing plant height at the moment of infestation; infestation effects however remained non-significant). The variation coefficients indicate that the experiment with the

TABLE 44. The effect of *D. lineolata* infestations on yield and plant development of two maize cultivars (two randomized block designs, between-plots analysis). Analysis of variance: F-values, significancies and means. (Exp. J)

A. Variety Nic-Synt-2; artificial infestations: Treatment W at whorl stage, Treatment S at silking stage. (± 40 plants per plot.)

Source of variation	df	Grain yield per plant	Kernel weight[1]	Ear size length	Ear size diameter	Stalk diameter
				F-values		
Blocks	3	2.54	.66	6.63*	2.66	8.70*
Treatments	2	1.35	3.66+	.47	1.42	3.01
Error: V.C.	6	7.57	4.07	3.45	3.60	2.68
Total	11					
				means		
		gram		cm		mm
Grand mean		73.0	1.40	14.4	3.99	12.2
		percentage deviation from grand mean				
Control		5	4	1	1	3
Treatment W		–3	–1	–1	–2	–1
S		–2	–3	0	1	–2

B. Hybrid X-105-A; Treatment NI: natural infestation after tasseling; treatment W + NI: artificial infestation at whorl stage and NI; (± 40 plants per plot).

Source of variation	df	Grain yield per plant	Kernel weight[1]	Ear size length	Ear size diameter	Stalk diameter	Plant height[2]
				F-values			
Blocks	3	.31	1.64	.31	1.02	.09	.27
Treatments	1	.17	.13	.10	.19	.14	.08
Error: V.C.	6	35.2	11.6	13.2	7.23	12.0	14.8
Total	10						
				means			
		gram		cm		mm	cm
Grand mean		95.4	1.16	13.2	3.91	16.1	115
		percentage deviation from grand mean					
Treatment NI		3	–1	1	–1	1	1
W + NI		–6	2	–2	1	–2	–2

[1] Per five kernels.
[2] X-105-A: measured 37 days after plant emergence.

Continued on the following page

Corresponding injury by *D. lineolata* per plant (average per cage).

Borer variables	Nic-Synt-2				X-105-A			
	W		S		NI		W + NI	
	Total	Below cob (%)	Total	Below cob (%)	Total	Below cob (%)	Total	Below cob (%)
Number of:								
injured internodes	4.9	62	2.7	80	1.4	65	2.7	85
perforations	8.2	66	3.2	79	1.5	61	4.9	89
borers	2.8	77	1.5	80	.57	70	.81	90

cultivar Nic-Synt-2 was more accurate than the one with X-105-A. The reduction in yield and plant development variables was too small to obtain significant effects with the number of replicates used.

Loss of yield in the variety Nic-Synt-2 was 8 and 7% by infestation at the whorl and silking stage respectively, while for the hybrid X-105-A a loss of yield of 9% is observed for the infestation at the midwhorl stage (table 44). Ear size in the variety Nic-Synt-2 seemed to be affected mostly by the infestation at the whorl stage, while the greatest reduction in kernel weight was by the infestation at the silking stage. The midwhorl infestation of hybrid X-105-A had hardly any effects on ear size and kernel weight. Stalk diameter and plant height were reduced by 3%.

4.4.3.3. Within-plots analysis[1]

The analysis for individual plants within treatments has been done using the statistical techniques, described in chapter 4.4.2.2.1. and 4.4.2.2.2.. The analysis was rather complicated, as differences in the development of individual plants showed effects on larval distribution over the stalk and on larval development (as suggested in diagrams 6 and 7). For an explication of the variables used in the analyses, see figure 32.

4.4.3.3.1. Variety Nic-Synt-2: infestation at whorl stage (Treatment W)

Plant development, the effect on the borer

The first/second instar larvae were introduced into the whorls about 10 days before tasseling and the larvae developed, when the plant differentiated morphologically from the whorl stage into a full grown plant.

In the correlation triangle rearranged by the COR program the borer variables made up clusters according to their position below or above the cob (table 45A). Within these clusters (feeding sites A1, A2, B1 and B2) the borer variables show

[1] For readers having some difficulties with the terminology of the correlation and regression analysis there is a summary of the results at the end of this chapter (4.4.4.).

TABLE 45. Correlation triangles of partial correlation coefficients (× 100) and plant development variables of maize plants (variety Nic-Synt-2 after whorl infestation by *D. lineolata*; see for specification of variables fig. 32). (Exp. J)

A. After controlling for cage rows.

tunnel lgth	(1)	100																									
A21	(2)	67																									
A22	(3)	61	68																								
A24	(4)	51	67	67																							
A23	(5)	44	60	60	54																						
intern BC	(6)	30	60	60	34	41																					
A11	(7)	50	21	21	17	17	4																				
A12	(8)	38	19	19	21	18	3	66																			
A14	(9)	40	12	12	8	15	5	71	51																		
A13	(10)	33	15	15	15	14	7	34	29	29																	
B21	(11)	24	10	10	11	1	-1	8	1	6	10																
B22	(12)	21	11	11	7	4	-5	6	3	12	8	80															
B24	(13)	0	-10	-10	-6	-1	-22	1	3	5	-7	44	41														
B23	(14)	16	5	5	12	0	-4	18	6	16	16	49	31	21													
intern AC	(15)	3	-7	-7	-8	-8	-20	9	10	11	-1	39	29	28	33												
grain yld	(16)	-1	6	6	0	3	10	-20	-14	-16	-6	30	19	-5	14	16											
ear diam	(17)	-4	1	1	-4	-4	4	-20	-16	-11	-3	14	12	-7	0	4	68										
ear lgth	(18)	1	5	5	-1	7	12	-8	-11	-7	1	13	8	0	0	16	67	36									
plant hght	(19)	20	28	28	24	23	24	-7	-8	-6	3	23	18	4	21	9	43	35	30								
stalk diam	(20)	7	5	5	5	13	10	0	15	7	3	21	18	13	10	20	29	4	31	36							
kernel wght	(21)	1	-5	-5	1	-6	2	5	-1	6	0	15	10	0	0	9	29	28	23	12	8						
B11	(22)	31	15	15	15	3	-7	8	19	-2	7	24	23	18	18	6	4	-5	-6	19	16	-11					
B14	(23)	26	14	14	4	12	-7	8	9	8	2	18	29	21	20	11	3	1	-3	15	4	-3	54				
B12	(24)	21	6	6	10	3	-8	1	9	3	9	26	12	13	22	8	11	1	5	11	10	-7	54	41			
B13	(25)	14	9	9	8	11	-6	-3	4	-10	12	0	-10	9	0	-9	-1	-5	-6	0	-11	-23	46	28	35		
inj ear shank	(26)	28	19	19	7	9	6	7	-6	4	14	7	4	0	2	-15	1	2	0	3	2	-1	14	13	14	19	100

A2 = internodes just below cob

A1 = lowest three internodes

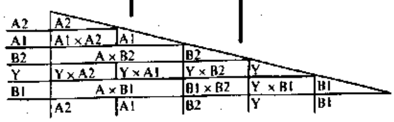
B2 = top internodes

Y = yield and plant development variables

B1 = first internode above cob

B. After controlling for cage rows, plant height and number of internodes below and above the cob

1	100																						
2	63																						
3	55	61																					
4	44	61	42																				
5	36	48	42	45																			
7	53	25	19	19	19																		
8	40	23	21	24	20	65																	
9	42	12	8	9	17	70	49																
10	33	12	8	13	12	34	30	29															
11	22	10	1	11	0	7	0	3	11														
12	20	14	7	8	5	5	2	10	9	77													
13	5	1	-6	0	8	0	2	4	-6	39	36												
14	14	4	-6	13	-1	18	5	15	17	39	21	12											
16	-13	-8	-9	-11	-7	-21	-13	-17	-8	19	9	-12	0										
17	-12	-7	-1	-13	-13	-18	-14	-10	-5	6	6	-12	-10	63									
18	-8	-8	-6	-11	0	-8	-12	-8	0	0	-1	-3	-12	62	29								
20	-1	-7	-7	-4	5	0	17	8	2	8	8	9	-2	13	-9	19							
21	-2	-11	-1	-1	9	5	-1	6	0	10	5	-1	-6	26	25	19	3						
22	34	22	18	16	4	11	22	0	8	21	19	15	14	-5	-14	-13	9	-14					
23	27	21	22	4	15	9	10	9	2	12	25	17	15	-5	-4	-9	-2	-6	52				
24	23	11	16	12	5	2	10	4	10	23	8	9	19	6	-3	1	6	-9	52	39			
25	18	17	12	10	15	-1	6	8	13	3	-8	11	3	0	-6	-4	-10	-22	47	29	36		
26	29	20	10	5	6	9	-4	7	13	14	9	4	7	1	2	1	4	0	15	15	15	18	100
	1	2	3	4	5	7	8	9	10	11	12	13	14	16	17	18	20	21	22	23	24	25	26
			A2				A1				B2					Y					B1		



high correlations. The number of internodes below the cob combined with borer variables below the cob (A1 and A2), but it correlates most with the internode group closest to the cob (A2). The number of internodes above the cob correlates best with the borer variables in the internode group below tassel (B2) and occurs with this group in one cluster. Yield variables and the plant development variables plant height and stalk diameter are together in one cluster.

From this description of correlations, may be deduced the following two processes in the larval distribution over the stalk. Firstly with a relative high position of the cob on the stalk, the larvae had more chance of entering the part of the stalk below the cob than the part above the cob and when the cob is relatively low, vice versa. Secondly, with a high number of internodes below the cob the larvae had more chance of tunneling the internode group just below the cob (A2) than the group of the lowest internodes (A1). This second effect can also be seen with regard to plant height[1] (the group of borer variables at the base of the plant (A1) weakly correlates negatively with plant height, while the group of borer variables just below the cob (A2) correlates positively with plant height; table 45A). Summarized, the number of internodes below, the number above the cob and plant height influence larval distribution over the stalk.

Plant height (at the time of larval infestation), besides affecting larval distribution, also affected larval development, because plant height (at whorl infestation) correlates positively with the number of borers per plant (table 46A). This is explained if larval survival is higher on the taller plants. The day following infestation many dead larvae were found in the plant whorl. This agrees with the observations on *O. nubilalis* by CHIANG and HOLDAWAY (1960), who reported an 80% mortality of first brood larvae during the first 24 hours of their life on the plant. The survival of *O. nubilalis* on vigorous plants was higher than on small plants of the same age (TAYLOR et al., 1952). Migration of larvae towards the tallest plants in a cage row is unlikely because migration of larvae between plants was never observed.

The injury variables (injured internodes and perforations) at internode numbers 5 to 7 above the cob, which was higher than the experimental average (4.5), remained at a high level and even showed a tendency to increase (fig. 33A). These high internode numbers are for tall vigorous plants. Apparently the borer reacts to plant vigour by increased injury at this feeding site. This phenomenon will be discussed later.

Correlation and regression procedure

Before investigating the effect of the borer variables on the yield variables it was necessary to remove from their relationship the effects of the number of internodes below and above the cob, and of plant height (control variables). This may be illustrated by plant height. Plant height is positively related to the yield variables and to borer variables. Thus tall plants on the one hand give a higher yield but on the other hand enable more larvae to survive. Without controlling for plant height the effect of larval injury on yield would be masked and more positive than with controlling. Table 46A shows this for the borer variables per single plant.

In the correlation triangles before and after controlling for plant development variables (table 45A en 45B respectively) the coefficients of both triangles were

[1] Plant height determined at the first infestation date strongly correlated ($r = .96$) with plant height measured one week later, the average of the two heights was used in all analyses for obtaining maximum accuracy.

TABLE 46. (Partial) correlation coefficients ($\times$ 100) between borer variables and plant development, and yield variables of maize plants (variety Nic-Synt-2 after infestations with *D. lineolata*) before (BC) and after (AC) controlling for various plant development variables[1] (from within-plots variation). (Exp. J)

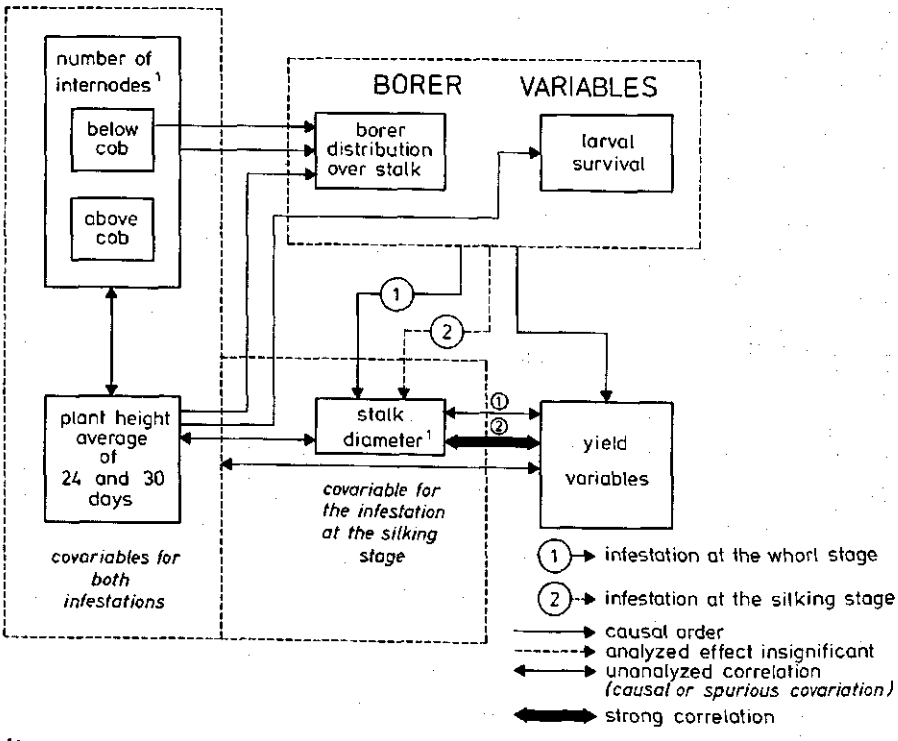
Borer variables (number per plant)	Plant development variables					Yield variables							
	Number of internodes		Plant height	Stalk diameter		Grain yield		Kernel weight		Ear length		Ear diameter	
	below cob	above cob		BC	AC	BC	AC	BC	AC	BC	AC	BC	AC
A. Infestation at whorl stage	*Q*					*P*							
Injured internodes	28^{***}	23^{**}	28^{***}	18^{*}	4	13	−3	6	0	5	−10	0	−11
Perforations	18^{**}	22^{**}	27^{***}	20^{**}	7	10	−5	4	−2	5	−8	5	−4
Exit holes	26^{***}	4	26^{***}	10	0	6	−7	12	-17^{*}	4	−7	−6	-17^{*}
Larvae	14	14	19^{**}	14	4	−8	-22^{**}	3	0	−5	-16^{*}	−11	-19^{**}
B. Infestation at silking stage	*P*			*Q*		*R*							
Injured internodes	13	4	−4	−6	−7	−11	−15	−4	−5	−7	−8	−13	−15
Perforations	3	12	−5	2	4	−8	-16^{*}	−6	−9	−9	−15	−15	-21^{**}
Exit holes	8	6	−7	−8	−5	0	2	0	1	−2	−1	2	4
Larvae	6	1	−1	4	5	−3	−10	1	−2	−3	−9	−10	−15

[1] Controlling for:	Cage rows	Internodes below cob	Internodes above cob	Plant height	Stalk diameter
P and B C	X				
Q (A C)	X	X	X	X	
R (A C)	X	X	X	X	X

* = P $\leqslant$ .05 ** = P $\leqslant$ .01 *** = P $\leqslant$ .001

about the same, except for two blocks (Y × A2 and Y × B2), which by the additional control became more negative or less positive. This because these two groups concerned those stalk parts of which length and/or number of internodes changed with differences in plant vigour and size. This is also true for tunnel length, because it related more to the borer variables of group A2 than to those of group A1. Correlations between some borer variables (B21 and B22) and the yield variables remained positive after the additional control. This will be dealt with later.

As the stalk diameter was determined at the moment of harvesting, borer injury could have affected stalk diameter. Therefore from the correlation matrix obtained after controlling (for cage rows, plant height, number of internodes below and above the cob) a multiple regression analysis was carried out to evaluate the effect of borer injury on stalk diameter. This effect appeared to be significant (table 47). Therefore stalk diameter is a criterion variable and cannot be used as a control variable.



[1]Determined at harvest.

DIAGRAM 6. Path analysis: causal structure for borer, plant development and yield variables after an infestation by *D. lineolata* of the maize cultivar Nic-Synt-2 at the whorl stage and one at the silking stage. (Exp. J)

The above discussion is summarized in a path diagram (diagram 6). The correlation matrix (table 45B) was used as an input for a multiple regression analysis of yield on borer variables (table 47).

Table 47 shows that almost half of the experimental variation in the grain yield, one fifth for kernel weight and about one third for ear size and stalk diameter could be explained (columns $100R^2$). The most important plant development predictor appeared to be 'plant height' at the time of infestation. If stalk diameter had been used as a predictor, its effect would have been insignificant for all variables except for ear length, probably because the diameter itself was affected by the borer (table 47). The regression analysis was also carried out using stalk diameter as a control variable. Almost similar results (not presented) were obtained, which means that yield was not affected by a smaller stalk diameter.

Borer variables

Borer variables explained about 10% of the variation for the criterion variables, except ear length (4%) (table 47). Tunnel length was never once selected into the regression equation. This variable was measured below the cob over all internodes and a subdivision into stalk parts was therefore impossible. Tunnel length shows high correlations with borer variables at feeding sites A1 and A2 (table 45B). However as both groups of borer variables had different effects, a combination of the groups is likely to have less effect.

For all yield variables ear shank injury was not selected. This was in contrast with the infestation at silking stage (table 49). The percentage of injured ear shanks was at the same level(26%) for both infestations (W and S). However the level of injury of the ear shank was probably greater when the plants are infested after tasseling, because the ear shank is then already fully developed.

The borer variables of feeding site B2 (the internode group below tassel) have regression factor structure coefficients (RFSC) with a different sign: the variables expressing injury (injured internodes and perforations) show positive coefficients and the variables expressing larval presence (exit holes and larvae) show negative coefficients (table 47). In block Y × B2 of the correlation triangles before and after controlling for plant development variables (table 45A and 45B) the coefficients became negative or more negative by controlling, only those for the injury variables remained positive; controlling apparently was not sufficient. The injury at internode number 5 to 7 above the cob (among B2), which belonged to vigorous plants, was relatively high (fig. 33A). These factors indicate that the injury to the feeding site B2 represented plant vigour, for which the relationship between injury and yield was not sufficiently controlled. Whenever injury variables of this feeding site entered into the regression equation the effect was an increase instead of a loss in the criterion variable (table 47). This shows how difficult the assessment becomes if the larvae react to plant vigour as in this experiment. However it should be remembered that the larvae is completely surrounded by plant tissue and that its development depends on plant conditions.

Generally grain yield and ear diameter had common significant predictor

TABLE 47. Multiple regression analysis of the effect of borer variables in different parts of the stalk on yield variables (grain yield, kernel weight and ear size) and stalk diameter of maize plants of the cultivar Nic-Synt-2 after whorl infestation by *D. lineolata*: percentage of variation explained and F-values of the covariables cage rows, plant height, number of internodes below and above the cob; Regression Factor Structure Coefficients (RFSC) and F-values (higher than one) of borer variables selected by a hierarchical multiple regression procedure; F-values, percentage of variation explained and percentage loss in criterion variables per feeding site. (Exp. J)

Multiple regression analysis		x̄ ± SD	Grain yield		Kernel weight[1]		Ear length		Ear diameter		Stalk diameter	
			$100R^2$	F	$100R^2$	F	$100R^2$	F	$100R^2$	F	$100R^2$	F
Percentage of variation explained ($R^2 \times 100$)												
Total			43.1		19.7		30.2		32.9		32.6	
cage row (Rep)			15.8		7.36		16.4		14.0		6.74	
plant development variables (Dev), after Rep			17.5		2.20		10.1		10.9		15.3	
F-values: plant height[2](cm)		84. ± 18.		31.8**		2.05		12.2**		21.9**		19.1**
no internodes below cob		5.8 ± .90		.15		.02		1.19		.32		.55
no internodes above cob		4.5 ± 1.2		3.13+		1.13		4.15*		.00		5.95*
stalk diameter (mm)		12. ± 2.0		(2.98+)		(.15)		(6.49*)		(1.43)		
selected borer variables, after Rep and Dev[3]			9.85		10.1		3.72		7.97		10.5	
Borer variables												
Below cob			RFSC	F	RFSC	F	RFSC	F	RFSC	F	RFSC	F
lowest three internodes												
injured internodes	(A11)	1.0 ± .91	–.55	7.77**	.17	1.24			–.58	3.54+	.02	4.97*
perforations	(A12)	1.4 ± 1.9					–.55	1.30			.48	7.13**
exit holes	(A13)	.24 ± .54										
larvae	(A14)	.65 ± .80									.23	1.20
rest												
injured internodes	(A21)	2.0 ± 1.1			–.35	2.50					–.21	3.63+
perforations	(A22)	3.9 ± 3.3										
exit holes	(A23)	1.1 ± 1.2			–.04	1.08			–.40	1.32	.15	2.62
larvae	(A24)	1.5 ± 1.1	–.29	1.85								
injured ear shank		.26 ± .44									.13	2.27
tunnel length (cm)		39. ± 26.										
Above cob												
first internode												
injured internodes	(B11)	.51 ± .50			–.43	.98	–.60	3.11+	–.44	2.06	.27	5.06*
perforations	(B12)	.84 ± 1.4					.07	2.12				
exit holes	(B13)	.29 ± .58			.68	4.91*					–.29	5.66*
larvae	(B14)	.26 ± .46			–.19	1.03					–.06	1.15
rest												
injured internodes	(B21)	1.3 ± 1.3	.50	14.7**	.31	4.91*			.12	6.29*		
perforations	(B22)	2.0 ± 2.3			.18	1.31						
exit holes	(B23)	.39 ± .74			–.19	3.66+	–.54	2.12	–.31	1.76		
larvae	(B24)	.39 ± .67	–.31	8.91**					–.38	4.50*		
							F-values					
Selected borer variables (all)			6.54**		2.05*		2.01+		2.95*		2.53*	
Below cob: A after B:	– A1 last		5.74**	7.77**	1.10	1.24	1.30	1.30	2.87+	3.54+	2.49*	3.03*
A alone	– A2 last		4.06*	1.85	1.33	1.26	2.41	–	3.55*	1.32	2.38*	1.98
Above cob: B after A:	– B1 last		8.61**	–	2.05+	2.98*	1.86	1.77	2.58*	2.06	2.67*	2.67*
B alone	– B2 last		6.90**	8.61**	2.52*	2.26+	2.23+	2.12	2.92*	2.78*	2.46+	–
Error: V.C.			31.2		16.4		15.0		9.72		15.3	
degrees of freedom			151		146		151		149		146	
			gram		gram		mm		mm		mm	
Grand mean			75.7		1.44		148.		40.6		12.2	
					variation explained by borers ($\% = r \times \beta \times 100$)							
Borer variables												
selected[4]	– all		14.8	17.6	11.2	12.7	5.06	7.32	10.6	12.5	13.5	15.4
below cob(A)	– A1		5.73	4.55	2.29	.51	1.16	1.16	4.04	2.83	8.66	5.89
	– A2			1.18		1.78		–		1.21		2.77
above cob(B)	– B1		9.03	–	8.92	5.53	3.90	1.77	6.58	1.64	4.83	4.83
	– B2			9.03		3.40		2.12		4.94		–
							percentage loss					
Damage by borer (– = increase)												
total			6.1		1.8		3.2		3.3		.5	
below cob(A)	– A1		11.8	7.5	.8	–1.7	1.0	1.0	2.9	1.7	1.7	.0
	– A2			4.3		2.5		–		1.2		1.7
above cob(B)	– B1		–5.7	–	1.0	2.5	2.2	1.3	.4	1.1	–1.2	–1.2
	– B2			–5.7		–1.5		.9		–.7		–

[1] Per five kernels.
[2] Average height for sampling dates 24 and 30 days after plant emergence.
[3,4] They indicate the same part of total variation, however the last is expressed as the fraction of the part of the variation ($100(1-(R^2_{Rep} + R^2_{Dev}))$), that is left unexplained by the plant development variables and replicates.

variables. In the correlation triangle (table 45A) these two criterion variables were located in the same cluster and had similar coefficients. The effect of the borer on both criterion variables apparently was similar.

Feeding site

Grain yield. The effect of injury of the lowest three internodes (A 1) was large and significant (table 47). The injury of this stalk part was only a fifth of the total stalk injury and less than one half of the injury that occurred in the other stalk part below the cob (A2). If the feeding site B2 (of which the injury variables represented plant vigour) was not considered the yield loss would have been 9.6% (compared to 8% for the between-plots analysis, table 44A) for which the borer variables of the lowest three internodes accounted for 6.7%[1].

Kernel weight. Injury to the internode above the cob (B1) had a significant and the largest effect on the kernel weight. Probably the translocation of assimilates from the upper leaves to the ear for kernel development was obstructed most by the injury of the internode closest to the ear. SOZA et al. (1975) found that the leaves above the cob contribute mainly to grain filling, while leaves below the cob had practically no influence (they also quoted a number of authors, who reported similar results). If group B2 was not considered percentage loss of kernel weight would have been 3.3 (compared to 5% for the between-plots analysis, table 44A), borer variables of feeding site B1 accounted for 2.3%[1]. The injury at this internode was only one ninth of the total stalk injury.

Ear length. From the borer variables selected, only one (in the internode above the cob) showed some significance. The variables above the cob participated by 4 of the total of 5% variation explained. Ear length showed a decrease of 3.2% (compared to 2% for the between-plots analysis, table 44A) of which the above cob predictors accounted for 2.2%.

Ear diameter. About the same remarks as those made for grain yield are valid for ear diameter. The predictors of the lowest three internodes appeared most important if feeding site B2 was not considered. Without B2 ear diameter decreased by 3.9% (compared to 4% for the between-plots analysis, table 44A) for which the borer variables of the lowest three internodes accounted for 1.7%[1].

Stalk diameter. Largest and significant effects were observed for the lowest three internodes (A1) and the internode just above the cob (B1). The predictors of the internodes below the cob (A2) explained twice as much of the variation as those of the internodes above the cob (B1).

4.4.3.3.2. Variety Nic-Synt-2: infestation at silking stage (Treatment S)

The distribution of borer variables over the stalk showed almost the same pattern as that for the whorl infestation (comparing fig. 33B with 33A). Al-

[1] These figures were obtained by another computer run (omitting feeding site B2) and cannot be deducted from table 47.

though the same amount of larvae was used for both infestations, borer establishment appeared to be lower in the later infestation. Injury above the cob was limited mainly to the first two internodes above the cob.

Correlation and regression

In the correlation triangle, rearranged by the COR program (table 48A) the variables were located in three clusters, namely 1. the yield variables and the plant development variables plant height and stalk diameter (Y), 2. the borer variables below the cob (A), and 3. the borer variables above the cob (B). The clusters of borer variables separated into two groups, representing the corresponding stalk parts. The number of internodes below the cob correlated positively with the borer variables in the stalk part just below the cob (A2) and negatively with all other borer variables. Plant height showed a similar effect. Apparently a taller plant with a larger number of internodes below the cob is responsible for the arrival of larvae in the stalk part just below the cob (A2), when artificially infested. Therefore there was controlled in the analysis for plant height and for the number of internodes below and above the cob.

With this correlation matrix (after controlling for these plant development variables) an investigation was made by multiple regression analysis, whether stalk diameter was influenced by the borer, but no predictors with a F-value higher than one were selected. Stalk diameter however still correlated highly with yield variables. Therefore it was decided also to control for stalk diameter. The above mentioned reflections are summarized in a path diagram (diagram 6).

The correlation triangle controlled for all plant development variables (including stalk diameter) is presented in table 48B. Considerable changes took place in the yield – borer correlations in block Y × B and Y × A2. In block Y × B coefficients became less negative[1] and coefficients in block Y × A2 negative or less positive. The latter correlation matrix was used for a multiple regression analysis.

Of the total amount of variation in grain yield nearly 60% was explained, for ear size 46% and for kernel weight 32% (table 49). Of the plant development variables stalk diameter was most important and of all the criterion variables an even better predictor than plant height. The difference in clearness of stalk diameter as a predictor between the infestations at whorl and silking stage (comparing table 47 with table 49) shows that stalk diameter was only affected by borer injury at whorl stage. The number of internodes below the cob also showed a significant effect in all cases, but the number of internodes above the cob did so only for grain yield and ear length.

Borer variables

The borer variables in this experiment explained 17% of the variation in ear diameter, 12% for grain yield and only 7 and 5% for kernel weight and ear length respectively (table 49).

[1] Variables B21 etc. have changed sign as expressed by the minus sign.

TABLE 48. Correlation triangles of partial correlation coefficients (× 100) between borer, yield and plant development variables of maize plants (variety Nic-Synt-2 after infestation at silking stage by *D. lineolata*; see for specification of variables fig. 32). (Exp. J)

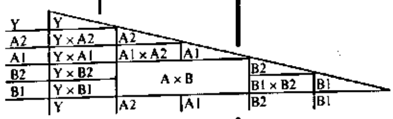
A. After controlling for cage rows

grain yld	(1)	100																									
ear diam	(2)	78																									
ear lgth	(3)	71	44																								
stalk diam	(4)	61	48	59																							
kernel wght	(5)	54	45	39	43																						
plant hght	(6)	39	29	38	59	25																					
A21	(7)	22	15	16	13	20	18																				
A22	(8)	10	3	7	15	10	13	66																			
A24	(9)	13	6	10	13	13	5	62	41																		
tunnel lgth	(10)	-4	-9	0	1	-1	9	53	48	28																	
A23	(11)	21	19	13	11	13	10	51	37	27	36																
intern BC	(12)	26	17	19	15	23	10	52	31	33	10	27															
A11	(13)	-23	-25	-7	-3	-12	-4	11	22	2	48	12	-5														
A14	(14)	-19	-25	-3	3	-3	2	18	23	3	37	18	-2	71													
A12	(15)	-12	-16	-5	-6	-9	-4	0	13	0	30	8	-12	62	25												
-inj ear shank	(16)	13	8	6	-2	12	-4	16	19	7	0	12	16	5	-3	6											
-B21	(17)	18	16	17	15	16	19	14	12	16	-6	9	35	-9	1	-9	-7										
-B22	(18)	11	15	10	7	19	16	16	16	16	3	10	32	3	6	5	-8	74									
-B23	(19)	13	8	13	11	14	8	6	10	7	-8	0	17	-13	1	-16	-13	61	39								
-B24	(20)	3	6	9	5	5	6	5	9	2	-11	-13	14	-16	-1	-23	-9	42	25	41							
-B14	(21)	5	0	11	11	8	7	4	4	12	-10	-2	19	0	0	3	-8	37	35	23	18						
-B11	(22)	25	15	27	24	19	23	1	3	0	-18	0	19	-2	-2	4	4	37	30	29	14	62					
-B12	(23)	28	21	28	20	11	25	3	5	-11	-18	11	17	-11	0	-13	6	29	14	22	9	15	54				
-B13	(24)	15	7	20	24	10	22	9	12	1	-2	12	15	8	15	8	-7	13	13	0	-1	25	51	35			
-intern AC	(25)	-14	-10	-15	-7	-3	-3	5	1	1	3	2	26	4	1	-1	16	19	25	5	0	8	11	7	7		
-A13	(26)	15	18	1	5	1	9	0	-9	-5	-10	2	4	-38	-29	-16	2	-7	-8	-2	-5	-6	-1	8	2	7	100

Y = yield and plant development variables
A2 = Internodes just below cob
A1 = lowest three internodes
B2 = top internodes
B1 = first internode above cob

B. After controlling for cage rows, plant height, stalk diameter and number of internodes below and above the cob.

	Y				A2					A1				B2				B1				
	1	2	3	5	7	8	9	10	11	13	14	15	16	17	18	19	20	21	22	23	24	26
1	100																					
2	70																					
3	52	18																				
5	36	29	16																			
7	6	4	3	8																		
8	-7	-10	-8	-2	61																	
9	-1	-4	-1	1	57	34																
10	-10	-13	-4	-4	56	48	27															
11	12	13	4	4	44	30	19	34														
13	-25	-26	-4	-11	18	26	4	50	15													
14	-27	-30	-6	-5	22	25	4	38	19	71												
15	-8	-13	0	-5	7	19	4	33	12	62	25											
16	18	11	11	13	11	17	2	-1	9	5	-3	8										
17	6	7	8	5	-6	0	6	-13	-1	-8	1	-4	-15									
18	4	12	7	14	-1	7	8	-1	1	5	6	11	-16	69								
19	5	1	6	7	-3	4	1	-10	-5	-12	1	-13	-16	60	36							
20	-4	2	5	1	-3	4	-2	-13	-19	-15	0	-22	-11	41	22	40						
21	-5	-9	4	0	-7	-2	5	-12	-8	1	0	6	-12	32	31	20	15					
22	12	3	16	7	-13	-5	-9	-23	-7	-1	-3	8	2	29	23	25	11	60				
23	19	12	20	0	-10	-3	-20	-23	5	-10	0	-10	4	21	6	19	6	11	49			
24	-2	-6	7	-1	0	5	-5	-5	7	10	15	12	-9	4	6	-6	-4	21	46	29		
26	16	18	-1	-1	-4	-11	-7	-12	0	-38	-30	-15	1	-12	-13	-4	-6	-8	-5	5	0	100



Tunnel length was never selected by the regression procedure into the regression equation as was the case with the whorl infestation. Tunnel length showed high correlations with borer variables of stalk parts below the cob (A1 and A2) (table 48B), however the separate effects of borer variables in these groups were apparently stronger than in combination.

Ear shank injury was now selected as a predictor for all yield variables (table 49). This in contrast to whorl infestation (see table 47). The effect of the injured

TABLE 49. *Multiple regression analysis of the effect of borer variables in different parts of the stalk on yield variables (grain yield, kernel weight and ear size) of maize plants of the cultivar Nic-Synt-2 after infestation at silking stage by D. lineolata*: percentage of variation explained and F-values of the covariables cage rows, plant height, number of internodes below and above the cob and stalk diameter; Regression Factor Structure Coefficients (RFSC) and F-values (higher than one) of borer variables selected by a hierarchical multiple regression procedure; F-values, percentage of variation explained and percentage loss in criterion variables per feeding site. (Exp. J)

Multiple regression analysis		$\bar{x} \pm SD$	Grain yield		Kernel weight[1]		Ear length		Ear diameter	
			100R²	F	100R²	F	100R²	F	100R²	F
Percentage of variation explained ($R^2 \times 100$)										
Total			57.5		32.1		46.6		45.7	
cage rows (Rep)			4.43		3.90		5.0		4.42	
plant development variables (Dev), after Rep			41.0		20.8		36.6		24.5	
F-values: plant height[2] (cm)		86. ± 17.		.42		.00		.29		.00
no internodes below cob		5.6 ± .89		12.0**		6.19*		4.77*		3.52+
no internodes above cob		4.2 ± .96		6.17*		.54		5.41*		2.03
stalk diameter (mm)		12. ± 1.8		50.0**		20.2**		45.9**		27.3**
selected borer variables, after Rep and Dev[3]			12.1		7.40		5.07		16.8	
Borer variables										
Below cob			RFSC	F	RFSC	F	RFSC	F	RFSC	F
lowest three internodes										
injured internodes	(A11)	.67 ± .79	–.55	1.04	–.38	2.82+				
perforations	(A12)	.54 ± .89								
exit holes	(A13)	.14 ± .41							–.38	1.13
larvae	(A14)	.36 ± .55	–.59	4.16*					–.63	16.2**
rest										
injured internodes	(A21)	1.5 ± .98	.14	3.78+	.28	3.32+	.12	3.10+	.08	4.15*
perforations	(A22)	1.9 ± 2.0	–.17	3.73+	–.07	2.13	–.28	4.56*	–.21	4.26*
exit holes	(A23)	.50 ± .80	.28	2.61					.28	3.26+
larvae	(A24)	.79 ± .78							–.10	1.67
injured ear shank		.25 ± .44	–.40	5.43*	–.41	5.00*	–.38	2.84+	–.23	2.37
tunnel length (cm)		38. ± 28.								
Above cob										
first internode										
injured internodes	(B11)	.27 ± .44	–.26	1.37						
perforations	(B12)	.24 ± .71	–.41	1.80			–.69	6.55*	–.26	1.67
exit holes	(B13)	.11 ± .35								
larvae	(B14)	.14 ± .37	.12	1.94					.19	2.47
rest										
injured internodes	(B21)	.29 ± .57			–.18	1.87				
perforations	(B22)	.43 ± 1.0	–.10	2.29	–.46	6.31*	–.24	1.52	–.27	9.33**
exit holes	(B23)	.12 ± .44			–.25	1.18				
larvae	(B24)	.15 ± .66								
			F-values							
Selected borer variables (all)			4.14**		2.32*		2.87*		4.51**	
Below cob: A after B:	– A1 last		5.13**	8.03**	2.68*	2.82+	2.34+	–	4.98**	10.84**
A alone	– A2 last		5.08**	3.89**	1.98+	2.74*	1.86	2.34+	4.49**	2.72*
Above cob: B after A:	– B1 last		2,43*	2.40+	2.79*	–	4.26*	6.55*	3.92**	1.84
B alone	– B2 last		2.29+	2.29	1.61	2.79*	3.56*	1.52	2.87*	9.33**
Error: V.C.			32.7		21.6		14.6		10.2	
: degrees of freedom			146		149		151		146	
			gram		gram		mm		mm	
Grand mean			74.0		1.39		147.		41.2	
Borer variables			variation explained by borers (% = $r \times \beta \times 100$)							
Selected[4] – all			22.1	23.2	9.83	11.6	8.67	10.5	23.6	24.7
Below cob (A)	– A1		16.9	8.99	5.87	1.63	3.92	–	18.2	11.4
	– A2			8.37		4.24		3.92		6.77
Above cob (B)	– B1		5.23	4.65	3.95	–	4.75	4.06	5.41	2.33
	– B2			.58		3.95		.69		3.08
Damage by borer (– = increase)			percentage loss							
Total			8.6		3.3		2.0		2.9	
Below cob (A)	– A1		4.8	7.8	2.1	2.5	.4	–	1.9	2.6
	– A2			–3.0		–.4		.4		–.7
Above cob (B)	– B1		3.8	2.2	1.2	–	1.6	.6	1.0	–.1
	– B2			1.6		1.2		1.0		1.1

[1] Per five kernels.
[2] Average height for sampling dates 24 and 30 days after plant emergence.
[3,4] They indicate the same part of total variation, however the last is expressed as the fraction of the part of the variation ($100(1-(R^2_{Rep}+R^2_{Dev}))$), that is left unexplained by the plant development variables and replicates.

ear shank appears to be independent, as is shown by its significance as a predictor of grain yield and kernel weight (table 49). The corresponding regression factor structure coefficients (RFSC) were rather high and negative. Because transport of assimilates to the ear have to pass the ear shank, injury at this feeding site will have serious consequences.

Injured internodes and perforations of the feeding site just below the cob (A2) were selected with significant or weakly significant effects in all cases. This was to be expected because half the total injury of the stalk was at this feeding site.

Feeding site

Grain yield. Borer variables below the cob explained 17% of the variation and borer variables above cob 5% (table 49). Both effects were significant. The borer variables of the lowest three internodes (A1) explained a similar amount of variation as those of the stalk part just below the cob (A2), although the injury to the feeding site A1 was 2 to 3 times less than that of A2. This again indicates the sensitivity of the plant to injury at the lowest internodes. Loss of yield was 8.6% (compared to 7% for the between-plots analysis, table 44A), mainly due to the infestation at the lowest three internodes.

Kernel weight. The effect of the borer variables was greatest for the part of the stalk just below the cob (A2) and the tassel (B2) (table 49). Both effects were significant, in the case of feeding site B2 in spite of the fact that the injury is only a very small fraction of the total injury.

Ear length. The greatest effect was observed for the borer variables in the stalk parts around the cob (A2 and B1), for those of B1 a significant and for A2 a weakly significant effect.

Ear diameter. The effects of the different groups of borer variables were almost similar to those for grain weight. Significant were the effects of the infestation of feeding sites A1, A2 and B2.

Reduction in grain yield was partly caused by a lighter kernel, but also by a smaller number of kernels, which is expressed by the smaller ear (length and diameter).

4.4.3.3.3. Hybrid X-105-A: natural infestation after tasseling (Treatment NI)

The cages were removed from plants which had been artificially infested at the midwhorl stage 55 days after plant emergence (just after tasseling) and from plants, which had not yet been subjected to a borer infestation. Figure 34B shows that the natural infestation, which occurred after tasseling was a very light one.

The injury above the cob to the whorl infested plants was completely due to the natural infestation after tasseling. (compare figs. 34A and 34B). The effect of this natural infestation (NI) on yield variables was studied for plants which had only this infestation. In a field experiment oviposition was closely related to the leaf area of the maize plant (Exp. AI, chapter 3.1.). Therefore the correlation matrix was controlled for all plant development variables, which could express plant vigour i.e. plant height (averaged over 3 sampling dates), number of internodes below and above the cob and stalk diameter. The obtained partial correlation

TABLE 50. Multiple regression analysis of the effect of borer variables in different parts of the stalk on yield variables (grain yield, kernel weight and ear size) of maize plants of the hybrid X-105-A after a natural infestation by *D. lineolata* after tasseling; percentage of variation explained and F-values of the covariables cage rows, plant height (average over three sampling dates), number of internodes below and above the cob, stalk diameter; Regression Factor Structure Coefficients (RFSC) and F-values (higher than one) of borer variables selected by a hierarchical multiple regression procedure; F-values, percentage of variation explained and percentage loss in criterion variables per feeding site. (Exp. J)

Multiple regression analysis	$\bar{x} \pm SD$	Grain yield		Kernel weight[1]		Ear length		Ear diameter	
		$100R^2$	F	$100R^2$	F	$100R^2$	F	$100R^2$	F
Percentage of variation explained ($R^2 \times 100$)									
Total		54.7		28.5		43.7		40.6	
cage rows (Rep)		21.9		19.7		19.2		19.8	
plant development variables (Dev), after Rep		28.9		7.08		24.5		17.6	
F-values: plant height[2] (cm)	80. ± 15.		7.98^{**}		.00		4.45^{*}		1.33
no internodes below cob	6.8 ± .80		.97		.02		.32		.22
no internodes above cob	4.8 ± 1.6		1.78		2.30		.31		5.31^{*}
stalk diameter (mm)	16.6 ± 2.5		50.9^{**}		11.0^{**}		42.8^{**}		25.9^{**}
selected borer variables, after Rep and Dev[3]		3.81		1.71		.00		3.20	
Borer variables		RFSC	F	RFSC	F	RFSC	F	RFSC	F
Below cob (A)									
injured internodes	.82 ± 1.1	–.16	1.35						
perforations	.87 ± 1.5	.12	5.57^{*}				no	.41	6.76^{*}
exit holes	.15 ± .40								
larvae	.35 ± .73			.64	3.44^{+}		variables		
tunnel length (cm)	8.5 ± 17.	–.61	8.86^{**}	–.10	1.05			–.46	7.56^{**}
Above cob (B)							selected		
injured internodes	.42 ± .82								
perforations	.51 ± 1.1	–.20	1.03	–.55	1.62				
exit holes	.06 ± .28								
larvae	.16 ± .44	.40	4.51^{*}					.40	2.30
					F-values				
All selected borer variables		3.44^{**}		1.65				3.72^{*}	
Below cob: A after B – A alone		4.27^{**}	4.09^{**}	1.72	1.66			4.70^{*}	4.40^{*}
Above cob: B after A – B alone		2.39^{+}	2.11	1.62	1.51			2.30	1.70
Error: V.C.		41.1		20.5				13.2	
: degrees of freedom		205		207				207	
		gram		gram		mm		mm	
Grand mean		92.2		1.17		142		41.4	
				variation explained by borer ($\% = r \times \beta \times 100$)					
Borer variables: selected[4] – all		7.75	8.11	2.34	3.08	.00	1.19	5.11	6.24
below cob (A) – above cob (B)		5.71	2.04	1.59	.75	–	–	4.19	.92
					percentage loss				
Damage by borer (– = increase): total		1.2		.2				–.7	
below cob (A)			2.2		–.6				–.2
above cob (B)			–1.0		.8				–.5

[1] Per five kernels.
[2] Average height for sampling dates 23, 30 and 37 days after plant emergence.
[3,4] They indicate the same part of total variation, however the last is expressed as the fraction of the part of the variation ($100(1-(R^2_{Rep}+R^2_{Dev}))$), that is left unexplained by the plant development variables and replicates.

matrix was used for a multiple regression analysis. The borer variables however explained not significantly the variation in kernel weight and ear length, but significantly about 3 to 4% of the variation in grain yield and ear diameter (table 50). These two yield variables again reacted very similarly to a borer infestation. The below cob borer variables showed the highest significant effects. Tunnel length was chiefly responsible for this. The below cob infestation caused about a 2% loss of yield.

TABLE 51. Correlation triangles of partial correlation coefficients (× 100) between borer, yield and plant development variables of maize plants (hybrid X-105-A after whorl infestation by *D. lineolata*; see for specification of variables fig. 32). (Exp. J)

A. After controlling for cage rows

A.1	(1)	100																		
A.2	(2)	80																		
A.3	(3)	79	75																	A = internodes below cob
tunnel lgth	(4)	66	59	62																
A.4	(5)	45	40	23	35															
–grain yld	(6)	16	15	8	20	11														
–ear lgth	(7)	15	18	6	18	13	85													
–ear diam	(8)	11	10	6	16	12	71	55												Y = yield variables
–kernel wght	(9)	0	–5	–9	–2	–5	52	44	41											
–B.1	(10)	–5	–4	–11	–5	–6	21	18	18	11										
–B.2	(11)	0	–1	–1	5	1	15	10	16	13	77									B = internodes above cob
–B.3	(12)	–7	–10	–17	–4	–11	5	2	24	3	51	45								
–B.4	(13)	5	2	–2	–11	–2	4	2	2	0	55	33	22							
–plant hght T_2	(14)	18	11	23	5	8	28	18	21	10	5	5	–1	5						
–plant hght T_1	(15)	–11	–16	–11	–4	4	7	5	8	8	9	8	3	5	68					D = plant
–stalk diam	(16)	–12	–13	–7	–6	0	34	27	21	19	15	9	0	4	54	43				development
–intern BC	(17)	4	5	10	2	5	19	23	2	14	–8	–8	–4	–3	39	27	31			variables
–intern AC	(18)	0	–5	–2	–0	–2	5	1	–4	6	6	4	0	10	23	14	40	14	100	

B. After controlling for cage rows, plant height before infestation (T_1), stalk diameter, number of internodes below and above the cob.

1	100													
2	79													
3	79	74												
4	66	59	62											
5	46	41	24	35										
6	21	19	9	24	11									
7	18	20	5	20	13	83								
8	16	14	9	19	12	70	54							
9	1	–3	–10	–1	–6	49	40	40						
10	–1	0	–8	–3	–6	20	18	15	9					
11	3	2	1	6	1	15	11	15	13	77				
12	–6	–9	–16	–3	–11	6	3	24	3	52	45			
13	6	4	–1	–11	–1	5	4	2	0	55	33	22		
14	42	35	46	14	7	20	8	18	–1	–3	0	–4	2	100
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
			A				Y				B			D

A	A			
Y	Y × A	Y		
B	A × B	Y × B	B	
D	D × A	Y × D	D × B	D
	A	Y	B	D

4.4.3.3.4. Hybrid X-105-A: midwhorl infestation (Treatment W + NI)

The injury above the cob was caused by the natural infestation (compare fig. 34A and 34B). As shown in the previous analysis the infestation of this part of the stalk did not cause any significant loss of yield and need not be considered in the evaluation of the midwhorl infestation. The injury by the infestation at midwhorl was restricted to the lowest five internodes below the cob (fig. 34A).

Correlation and regression

In the correlation triangle, rearranged by the COR program (table 51A) the variables were ordered in four clusters, namely yield variables (Y), plant development variables (D) and the borer variables below (A) and those above the cob (B).

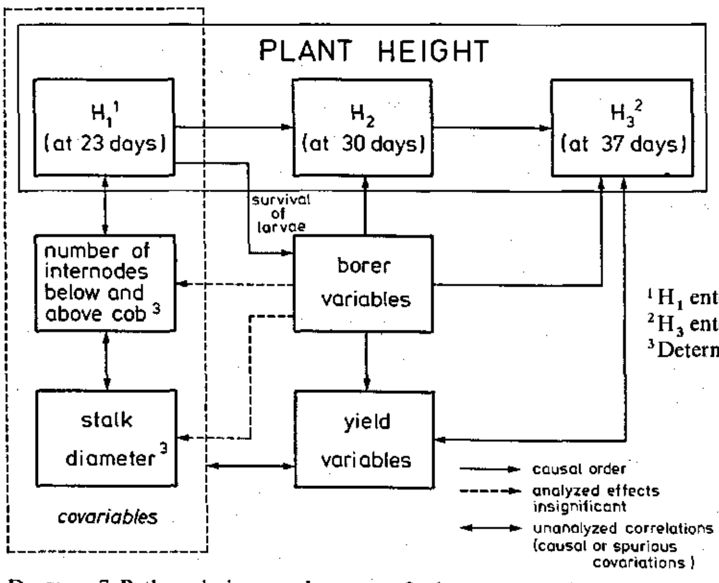
Plant height T_1, measured on the first infestation day correlated positively to borer variables below the cob (A) (table 51A). As discussed earlier the assumption is that larval survival increased with plant height. Plant height T_2 however, measured two weeks after T_1, showed negative coefficients with borer variables below the cob. The explanation can only be that plant height was reduced by the infestation.

Because plant height T_2 is affected by the borer, it has to be analyzed as a criterion variable and cannot be used as a control variable. In a multiple regression analysis, controlling only for plant height T_1 (after control for cage rows) an investigation was carried out to see if stalk diameter and/or number of internodes below the cob were possibly influenced by the borer variables. Because no significant effects were found, the final path diagram could be drawn (diagram 7). A correlation matrix was computed, controlling cage rows, plant height T_1, number of internodes both below and above the cob, and stalk diameter.

The correlation coefficients of the borer variables below the cob with the yield variables (block Y × A) and the plant height (block D × A) became more negative (compare table 51A and 51B). The coefficients of the borer variables above the cob (B) with others remained almost the same. The last partial correlation matrix that was obtained was now used for a multiple regression analysis.

Fourty-six and 33% of the total amount of variation was explained in grain yield and kernel weight, 38 and 25% in ear length and -diameter respectively and 82% in plant height T_2 (table 52). For yield variables, stalk diameter was the most effective predictor, but for plant height T_2 the most effective was plant height T_1, measured two weeks earlier.

Tunnel length was selected as a predictor for all criterion variables when a subdivision into stalk parts below the cob was made (lowest three internodes and the rest). Because tunnel length was measured per internode and could not be assigned to the stalk parts below the cob, two computer runs were made. The first



[1] H_1 enters the analysis as T_1.
[2] H_3 enters the analysis as T_2.
[3] Determined at harvest.

DIAGRAM 7. Path analysis: causal structure for borer, plant development and yield variables after a midwhorl infestation by *D. lineolata* of the maize hybrid X-105-A. (Exp. J)

TABLE 52. Multiple regression analysis of the effect of borer variables in different parts of the stalk on yield variables (grain yield, kernel weight, ear size and plant height T_2 two weeks after infestation) of maize plants of the hybrid X-105-A after midwhorl infestation by *D. lineolata*: percentage of variation explained and F-values of the covariables cage rows, plant height T_1 (at infestation), number of internodes below and above the cob, and stalk diameter; Regression Factor Structure Coefficient (RFSC) and F-values (higher than one) of borer variables selected by a hierarchical multiple regression procedure; F-values, percentage of variation explained and percentage loss in criterion variables per feeding site. (Exp. J)

Multiple regression analysis	$\bar{x} \pm$ SD	Grain yield		Kernel weight[1]		Ear length		Ear diameter		Plant height T_2[3]	
		100R²	F	100R²	F	100R²	F	100R²	F	100R²	F
Percentage of variation explained ($R^2 \times 100$)											
Total		45.6		33.1		38.5		24.7		81.7	
cage rows (Rep)		29.7		26.1		21.8		20.0		41.0	
plant development variables (Dev), after Rep		10.6		3.28		9.77		1.95		33.8	
F-values: plant height T_1[2] (cm)	45. ± 8.1		1.53		.02		1.65		.02		64.2**
no internodes below cob	6.9 ± .89		1.89		1.05		4.65*		.26		7.49**
no internode above cob	4.6 ± 1.7		1.54		.03		1.92		2.77^{+}		.24
stalk diameter (mm)	16. ± .25		16.2**		2.59		9.57**		8.18**		11.9**
Selected borer variables, after Rep and Dev[4]		5.34		3.72		6.93		2.84		6.99	
Borer variables		RFSC	F	RFSC	F	RFSC	F	RFSC	F	RFSC	F
Below cob											
injured internodes	2.4 ± 1.8	−.72	3.20^{+}	−.08	5.23*	−.59	1.01			−.80	4.42*
perforations	4.5 ± 4.9	−.32	3.18^{+}	.44	5.84*	−.17	6.25*			−.88	11.1**
exit holes	1.7 ± 1.9					−.65	2.63				
larvae	.74 ± 1.1			.28	2.08						
tunnel length (cm)	19. ± 20.	−.82	3.69^{+}			−.66	2.48	−1.00	4.63*	−.27	8.94**
All selected borer variables			3.95**		2.24^{+}		3.38*		4.63*		15.4**
Error: V.C.			40.6		21.8		20.3		11.2		17.4
: degrees of freedom			121		121		120		123		121
			gram		gram		mm		mm		cm
Grand mean			94.5		1.21		142.		42.6		114.
		variation explained by borer (% = $r \times \beta \times 100$)									
Borer variables: selected[5] *and all*		8.93	9.63	5.26	5.30	10.1	10.2	3.63	4.81	27.6	27.9
		percentage loss									
Damage by borer			12.8		1.5		5.6		2.1		8.9

Limited analyses of the sensitivity of feeding sites below cob to injury without tunnel length

Borer variables	$\bar{x} \pm$ SD	RFSC	F	RFSC	F	RFSC	F	RFSC	F	RFSC	F
lowest three internodes (A1)											
injured internodes	1.2 ± 1.1	−.56	1.88	.25	1.39	−.42	2.94^{+}	−.59	2.14	−.87	4.27*
perforations	2.6 ± 3.3			.59	5.36*	−.06	3.54^{+}	−.17	1.65	−.90	5.35*
exit holes	.88 ± 1.0			.18	1.21						
larvae	.33 ± .61										
rest (A2)											
injured internodes	1.3 ± 1.2	−.69	2.39	−.31	4.31*					−.69	2.66
perforations	1.9 ± 2.4	−.27	2.99^{+}	.19	1.03	−.81	6.83**	−.82	3.86^{+}	−.34	1.78
exit holes	.85 ± 1.3	−.74	1.48								
larvae	.42 ± .72										
		F-values									
All selected borer variables		2.46*		1.82		3.63*		2.36^{+}		10.6**	
lowest three internodes: A1 after A2 – A1 alone		1.88	3.02^{+}	2.27^{+}	1.56	1.87	1.93	1.18	1.57	10.6**	19.5**
rest : A2 after A1 – A2 alone		2.25^{+}	2.64^{+}	2.17	1.11	6.83**	7.05**	3.86^{+}	4.71*	1.50	9.04**
		variation explained by borer (% = $r \times \beta \times 100$)									
Borer variables: selected – all		7.59	8.84	7.11	7.72	8.25	9.37	5.53	6.06	26.0	27.8
A1 – A2		2.08	5.51	4.73	2.38	2.47	5.78	1.85	3.67	22.0	4.13
		percentage loss									
Damage by borer (− = increase): total below cob		11.1		.8		4.3		2.1		8.4	
lowest three internodes (A1)			5.4		−3.2		.9		.6		7.4
rest (A2)			5.7		4.0		3.4		1.5		1.0

[1] Per five kernels.
[2] Plant height 23 days after plant emergence.
[3] Plant height 37 days after plant emergence.
[4, 5] They indicate the same part of total variation, however the last is expressed as the fraction of the part of the variation ($100(1-(R^2_{Rep} + R^2_{Dev}))$), that is left unexplained by the plant development variables and replicates.

with all aggregated borer variables below the cob including the tunnel length. The fact that tunnel length entered into the equation may indicate that a detailed subdivision into stalk parts is not very effective (as the regression analysis shows, table 52); moreover it was observed that intercorrelation between the borer variables of these stalk parts was high. The subdivision (second computer run without tunnel length) however was useful in the evaluation of the importance of feeding sites for ear length and plant height T_2, as will be discussed later.

Borer variables

The borer variables, selected by the regression procedure explained, in this experiment, 5 and 4% of the variation in grain yield and kernel weight, 7 and 3% for ear length and diameter respectively and 7% for plant height T_2 (table 52).

In the analysis including tunnel length, this was selected as a predictor for all criterion variables, except kernel weight (table 52). In general the injury variables (injured internodes, perforations and tunnel length) were more effective predictors than the variables expressing larval presence (exit holes and larvae). An explanation may be that the number of larvae could not be measured accurately. This figure was based chiefly on the count of pupal skins, which could not always be recovered. Therefore larval presence is better represented by exit holes.

Feeding site

Grain yield was significantly affected (table 52). Loss of yield was estimated about 13%. However the natural infestation after tasseling caused a loss of yield of about 2%. Assuming that there are no interactions between the whorl and the after-tassel infestation, the loss of yield caused by the whorl infestation is about 11% (compared to 9% for the between-plots analysis, table 44B). *Kernel weight* was hardly influenced by the whorl infestation. *Ear size* was reduced significantly, the greatest reduction was in ear length (6%). The midwhorl infestation highly significantly reduced plant height T_2 (only two weeks later) by an estimated 9%.

In the regression analysis, excluding tunnel length, the effect of the borer variables of the stalk parts below the cob (the lowest three internodes and the rest of this stalk part) was investigated (table 52). The infested stalk parts did not show significant effects on grain yield, kernel weight and ear diameter. The infestation of the stalk part just below the cob (A2) affected ear size most (the length more than the diameter). Plant height T_2 was lowered almost exclusively by the borer variables of the lowest internodes (A1).

4.4.4. *Summary and general discussion*

4.4.4.1. Methods of crop loss assessment

Two maize cultivars grown in field cages (to exclude *S. frugiperda*) were artificially infested with *D. lineolata* at two developmental stages of the plant. The yield loss in maize caused by the borer was assessed by two independent methods. Firstly, whole plots were considered (between-plots analysis) and secondly, individual plants within separate treatments (within-plots analysis). In the between-plots analysis (analysis of variance of a randomized block design) the average reductions caused by the borer, in yield and plant development, were small and not significant (by a low number of replicates). However, as measurements had been carried out per plant, also a within-plots analysis (a multiple correlation and regression analysis) could be made. Although both analyses were independent, they gave similar results of the effect of the borer on yield and plant development.

This chapter mainly deals with the within-plots analysis. A number of borer variables (i.e. number of injured internodes, perforations, exit holes, larvae, injured ear shanks and tunnel length below the cob) were used as possible predictors of yield loss. Simultaneously the relative sensitivity of stalk parts to injury was investigated (2 feeding sites below the cob and 2 above the cob).

The within-plots analysis revealed a number of unexpected complications due to the effect of the plant on the borer. In the experiment there were phenotypical differences between plants e.g. in height and the number of internodes below and above the cob. The consequences of this were: 1. the position of the cob on the stalk influences the place where a larva enters the stalk (below or above the cob; the effect of the borer on the yield may be different for these two feeding sites); 2. plant height (before the whorl infestation) correlated positively with the number of larvae at harvest (table 46A), showing that on the taller plants more larvae survived. These differences between individual plants gave different yields, directly because e.g. taller plants yield more, and indirectly because more larvae survive on taller plants, causing a greater loss of yield. If the increase of yield by taller plants (plant height before the infestation) is more than the loss of yield by a larger number of larvae (because of increased survival) then the correlation between borer variables and yield is more positive than it would have been without these differences in plant height.

Therefore the effect of these plant differences had to be removed from the relationship between the borer and yield variables before the effect of the borer on yield loss could be assessed. This 'controlling' was carried out by partial correlation analysis. Table 46A shows that in the whorl infestation of the maize variety Nic-Synt-2 the correlations between the borer and yield variables were more negative after controlling. Only the plant development variables which were not affected by the borer could be used as control variables. Stalk diameter was determined at harvest and therefore the possible reduction by the borer was investigated. When it was not significantly affected the stalk diameter was used as a control variable.

By means of the controlled (partial) correlation coefficients, the effect of the borer on maize was assessed by carrying out a multiple regression of yield on borer variables. A regression analysis selected those borer variables which best predicted the yield.

4.4.4.2. The effect of borer variables

For the variety Nic-Synt-2 the borer variables that best correlated with yield variables for the infestation at whorl stage were those that expressed borer presence (exit holes and larvae) whereas for the silking stage the variables were those that expressed injury (injured internodes and perforations) (see tables 46A and 46B of correlation coefficients after controlling). For whorl infestation the injury variables of one stalk part (just below the cob) unexpectedly indicated a yield gain instead of a loss (this is probably explained by an effect of plant vigour on injury). EVERETT et al. (1958) also found that first brood larvae and cavities of *O. nubilalis* had a stronger association with yield than second brood larvae. For the maize hybrid X-105-A infested at midwhorl stage, yield was best predicted by the injury variables (injured internodes, perforations and tunnel length). The number of larvae (= pupal skins) was an ineffective predictor, mainly because it could not be sampled accurately as the skins could not always be recovered at harvest.

The variety Nic-Synt-2 showed that the percentage of injured ear shanks for the infestation at whorl stage was similar to that at silking stage, but only for the latter was it an effective predictor of the yield. Probably because the ear shank injury was higher for plants infested at silking stage than at whorl stage.

The results indicate that for an adequate assessment of loss a set of predictors should be used. The borer variables that best predict yield depend on factors such as the stage of growth of the plant in which the infestation occurs, the injury level and the maize variety. EVERETT et al. (1958) also mentioned that it is not advisable to use a single figure only as an index to evaluate yield loss by *O. nubilalis*.

4.4.4.3. The effect of feeding site

In the variety Nic-Synt-2 loss of yield for both moments of infestation was mainly caused by the injury of the lowest internodes. Similar results were obtained by CHIANG (1964) for *O. nubilalis*. For the midwhorl infestation of the hybrid X-105-A the injury was restricted to a few internodes below the cob and the effect on the grain yield was not different for the feeding sites below the cob.

Kernel weight did not seem much affected by the midwhorl infestation of the hybrid X-105-A. In the variety Nic-Synt-2 for both times of infestation the injury of the plant parts responsible for the translocation of assimilates to the ear (internodes above the cob and ear shank) resulted in less kernel weight. Ear length was most affected by the feeding sites directly around the cob. Ear diameter reacted in all infestations very similarly to grain yield. Plant height of the hybrid X-105-A was lowered by 9 per cent two weeks after the midwhorl infestation, this was almost entirely due to the injury of the lowest internodes.

A further knowledge on how the functioning of the two independent vascular systems of maize (as described by KUMAZAWA, 1961) is obstructed by the borer, may give further insight into the mechanisms of physiological damage.

4.4.4.4. Tunneling activity

The infestation at the silking stage of the variety Nic-Synt-2 by tunneling was twice as high as at whorl stage (expressed per larva the tunnel length was 26.3 and

13.8 cm respectively and expressed per perforation 12.1 and 4.8 cm respectively). Also for the maize hybrid X-105-A tunneling activity doubled for the natural infestation after tasseling when compared with the midwhorl infestation (expressed per larva the tunnel length was 24.3 and 11.2 cm respectively, expressed per perforation 9.8 and 4.2 cm respectively; for 'per larva' in the midwhorl infestation one has to read 'per exit hole', which in this case gives the best estimate of larval presence). GHIDIU et al. (1979) also mentioned a higher linear regression coefficient of stalk cavities on entrance holes for a second generation *O. nubilalis* as compared to the first generation.

The larvae from an infestation after tasseling, tunnel more than those before tasseling, possibly because: firstly more larvae from infestations after tasseling enter diapause than from an earlier infestation. Pre-diapausing larvae usually have a larger food intake (SCHELTES, 1978). For the variety Nic-Synt-2 the number of diapausing larvae was 72 and 86 per cent for the infestations at whorl and silking stage respectively. For the maize hybrid X-105-A 75 per cent of the larvae from the natural infestation after tasseling entered diapause, while for the midwhorl infestation no diapausing larvae were found (the midwhorl infestation plus the natural infestation after tasseling produced a lower number of diapausing larvae per plant than the natural infestation after tasseling alone; therefore all larvae from the midwhorl infestation pupated). Secondly, the sugar content of the stalk increases considerably after tasseling (SCHELTES, 1978; USUA, 1973; JONES and HUSTON, 1914). CHIPPENDALE and REDDY (1974) mentioned as feeding stimulants for *D. grandiosella* several sugars that permitted optimum growth and development of the larvae.

4.4.4.5. Yield loss

Yield loss for all infestations was only partly due to the the loss in kernel weight, so it must have been due to a reduced number of kernels. This is in accordance with the findings of SCOTT and DAVIS (1974) for *D. grandiosella.*

Table 53 shows the estimated yield loss for each infestation for the between- and within-plots analysis with corresponding values for the borer variables. Yield loss per borer per plant for the early variety Nic-Synt-2 was about 3 per cent for the whorl infestation and 5 to 6 per cent for the infestation at silking. Damage almost doubled when infestation occurred at the silking stage in comparison to whorl stage which coincides with a doubled tunneling activity (see chapter 4.4.4.4.). Generally however infestations by second generation borer larvae of *O. nubilalis* have been found to cause less damage (JARVIS et al., 1961; CHIANG et al., 1954; HU and SUN, 1979).

Our results amounted to 3 to 6 per cent loss of yield per borer per plant (table 53). This is higher than the often cited index of 3 per cent for *O. nubilalis* in the United States, although higher percentages have been recorded (CHIANG, 1964), in China even as high as 24 per cent per borer (HU and SUN, 1979).

In 1978 extension workers sampled maize stalks at harvest for *D. lineolata* injury from fields in different parts of the country (table 54). The level of injury was generally low except for some fields in two departments. When applying the

TABLE 53. Percentage loss of yield by *D. lineolata* after infestations at whorl and silking stage of the maize variety Nic-Synt-2, and after a midwhorl infestation of the hybrid X-105-A. (Exp. J)

Cultivar	Time of infestation	Borer variables: number per plant				Yield loss (%)			
		Injured internodes	Perfo-rations	Exit holes	Borers[1]	Between-plots analysis		Within-plots analysis	
						total	per borer per plant	total	per borer per plant
Nic-Synt-2	whorl stage	4.9	8.1	2.0	2.8	8	2.6	9.6	3.5
	silking stage	2.7	3.1	.9	1.4	7	5.0	8.6	5.9
X-105-A	midwhorl stage	2.4	4.5	1.7	.7	9	5.3[2]	11.	6.5[2]

[1]Borers = larvae.
[2]Per borer = per exit hole.

TABLE 54. Incidence of *D. lineolata* injury in maize fields in different parts of Nicaragua (first growing period, 1978).

Region	Department (number of municipals)	Number of maize fields sampled[1]		Maize variety	Percentage of injured plants		Number of injured internodes per plant	
Pacific Central		26		X-105-A	43		.75	
	Granada (1)		9	X-105-A		45		.87
	Masaya (2)		7	X-105-A		53		.83
	Carazo (3)		10	X-105-A		34		.59
Pacific South	Rivas (2)	2		X-105-A	97		4.08	
Interior South		5		X-105-A	29		.71	
	Boaco (1)		1	X-105-A		43		1.15
	Chontales (1)		4	X-105-A		25		.60
Interior North	Nueva Segovia (5)	8		NB-2/Tuxpeño	79		2.56	
			5	NB-2		68		1.75
			3	Tuxpeño		98		3.90
Republic		41		X-105-A/NB-2/Tuxpeño	51		1.26	

[1] Sampling: 10 plants in each of four random sites per field.

results of the crop loss assessment (table 53) to these injury levels, the loss of yield in the first growing period was in most maize fields less than 3 per cent. Only in some fields a yield loss of more than 10 per cent must have occurred. To make an estimation of yield loss of maize grown in the second growing period, injury estimates will have to be made similar to those made in the first growing period.

The aspect of economic thresholds and chemical control of the borer will be discussed in chapter 6.2..

5. CONTROL OF *S. FRUGIPERDA* AND *D. LINEOLATA*

5.1. CHEMICAL CONTROL OF *S. FRUGIPERDA*: EVALUATION OF INSECTICIDES, ECONOMIC THRESHOLDS, SELECTIVE APPLICATIONS AND TIMING

5.1.1. *Introduction*

Investigations evaluating insecticides used in controlling *S. frugiperda* in maize have been carried out in different parts of America. USA: HARRIS et al. (1975); Mexico: VALENCIA et al. (1972), CORIA and DELGADO (1973), MEDINA (1976), RAMIREZ (1971), ALVARADO (1975a and b, 1977b); El Salvador: GARCIA (1977); Nicaragua: MEDRANO (1978); Costa Rica: ALVAREZ (1977); Columbia: ICA (1974); Peru: PEÑA (1974). In all these investigations a number of insecticides were found to be statistically equally effective in reducing *S. frugiperda* infestations and in increasing yields. Formulations and concentrations of some insecticides differed, and *S. frugiperda* injury occurred at different stages of plant development and varied in intensity; it is therefore very difficult to draw a general conclusion. Only in some cases were the timing of applications (ALVARADO, 1977b) and the use of economic thresholds considered (YOUNG and GROSS, 1975; OBANDO, 1976; SARMIENTO and CASANOVA, 1975). Generally a reduction in the number of injured whorls by the insecticides and increases in yield were reported, but OBANDO (1976) and ALVARADO (1975a and 1977b) also gave data on plant loss.

Granular insectides are recommended against *S. frugiperda* and *D. lineolata* because the small farmers can easily apply them to the whorl by hand or using a jar with a perforated lid. Granules are also ecologically selective, because applications are directed only towards the part of the plant where they are needed. In Nicaragua granular phoxim (Volaton 2.5%) proved to be an effective insecticide (MEDRANO, 1978), this is affirmed by results obtained in El Salvador and Costa Rica (GARCIA, 1977 and ALVAREZ, 1977, respectively). During early plant development granules are difficult to apply because the whorl is small, therefore liquid insecticides are generally recommended. The control with granular trichlorphon (Dipterex 2.5%) was inadequate. (MEDRANO, 1978; OBANDO, 1976). This chemical had been recommended in Nicaragua (BNN/INCEI/IAN/MAG, 1974) and was still being used in 1977 by many farmers using insecticides. In Nicaragua a method was developed in which a mixture of chlorpyrifos (Lorsban 480E) and sawdust was applied to the whorl (MAG/FAO/PNUD, 1976). In this way the recommended concentration could be reduced to a half or even a fifth. Several farmers replied in a survey, that they applied mixtures of wettable powder insecticides and soil to the whorl. Many farmers save a considerable amount of insecticide by applying them only to the injured whorls. Another control practice, which is used by some farmers, is the application of soil only to the whorl.

MCMILLIAN et al. (1969) reported that an extract of the leaves of *Melia azedarach* L., a common tree in Nicaragua, deterred feeding, retarded development and caused mortality of the larvae of *S. frugiperda*, when incorporated in a meredic diet or when applied to the maize seedlings in the greenhouse. In Nicaragua, the possible use of this method by the small farmer was investigated in a preliminary experiment. A dilution with water of an extract of mortar-crushed leaves of this tree was applied by knapsack sprayer on a heavily infested maize (midwhorl stage) plot, but no signs of control could be detected.

Synthetic pyrethroids for the control of *S. frugiperda* have shown to be rather promising (GARCIA, 1977; MEDRANO, 1978; TYSOWSKY and GALLO, 1977). The latter authors found in a bioassay that egg hatching of *S. frugiperda* was prevented by permethrin.

Carbofuran has been recommended when a very heavy attack of *S. frugiperda* at the early whorl stage is expected. It has also been recommended to control *Dalbulus maidis*, the vector of corn stunt spiroplasma and rayado fino virus (ANAYA and DIAZ, 1974). YOUNG and GROSS (1975) bioassayed excised whorls of carbofuran-treated plants against 4-days old larvae of *S. frugiperda*; the percentage mortality was recorded 48 hours later. Carbofuran applied in the furrow gave an acceptable control for about 15 days which declined rapidly thereafter. Placing carbofuran in a .15 m band on the row and incorporating it at sowing gave erratic control.

The highest yield obtained by SARMIENTO and CASANOVA (1975) was when they used an economic threshold of 20% of plants infested by *S. frugiperda*, the difference between the 10 and 30% levels was not significant; when levels were above 40% yields diminished significantly. In a second experiment the best results were obtained with a threshold of 10% of injured plants and a significant reduction in yield occurred when the 30% level was used. YOUNG and GROSS (1975) and OBANDO (1976) found no significant differences between the 20 and 50% levels.

The importance of early protection of maize plants against *S. frugiperda* has been recommended in several extension bulletins, such as SIFUENTES (1976) in Mexico and ARGUELLO and PINEDA (1976) in Nicaragua. This may be due to the effect of early protection on the yield per plant as well as on the prevention of plant loss; early *S. frugiperda* attacks may kill the plant by tunneling larvae feeding on the meristematic tissue of the bud ('dead heart'). SARMIENTO and CASANOVA (1975) stress the importance of early plant protection, as with a lower threshold, insecticide applications occur earlier (see last paragraph). They however, do not give data on plant loss. OBANDO (1976) obtained in Nicaragua with the 20% economic threshold, a significant yield increase of 34% over the control, and 29% by preventing plant loss. ALVARADO (1977b) protected an inland and hybrid maize cultivar at 10 and 17 days and observed in the untreated check, a yield reduction of 32 and 40% and a plant loss of 22 and 38% respectively, which indicates that largest loss of yield occurred by elimination of plants by *S. frugiperda*. In another experiment he found that yield increase obtained by an insecticide application to 5 days old maize plants was mainly because it prevented plant loss (ALVARADO, 1975a). The highest yield per plant was observed for treatments that included applications at 30 or 35 days.

Crop loss assessment of stem borers in maize is virtually absent in tropical America and chemical control in general is not directed towards this pest. However a chemical treatment against *S. frugiperda* is frequently also evaluated for its effectiveness in controlling maize stem borers.

In experiment K I (chapter 5.1.2.), economic thresholds, timing and methods of application against *S. frugiperda* and *D. lineolata* were evaluated. In experiment K II (chapter 5.1.3.), chemical control methods of practical importance for the small farmer were studied including economic thresholds. In experiment K III (chapter 5.1.4.), the traditional control method of applying soil to the whorl was evaluated.

5.1.2. *Control of S. frugiperda and the effect on D. lineolata*

5.1.2.1. Material and methods (Exp. K I)

The open pollinating maize variety Salco developed in Nicaragua, was sown on June 28, 1976 at the experimental station La Calera, Managua. Germination was completed by July 2. At sowing NPK fertilizer (10–30–10) and urea were applied at a rate of 130 and 65 kg ha^{-1} respectively. The urea treatment was repeated 3 weeks after plant emergence. The experiment was laid out in a randomized block design with 11 treatments (T) and 8 replicates. The specification of the treatments is given in table 55.

Economic thresholds of 20 and 50% of injured whorls were maintained with a chlorpyrifos-sawdust mixture (T_2, T_3) in combination with carbofuran applied at sowing (T_5, T_6). The effect of carbofuran alone was evaluated in T_4 (carbofuran is a systemic insecticide and nematicide; in soil its half life is 30 to 60 days and in plants less than 5 days). The timing of applications of chlorpyrifos-sawdust was investigated in the treatments T_7, T_8, T_9. Control by granular mefosfolan, a systemic insecticide, was investigated in T_{10} (besides its control of *S. frugiperda*, the effect on *D. lineolata* could be evaluated). In treatment T_{11} (weekly applications of the chlorpyrifos-sawdust mixture) an attempt was made to prevent all whorl injury by *S. frugiperda* (chlorpyrifos is a non-systemic insecticide of reasonable persistence). A control was added (T_1). Plant protection from tasseling onwards in 4 out of 8 replicates aimed at the prevention of ear injury by *S. frugiperda* and *Heliothis zea* (table 55, note 1). The effect on injury by *D. lineolata* was evaluated in all treatments, the economic aspects were also considered.

Each plot consisted of 4 rows, .9 m apart of 5 m length, the sampling unit being the 2 inner rows. In the row, plants were spaced .15 m. Twice a week in each plot, all the plants and the number of whorls injured by *S. frugiperda* were counted and the height of 2 plants was measured. When the assigned economic threshold was reached in a plot, chlorpyrifos was applied to all whorls on the same day. At harvest the number of plants was counted and grain weight (adjusted to 15% moisture) was determined. In each plot the injured internodes and the perforations of *D. lineolata* per stalk were counted on 20 plants.

In the analysis of variance (Appendix 2) sets of contrasts were tested for replicates and treatments. Table 56 specifies these contrasts. Treatment sum of squares was partitioned for a part of the treatments into linear, quadratic and cubic components. The percentage of whorls injured (100x) by *S. frugiperda* was transformed by arcsin $\sqrt{x}$. A multiple regression analysis was carried out to predict grain yield per plot from variables representing treatments, injury by *S. frugiperda* and injury by *D. lineolata*. The three groups of variables were entered into the regression equation in different sequences to compare the amounts of variation in yield explained by each group, and check the independence of each group in predicting yield. The statistical analyses were carried out by means of the computer program SPSS.

For the calculations of the costs of the applications of insecticides (expressed in kg grain of maize) the following prices (page 170) were used (1978):

TABLE 55. Specification of treatments used in experiment K I.

Treatments within (8) blocks[1]		Economic thresholds in percentage of injured whorls	Programmed applications of insecticides (days after plant emergence)	Applications of		Carbofuran applied at sowing[4]
Number	Symbol			Chlorpyrifos-sawdust mixture[2]	Mefosfolan[3]	
T_1	C_c (= Control)	∞	–	–	–	–
T_2	Thr_{50}	50	–	+	–	–
T_3	Thr_{20}	20	–	+	–	–
T_4	C_c (= Control + carbofuran)	∞	–	–	–	+
T_5	Thr_{50} (+ carbofuran)	50	–	+	–	+
T_6	Thr_{20} (+ carbofuran)	20	–	+	–	+
T_7	T15	–	15	+	–	–
T_8	T15 + 30	–	15 + 30	+	–	–
T_9	T10 + 15 + 30	–	10+15 + 30	+	–	–
T_{10}	Me (= Mefosfolan)	–	15 + 30	–	+	–
T_{11}	Chl (= Chlorpyrifos)	–	weekly	+	–	–
$T_1 + T_4$	Thr ∞ ($C + C_c$)					

[1] Four blocks at the lee-side of the experimental field were treated with methyl-parathion (48% EC, .7 l ha^{-1}) by knapsack sprayer, 5 times at weekly intervals, starting from tasseling (48 days after plant emergence).
[2] .35 l of chlorpyrifos (Lorsban 480E) was mixed with 26 kg sawdust and 8 l water (per ha). Application was to the whorl and by hand.
[3] 13 kg ha^{-1} of granular mefosfolan (Cytrolane 5%), a systemic insecticide. Application was to the whorl and by hand.
[4] 13 kg ha^{-1} of granular carbofuran (Furadan 5%).

	Dollar price (1978)	Costs in kg maize per application per ha
carbofuran (Furadan 5% G)	108.7 per 100 kg	144
mefosfolan (Cytrolane 2% G)	72.4 per 100 kg	107
chlorpyrifos (Lorsban 480E)	7.55 per litre	54
methyl parathion (48% EC)	3.77 per litre	54
labour	4.08 per application	
maize (price to producer)	12.60 per 100 kg	

TABLE 56. Specifications (by vectors) of various contrasts (e.g. in partitioning the sum of squares) in the analysis of the effects of different insecticide treatments to protect the maize plant against *S. frugiperda* and *D. lineolata*. (Exp. K 1)

Replicates

Block	Weekly applications of methyl parathion starting at tasseling (48 days) up till harvest	Contrast vectors A	B	C	A×C
1	+	1	0	3	3
2	+	1	1	-1	-1
3	+	1	1	-1	-1
4	+	1	1	-1	-1
5	–	-1	-1	-1	1
6	–	-1	-1	-1	1
7	–	-1	-1	-1	1
8	–	-1	0	3	-3

Treatments

Treatment number	Carbofuran at sowing	Economic threshold[1] (injured whorls)	Contrast vectors: Carbo-furan D	Threshold effects E	F	G (linear)	H (quadratic)	J	Interactions D×E	D×F	D×G	D×H	D×J
T_1	–	Control[2] (C)	1	2	1	1	-1	0	2	1	1	-1	0
T_2	–	50%	1	-1	-1	0	2	1	-1	-1	0	2	1
T_3	–	20%	1	-1	0	-1	-1	-1	-1	0	-1	-1	-1
T_4	+	Control (C_c)	-1	2	1	1	-1	0	-2	-1	-1	1	0
T_5	+	50%	-1	-1	-1	0	2	1	1	1	0	-2	-1
T_6	+	20%	-1	-1	0	-1	-1	-1	1	0	1	1	1

Treatments

Treatment number	Programmed applications (chlorpyrifos) days after emergence	Contrast vectors K (linear)	L (quadratic)	M (cubic)
T_1	Control[2]	3	1	1
T_7	15	1	-1	-3
T_8	15+30	-1	-1	3
T_9	10+15+30[3]	-3	1	-1

Treatments

Treatment number	Other treatments	Contrast vectors N	O
T_1	Control[2]	2	0
T_{10}	Mefosfolan (15 + 30 days) (Me)	-1	1
T_{11}	Chlorpyrifos (weekly) (Chl)	-1	-1

[1] When the threshold was reached chlorpyrifos was applied.
[2] Used in three different sets of contrasts and in partitioning of sum of squares.
[3] Short for 'applications 10, 15 and 30 days after plant emergence'.

5.1.2.2. Results and discussion

The effect of treatments on yield and plant development, and on injury by *S. frugiperda* and *D. lineolata* is presented in an analysis of variance (Appendix 2).

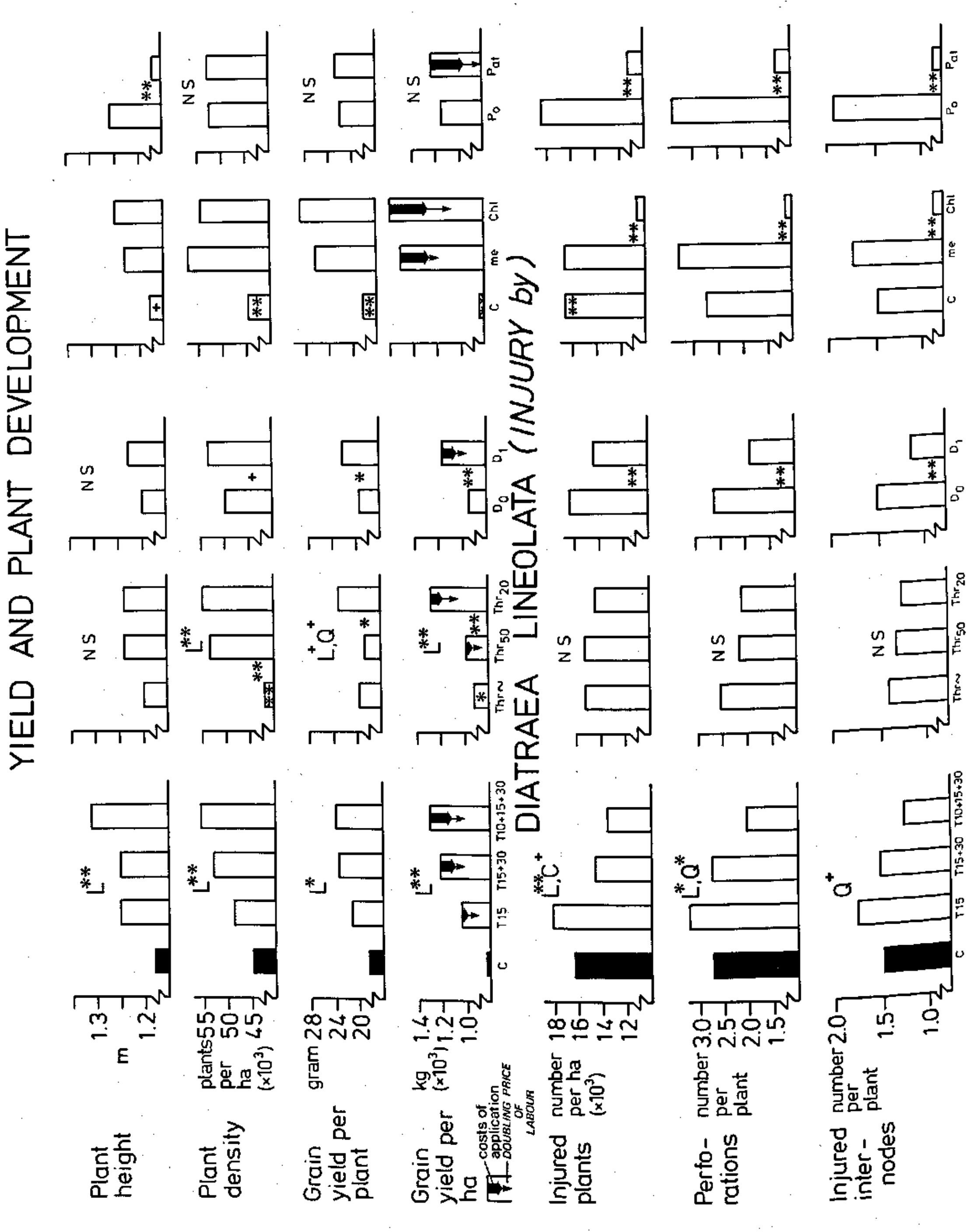
The experiment as a whole showed that the two outer blocks of the experimental field produced more than the inner blocks (Appendix 2). This significant difference accounted for almost all the variation in the yield between the blocks (the cause of this border effect is not known). Interactions between replicates and treatments were considered, but they were not significant for all the variables analyzed. Drought, which occurred in the third week after plant emergence and in the four weeks after tasseling (fig. 36A) was responsible for the rather low average yield of 1183 kg ha^{-1}. This has in recent years been the national average yield in Nicaragua (fig. 1). Drought is a very common phenomenon in Nicaragua (fig. 1). From the results of the analysis, chemical control effects can now be judged under the adverse climaticalogical conditions, that frequently occur in this area.

In the following paragraphs we deal with various groups of treatments. All the results have been presented in figure 35.

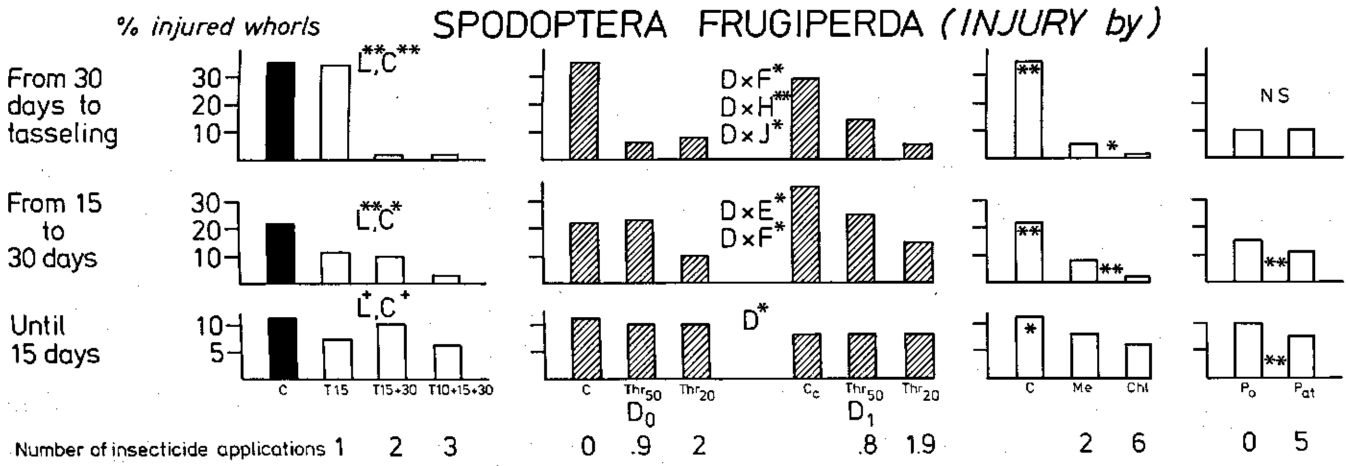
5.1.2.2.1. Programmed applications

The series of control and applications of chlorpyrifos at 15, 15+30 and 10+15+30 days after plant emergence showed in this order a significant linear increase in yield and plant development variables (fig. 35). When the applications at 15 and 30 days (T15+30) were preceded by one at 10 days (T10+15+30), yield per plant did not change, but plant height and the number of plants per ha increased. This may be explained by the small reduction in the number of whorls injured by *S. frugiperda* before the 30th day. The greatest effect on the number of injured whorls was caused by the applications at 30 days which reduced this injury by about 30% to almost zero and increased yield per ha by about 36% of the control.

D. lineolata injury showed significant linear and quadratic components. The quadratic components consisted of an increase in injury by the application at 15 days compared to the untreated control. As an explanation it is noted that oviposition by *D. lineolata* correlates positively with leaf area (Exp. A I, chapter 3.1.). Leaf area increases during whorl development. The application at 15 days (i.e. before the moment of highest oviposition) did not result in a significant control of *D. lineolata*. However it increased plant height and probably leaf area, resulting in a higher oviposition by *D. lineolata* (and/or larval survival; see Exp. F chapter 4.1. and Exp. J, chapter 4.4.) and hence infestation. This may also be expected from the treatments which include an application at 30 days. At this later stage of plant development however, the number of larvae of *D. lineolata* in the whorl is higher, due to increased oviposition, insecticide applications at this stage will cause mortality of these larvae. Thus application of insecticides against *S. frugiperda* may result in a higher infestation by *D. lineolata* (probably more oviposition because of the increased leaf area), however it lowers this infestation by controlling the borer larvae. The extent to which this occurs depends on the developmental stage of the plant.



YIELD AND PLANT DEVELOPMENT
DIATRAEA LINEOLATA (INJURY by)
Plant height
Plant density
Grain yield per plant
Grain yield per ha
costs of application
DOUBLING PRICE OF LABOUR
Injured plants
Perfo- rations
Injured inter- nodes
NS



PROGRAMMED INSECTICIDE APPLICATIONS

Tx= application at day x

C = untreated control

Tested: the linear (L) quadratic (Q) and cubic (C) components[1]

ECONOMIC THRESHOLD AND CARBOFURAN

Thr_y = threshold of y per cent of whorls injured by *S. frugiperda*

D_1 = carbofuran applied at sowing (D_0 = without)

C = untreated control

C_c = control plus carbofuran at sowing

Thr ∞ = C + C_c (averaged)

Tested: the linear (L) and quadratic (Q) components[2]; Thr ∞ – Thr_{50}, Thr_{20} (E) $\boxed{*}$; Thr ∞–Thr_{50} (F); Thr_{50}–Thr_{20}(J); and the interactions[3] with D_0–D_1; D_0–D_1

MEFOSFOLAN AND CHLORPYRIFOS

Me = mefosfolan applied at 15 and 30 days

Chl = chlorpyrifos applied weekly

C = untreated control

Tested: C–Me, Chl $\boxed{*}$; Me–Chl

PLANT PROTECTION AFTER TASSELING

P_{at} = protected blocks 1 to 4

P_0 = unprotected blocks 5 to 8

Tested: P_{at}–P_0

[1] L, Q and C in this column have been called K, L, and M, respectively in the text.
[2] L and Q in this column have been called G and H respectively in the text.
[3] With significant interactions the presence of main effects is implied.

FIG. 35. Various chemical control methods. The effect on yield and plant development of the maize variety Salco and on the injury by *D. lineolata* and *S. frugiperda* (see for specifications of the tested effects table 56 and Appendix 2. (Exp. K I)

5.1.2.2.2. Economic thresholds for *S. frugiperda* and carbofuran applied at sowing

Both thresholds of 50 and 20% of whorls injured by *S. frugiperda* (Thr_{50} and Thr_{20}) prevented plant loss significantly. As far as yield per plant and per ha are concerned the threshold of 20% performed much better than the one of 50%, which hardly showed differences with the untreated control ($Thr\infty$). The 20% threshold increased yield significantly (by 24%). The effect of the thresholds on injury by *S. frugiperda* is presented in figure 35 separately for treatments with (D_1) and without (D_0) carbofuran to illustrate some interactions. Initially (until 15 days) carbofuran caused a small, but significant decrease in the number of infested plants (= % of injured whorls). From 15 to 30 days however the carbofuran treatment showed a significant increase in the percentage of infested plants, that caused the significant interactions (D × E, etc.), that are observed between thresholds and carbofuran for the number of infested plants from 15 days onwards. This is also shown by the curves of the percentage of injured whorls against time with and without (C_c, C) carbofuran (P, Q) in figure 36A. In the second growing period, a similar experiment with the same treatments was carried out (OBANDO and VAN HUIS, 1978, unpublished report) and a similar effect of carbofuran was observed (fig. 36B).

The carbofuran treatment increased yield significantly (by 20% per ha and by 15% per plant; D_1 versus D_0, fig. 35). A reduction of *S. frugiperda* infestation was not the cause. Injury by *D. lineolata* decreased significantly by about 30%, probably by the systemic effect of the treatment. It seems unlikely (see chapter 4.4 and 5.1.2.2.6.) that this lower borer injury was responsible for the yield increase obtained with carbofuran. Yield increase in maize with carbofuran that cannot be explained by control of insects has been reported by APPLE (1971) and DAYNARD et al. (1975), however ROGERS and OWENS (1974) did not find this stimulative effect. DAYNARD et al. (1975) concluded that carbofuran should not be recommended as a yield stimulator of maize until the causes of occasional yield increases have been determined.

In our experiment *D. lineolata* injury was less with lower economic thresholds for *S. frugiperda*, but not significantly so.

5.1.2.2.3. Mefosfolan and chlorpyrifos

Mefosfolan applied at 15 and 30 days and chlorpyrifos applied weekly, both reduced plant loss and increased yield significantly (Me, Chl versus C, fig. 35). Yield per ha showed an increase of 57 and 64% respectively. The percentage of whorls injured by *S. frugiperda* was significantly reduced by both treatments and more by the weekly applied chlorpyrifos.

The mefosfolan treatment did not affect *D. lineolata*, borer injury was even higher than in the control. The mefosfolan treatment prevented injury by *S. frugiperda* and hence increased the leaf area, which probably provoked increased oviposition by *D. lineolata*. With a deficient control by mefosfolan of *D. lineolata* larvae, its injury with this treatment might be higher than in the untreated control. This again shows that *D. lineolata* infestation may increase after appli-

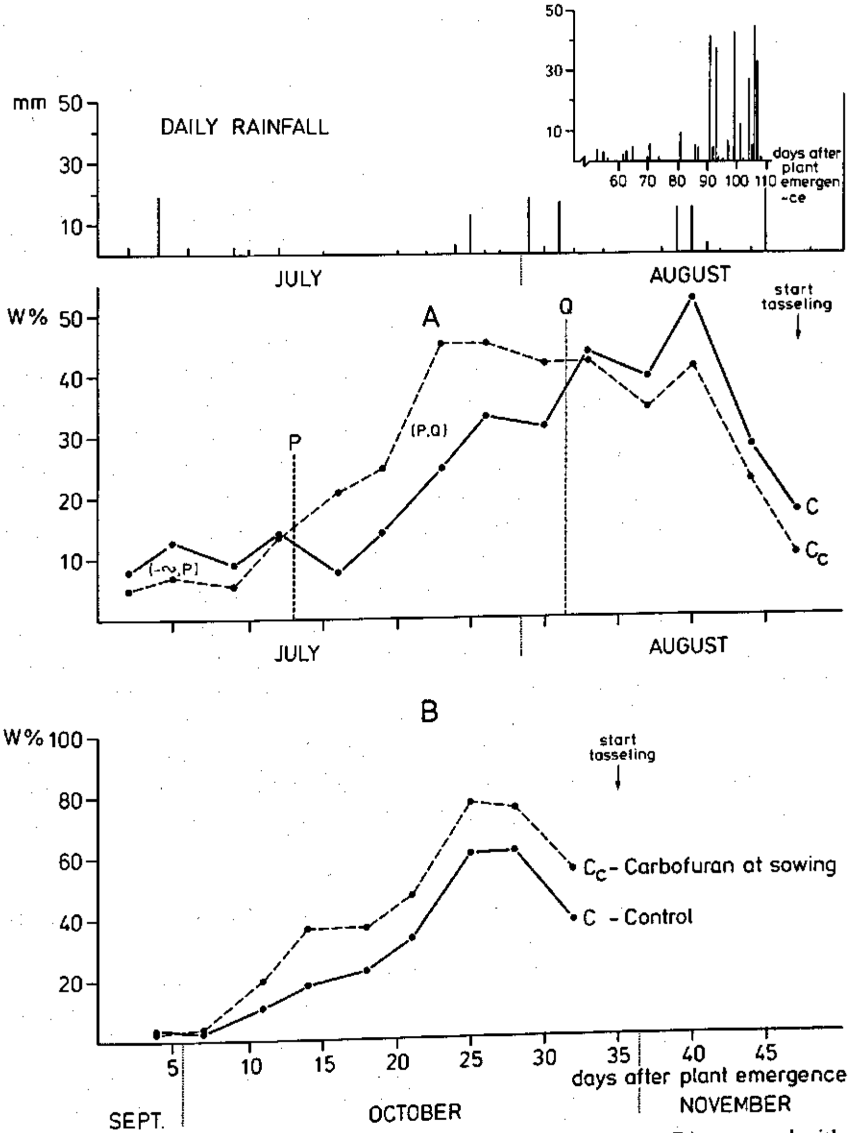


FIG. 36. The systemic insecticide carbofuran applied at sowing to maize (C_c) compared with the untreated control C. Percentage of whorls injured (W) by *S. frugiperda*.
A. Maize variety Salco, first growing period of 1976 (compare C and C_c in fig. 35; Exp. K 1).
B. Maize variety Nic-Synt-2, second growing period of 1976 (under irrigation).

cations of insecticides directed against *S. frugiperda*.

5.1.2.2.4. Chemical control after tasseling

The five applications of methyl parathion after tasseling (P_{at}) decreased injury by *D. lineolata* (injured internodes and perforations) by about 70% and the number of plants infested by the borer by about 40%, when compared to the control (P_0) (fig. 35). The yield increase as a result of the after-tassel applications was 6% per plant and 7% per ha (non-significant). Ear injury by *Heliothis zea* and *S. frugiperda* was very small. The increase in yield was possibly a result of less damage by *D. lineolata*.

Block 1 to 4 (see table 55, note 1) on the lee-side of the experimental field initially had a significantly lower percentage of whorls injured by *S. frugiperda*. The difference was small and disappeared 30 days after plant emergence. The cause is not known.

5.1.2.2.5. Chemical control and yield: regression analysis

The variation in yield per plot is mainly a result of the treatments and *S. frugiperda* damage, both are strongly linked (combined about 38%), which is natural as the treatments are mainly against *S. frugiperda* (table 57). Treatments are responsible for at least 13% and at most 33% of the variation, leaving at most 25% and at least 3% for *S. frugiperda* impact. This may indicate the following. Firstly that the percentage of injured whorls is a fairly accurate predictor of *S. frugiperda* damage and secondly that the treatments have affected maize yield mainly by varying *S. frugiperda* damage as shown by the percentage of injured whorls. Treatments however still showed an independent effect. Probably this was mainly caused by the systemic insecticides, which increased maize yield more positively than might have been expected when only *S. frugiperda* was controlled. This has already been explained for carbofuran. The effect of mefosfolan is shown in figure 35 by the applications of chlorpyrifos and mefosfolan at 15 and 30 days. Both treatments brought about an equal reduction in the *S. frugiperda* infestation, however yield increase was much higher for mefosfolan.

5.1.2.2.6. Economic analysis

In figure 35 the costs of the insecticide applications (indicated by ⬇ in the histograms) have been expressed in kg maize (based on prices in 1978). This figure will vary from year to year as insecticide prices and labour costs increase, and the price of maize fluctuates. For example increased labour costs mean that the number of applications becomes a limiting factor (indicated by ↓ when labour costs double). These calculations and a subsequent evaluation of the different treatments should be made each year, using current prices. The merits of chemical control should however not be judged without the well known side effects, as discussed in chapter 1.1.. Mefosfolan applied at 15 and 30 days, shows the best results in terms of yield and returns. Its effect on *S. frugiperda* injury was however comparable to that of chlorpyrifos applied on the same dates (T15 + 30) and also to that of the economic threshold of 20% (Thr_{20}) of injured whorls. These last two treatments both had two applications of the same insecticide (see one of the lower lines in fig. 35), but the economic threshold of 20% yielded the most. Therefore, preference should be given to the in Central America already widely recommended threshold of 20% of injured whorls. A threshold is a more rational method than a programmed application, as the magni-

TABLE 57. Percentage of variation in maize yield per plot explained ($R^2 \times 100$) by replicates, treatments and injury by *S. frugiperda* and by *D. lineolata*, when the last three groups of variables are entered in different sequences (SEQ) in the multiple regression equation. (Exp. K I)

Source of variation	df	SEQ	$R^2 \times 100$	SEQ	$R^2 \times 100$	SEQ	$R^2 \times 100$	SEQ	$R^2 \times 100$
Replicates	7	1	29.40	1	29.40	1	29.40	1	29.40
Treatments	10	2	33.57	2	33.57	4	13.28*	4	13.28*
S. frugiperda injury[1]	3	3	2.86	4	4.63*	2	25.09	3	22.12
D. lineolata injury[2]	2	4	5.12*	3	3.35	3	3.18	2	6.15
Total			70.95		70.95		70.95		70.95

[1] Variables: percentage of injured whorls (arcsin – transformed) before 15, between 15 and 30, and after 30 days of plant emergence.
[2] Variables: number of injured internodes and number of perforations.

tude of a natural infestation cannot be foreseen.

5.1.3. *Chemical control appropriate to small farmer's conditions*

In this experiment chemical control practices appropriate to the small farmer were investigated. Chlorpyrifos mixed with soil or sawdust was compared to granular phoxim and an untreated control. Insecticides were applied at thresholds of 20 and 50% of infested plants on all whorls, and on injured whorls only (selective applications).

5.1.3.1. Material and methods (Exp. K II)

The maize hybrid X-105-A was sown on June 13, 1978 at the experimental station, La Calera, Managua. At sowing 130 kg NPK fertilizer (10–30–10) per ha was given and 5 days after sowing 65 kg urea. The urea treatment was repeated 30 days after plant emergence.

The experimental design was a split-plot with 4 replicates. The main plots were each assigned a control and 3 insecticide applications, namely 10 kg granular phoxim (Volaton 2.5%), chlorpyrifos wettable powder (Lorsban 5%), of which 7.1 kg was mixed with soil, and chlorpyrifos (Lorsban 480E) of which .14 l was mixed with 26 kg sawdust and 8 l water (all rates per ha). In the 4 subplots of each plot the treatments were applied by hand when 20% or 50% of the whorls showed injury by *S. frugiperda* (economic thresholds); moreover the application in the subplots was applied on all whorls or on injured whorls only (selective applications). The subplots thus each consisted of a different combination of economic thresholds and selective applications. In this way a total of 60 subplots was obtained. Each subplot consisted of 4 rows 5 m long, the 2 inner rows being the sampling unit. Rows were .9 m apart. At 2.5 weeks after plant emergence plants were thinned out to a distance of .15 m in the row.

Twice a week during the whorl stage the number of plants and injured whorls per subplot were counted and the height of 6 consecutive plants in a row measured. At each sampling date the percentage of injured whorls was determined per subplot, and if the injury was higher than the subplot's assigned threshold, an insecticide was applied that day. After harvesting the number of plants and cobs were counted and grain weight (adjusted to 15% moisture) was determined.

Eleven subplots received incorrect treatment and so had to be excluded from the analysis. Because of the complexity of an analysis of variance including the missing subplots, the subplot analysis was carried out by means of a multiple regression analysis, in which the control was excluded and the plots were entered first into the equation as covariables. The effect of the different insecticides (main plots) was investigated by an analysis of variance with and without the control. Means were adjusted by standard techniques. Analysis of variance and regression analysis were carried out by means of the computer program SPSS.

5.1.3.2. Results and discussion

Infestation patterns of *S. frugiperda* are shown for all treatments in figure 37. The analysis of variance for maize yield and plant development is presented in table 58. For the untreated control the infestation pattern was as follows (fig. 37A): from 5 to 10 days after plant emergence the percentage of injured whorls increased from about 10 to 60 per cent; from 10 to 30 days it remained at a level of 60 to 80 per cent; after 30 days the percentage of injured whorls decreased sharply.

The differences brought about by the insecticide application occurred mainly between 10 and 35 days. Figure 37 shows that between 18 and 23 days the infestation sharply increased in the insecticide treatments and only moderately in the control. This is probably because a high oviposition and subsequent colonization of plants by *S. frugiperda* will be more obvious in healthier plots.

TABLE 58. Insecticide treatments, economic thresholds and selective applications (to injured whorls only). The effect on yield and plant development of maize. Analyses of variance and multiple regression: F-values, significancies and means. (Exp. K II)

Source of variation	df	Grain yield per plot	Grain yield per plant	Number of plants	Number of cobs	Plant height[1]
Analysis of variance (including control)				F-values		
Block (B)	3	.25	.19	.85	.61	.29
Insecticides (I_1)	3	3.78$^+$	4.26*	.82	2.36	21.3**
Error (B × I_1): V.C.	9	17.2	15.6	11.2	13.1	4.73
Analysis of variance (without control)				F-values		
Block (B)	3	.12	.09	.68	.31	.34
Insecticides (I_2)	2	1.12	1.82	.74	.81	.80
Error (a) (B × I_2): V.C.	6	19.0	17.2	11.6	14.7	5.36
Regression analysis (without control)				F-values		
Main effects (plots)	11					
damage thresholds (T)	1	.17	.01	.00	.93	2.18
selective applications (S)	1	5.61*	3.96$^+$	.28	2.54	.25
Two-way interactions						
$I_2 \times T$	2	.89	.07	.27	2.08	1.38
$I_2 \times S$	2	2.16	.09	1.27	2.50	2.53
$T \times S$	1	.00	1.66	1.83	.02	.03
Three-way interactions						
$I_2 \times T \times S$	2	.05	1.04	1.01	.92	1.86
Error (b): V.C.	13	10.8	15.4	14.7	9.82	5.40
Total	33					
				means		
		kg ha^{-1}	gram	number per ha		cm
Grand mean		5671	105.	54.9	58.0	144.
		percentage deviation from grand mean[2]				
(Control)		–15	–13	–3	–9	–11
Insecticides						
phoxim		3	2	1	3	–2
chlorpyrifos/soil		–5	–7	3	2	0
chlorpyrifos/sawdust		3	6	–3	–4	1
Economic threshold						
injured whorls: 50%		–1	–0	–0	2	–2
20%		1	0	0	–2	2
Selective applications						
all whorls		5	6	–2	3	1
only injured whorls		–4	–5	1	–3	–0

[1] Average of 35, 38, 42 and 45 days after plant emergence.
[2] Percentage deviations of corrected values do not always add up to zero.

5.1.3.2.1. Insecticide treatments

The different insecticides reduced the infestation (injured whorls) by about 50% (fig. 37A). Chlorpyrifos appeared to be most effective when the emulsion was mixed with sawdust and least effective when the powder form was mixed with soil. The difference however in the percentage of infested plants was small. The various insecticides showed significant effects on maize yield and plant development when the untreated control was included in the analysis (table 58). The yield increase by controlling *S. frugiperda* was not as high as was observed in other experiments. This is probably due to the decreasing infestation in the untreated control after the midwhorl stage (fig. 37A). It indicates that whorl injury by *S. frugiperda* during early plant development does not cause much damage. The significant differences in yield per plot were obtained by yield per plant and not by effects on the number of plants. An explanation may be that plants were thinned out at 2.5 weeks after plant emergence. There were no significant differences between the insecticide treatments, although it seems that the chlorpyrifos-soil mixture was the least effective in increasing yield. Granulated phoxim and the chlorpyrifos-sawdust mixture showed similar and better results.

5.1.3.2.2. Economic thresholds.

The highest average number of applications occurred for both thresholds (20 and 50% of injured whorls) 10 and 22 days after plant emergence (fig. 37B). Because the number of infested plants had increased sharply on these dates it did not make much difference which threshold was used. With the 20% threshold, the average number of applications was only .7 higher than with the 50% threshold (fig. 37B). The percentage of infested plants was slightly higher for the 50% threshold. The difference was not significant and there was no appreciable effect on maize yield or plant development (table 58).

In the foregoing experiment K I the 20% threshold was significantly and considerably better than the 50% threshold. These results indicate that it may depend on the pattern of natural infestation whether both thresholds will or will not show a significant difference in maize yield and plant development. With sharply increasing infestations above the 50% level, it may be expected that both thresholds will show similar effects. With moderate infestations however, when the 50% threshold is hardly attained, a better performance of the 20% threshold may be anticipated (as shown by the results of the experiment K I). In this experiment only a small saving of insecticides was observed when using the 50% threshold. Moreover, because it is difficult to forecast a natural infestation pattern for *S. frugiperda* in Central America, the 20% threshold should be used.

5.1.3.2.3. Selective application

Irrespective of the applications being made to all whorls or to injured whorls only, the percentage of infested whorls remained nearly the same (fig. 37C). Selective treatment (to injured whorls only) increased the average number of applications by .5 to maintain the desired threshold, but the quantity of insecticides used was 2.6 times less than required by the application to all whorls.

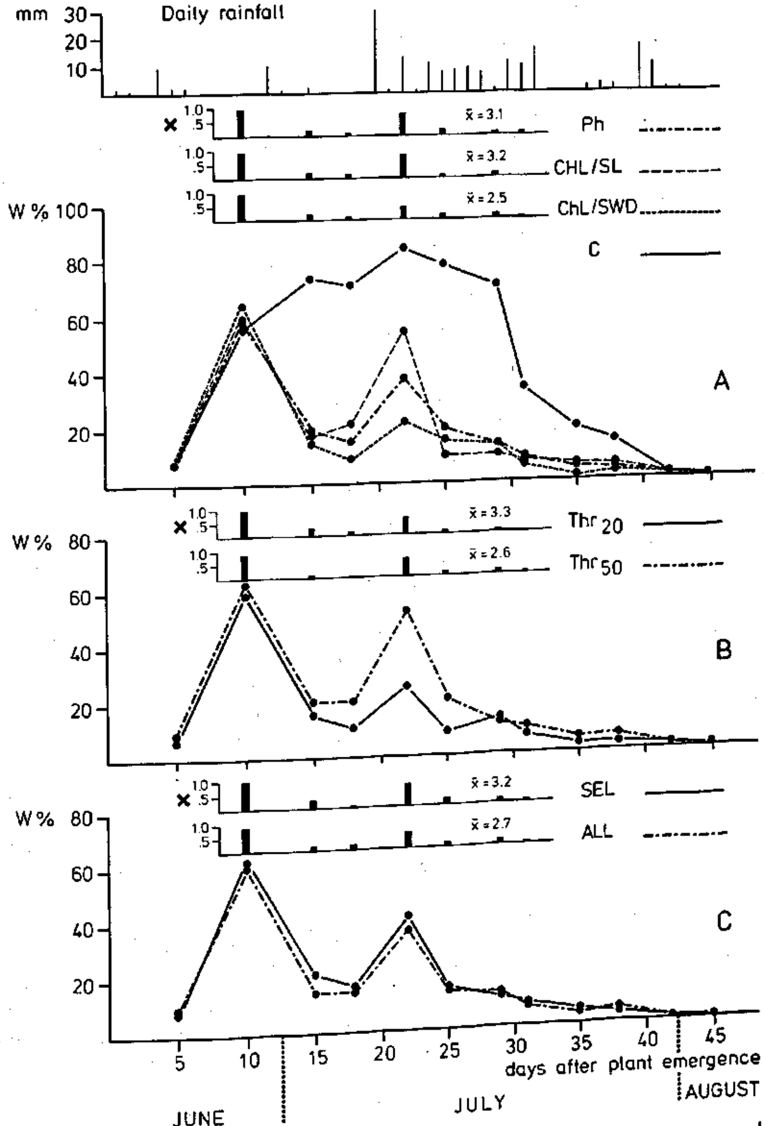


FIG. 37. Percentage of whorls injured (W) by S. frugiperda in maize and average number x of insecticide applications obtained by the use of
A. Various insecticide treatments (PH = phoxim; CHL/SL = chlorpyrifos-soil; CHL/SWD = chlorpyrifos-sawdust; C = control).
B. Economic thresholds of 20 and 50 per cent of infested plants (Thr_{20} and Thr_{50}).
C. Applications directed to all whorls (ALL) or to injured whorls only (SEL).

Because both methods were equally effective in controlling *S. frugiperda* but selective application saves a considerable amount of insecticide, the latter should be recommended.

However table 58 shows that the yield per ha was significantly lower (by 9% = 504 kg) using the selective application. As *S. frugiperda* injury was about the same for both treatments, the cause of this effect is uncertain. A possibility is *D. lineolata*. Although *D. lineolata* causes some whorl injury, it was not specifically considered as a criterion for the applications in this experiment. Also no evaluation of stalk injury by *D. lineolata* was made at harvest time. Treating injured whorls only, the others remained without protection. Thus a *D. lineolata* infestation might have taken place. Efforts should first be made to gain more information on why and how much of a yield increase will be obtained by protecting plants that do not show *S. frugiperda* injury, before the farmers, who are used to applying selectively, can be advised to change their practice.

5.1.4. *Soil applied to the whorl as a control method against S. frugiperda*

In a survey it appeared that 8% of the 200 farmers interviewed controlled *S. frugiperda* in maize by applying soil in each whorl or to injured whorls only. Seventeen per cent said they knew of the existence of this method but did not practice it. In two experiments the effect of this traditional practice of controlling *S. frugiperda* was investigated and the results compared with those of an untreated control and an insecticide treatment.

5.1.4.1. Material and methods (Exp. K III)

In the first experiment the maize hybrid B-666 was sown on May 27, 1977 in a randomized block design with 3 treatments and 4 replicates. Treatments consisted of 1. soil and 2. a chlorpyrifos-sawdust mixture (.14 l Lorsban 480E, mixed with 26 kg sawdust and 8 l water per ha), both applied by hand 21 and 31 days after plant emergence. An untreated control was added. Each plot consisted of 4 five-metre rows, 1 m apart, planting holes .7 m apart in the rows and 2 plants per plant hole. The 2 inner rows in each plot were sampled. On 21, 28, 35 and 42 days after plant emergence the number of plants and injured whorls were counted. Forty-nine days after plant emergence, the height of 3 consecutive plants in a row were measured. Grain yield could not be determined.

In the second experiment the maize hybrid X-105-A was sown on May 28, 1978 in a randomized block design with 3 treatments and 4 replicates. Treatments consisted of 1. soil and 2. granular phoxim (Volaton 2.5%, 10 kg ha^{-1}), both applied by hand 24 and 38 days after plant emergence. Each plot consisted of one maize row of 10 m, plant holes .4 m apart in the row, 2 plants per hole. Rows were 2.1 m apart and intercropped with 3 rows of beans. Twenty-two, 34 and 47 days after plant emergence the number of plants and number of injured whorls were counted. After harvesting the number of plants was counted and the grain yield (adjusted to 15% moisture) determined.

Statistical treatment consisted of an analysis of variance and of testing various contrasts among treatments. The percentage of injured whorls (100x) was tranformed by arcsin $\sqrt{x}$.

5.1.4.2. Results and discussion

In both experiments the insecticide treatments reduced *S. frugiperda* infestation drastically and significantly (table 59). The soil applications did not exert any control on *S. frugiperda*. On the contrary in the first experiment 35 and 42 days after plant emergence the soil treated plants were significantly more infested than the control, mainly due to a sharper decrease in the percentage of infested plants in the control that occurred between 21 and 28 days after plant emergence. Maybe the soil application impeded natural mortality, such as by predators, parasites or rain.

TABLE 59. Soil and insecticides applied to the maize whorl. The effect on whorl injury by *S. frugiperda*, yield and plant height of maize during two growing periods. Analysis of variance: F-values, significancies and means. (Exp. K III)

Source of variation	df	First growing period, 1977 maize hybrid B-666					First growing period 1978 maize hybrid X-105-A				
		S. frugiperda Percentage (100 x) injured whorls (arcsin $\sqrt{x}$) at date[1]				Plant height at 49 days	*S. frugiperda* Percentage (100 x) injured whorls (arcsin $\sqrt{x}$) at date[1]			Grain yield per	
		21	28	35	42		22	34	47	plot	plant
						F-values					
Block	3	1.79	.65	2.98	3.05	9.09*	.08	3.49^{+}	2.49	7.66*	.61
Treatment	2	2.13	90.7**	64.9**	46.6**	6.48*	.12	44.7**	15.4**	27.9**	4.91^{+}
Soil (S) vs. Control (C)	1	.15	3.56	4.48^{+}	7.64*	.38	.15	2.00	.01	.24	.13
Insecticide vs. S, C	1	4.12^{+}	178.**	125.**	85.5**	12.6*	.09	87.3**	30.7**	55.6**	9.67*
Error: V.C.	6	10.6	16.1	16.9	20.6	7.22	19.6	14.2	28.0	7.37	13.5
Total	11										
						means					
		percentage[2]				cm	percentage[2]			gram	
Grand mean		71.5	29.0	32.7	28.0	128.	59.5	33.2	21.8	6263	131.
										deviation from grand mean (%)	
Control		74	47	48	39	123	61	54	35	−10	−10
Soil		77	59	63	63	119	56	45	35	−13	−7
Insecticide		63	1	2	1	141	62	8	3	23	17
Insecticide used		Chlorpyrifos/sawdust mixture applied 21 and 31 days after plant emergence					Granular phoxim applied 24 and 38 days after plant emergence				

[1] Date = days after plant emergence.
[2] Backtransformed.

Plant height in the first experiment and grain yield in the second experiment increased significantly when insecticides were used. Phoxim caused some phytotoxicity with the concentrations used. In the second experiment the insecticide applications at midwhorl stage caused a decrease in the number of injured plants by about 50%. Yield per plot increased by 33 to 36% and yield per plant by 24 to 27% (table 59). In the planting system used this resulted in a yield increase of about 1000 kg ha^{-1}.

As a conclusion it may be stated that the soil treatment in these experiments did not exert any control of *S. frugiperda*. It also became apparent that chemical protection of moderately infested plants could increase yield significantly and considerably.

5.1.5. *Summary and conclusions*

The systemic insecticides mefosfolan and carbofuran increased yields more than could be expected considering the effect they have on *S. frugiperda*. These insecticides should however not be recommended for the stimulating effect they have on the maize yield, until the cause for this stimulation has been determined.

Applications of insecticide against *S. frugiperda* may increase injury by *D. lineolata*. This effect was observed when mefosfolan was applied at 15 and 30 days and when chlorpyrifos was applied at 15 days. These control actions created a healthier plant, i.e. more leaf area, which probably received a higher oviposition by *D. lineolata* (see chapter 3.1.). This higher infestation by *D. lineolata* was not controlled by the mefosfolan treatment and the early chlorpyrifos treatment missed the later borer infestation. In an experiment by SARMIENTO and CASANOVA (1975) insecticide treatments possibly caused a similar effect on *Diatraea saccharalis* infestations. They could not find a satisfactory explanation.

In one of the experiments the economic threshold of 20 per cent of whorls injured by *S. frugiperda* performed better than the 50 per cent level. It seems to depend on the rate of increase in the number of injured whorls whether the use of the 20 per cent level achieves better results. As infestation patterns cannot be forecasted, the 20 per cent economic threshold deserves preference over the 50 per cent level.

It does not make any difference to the level of infestation by *S. frugiperda* if plants are either cured of *S. frugiperda* injury (applications in injured whorls only) or if besides curing, injury is prevented (applications in all whorls). By using therapeutic treatments only, almost three times less insecticides were used, a small yield reduction however was observed that may have been caused by a *D. lineolata* infestation in the non-treated plants. The therapeutic method is favoured by the small farmer as it saves a considerable amount of insecticides. The practice is appropriate to his socio-economic conditions and should be investigated further.

By use of the chlorpyrifos-sawdust mixture the recommended insecticide concentrations can be reduced by one fifth without loss of control. Granular phoxim seemed effective. Investigations may show that the recommended concentration can be lowered. Soil, whorl-applied, a practice carried out by a small percentage of the farmers, did not show any control of *S. frugiperda* in two experiments (K III).

Yields were reduced more by infestations of *S. frugiperda*, which increased during whorl development (Exp. K I) than by infestations which started at a high level and decreased during whorl development (Exp. K II). This indicates the higher sensitivity of the plant to late whorl injury. This has also been observed in experiments G and H (chapter 4.2. and 4.3.). Plants are able to withstand considerable injury before midwhorl. If plant loss is the main effect of injury by *S. frugiperda* in the early whorl stage (as discussed in the introduction), then a higher plant density and thinning out the less vigorous plants at 2 to 3 weeks after plant emergence would make control of *S. frugiperda* unneccesary at this stage of plant development. Insecticide treatments during this early period would have to be made with the contaminating and costly sprays of liquid insecticides (plants are too small for whorl directed applications such as granules). These sprays could then be omitted, making full use of natural mortality factors such as rain, predators and parasites. After the midwhorl stage granules or insecticide baits can be applied selectively to the whorls. Besides controlling *S. frugiperda*, *D. lineolata* infestations (which occur now) will also be controlled. The strategy to control *S. frugiperda* and *D. lineolata* will be further discussed in chapter 6.

5.2. Biological control

5.2.1. *Introduction of parasites*

In general this component of integrated pest management has many advantages for the small farmer. The control of pests by introducing and establishing exotic parasites does not require significant efforts or costs from the peasant and does not contaminate the environment.

S. frugiperda

In 1975, Dr. F. D. Bennett[1] evaluated the possibilities of biological control of foodgrain pests in Nicaragua. He recommended among others the introduction of the egg parasite *Telenomus remus* Nixon (Hymenoptera: Scelionidae) for the control of *S. frugiperda* in maize and sorghum. This parasite would only have to compete for the eggs of *S. frugiperda* with *Chelonus* spp., which oviposits in eggs and completes the development in the host larvae. Natural parasitism by the egg parasite *Trichogramma* sp. is virtually absent. Parasitism by *T. remus* would provide control before *S. frugiperda* is able to cause any injury. This parasite, originating from India and New Guinea, has been introduced into several countries. In Barbados it was established succesfully and attacks over 80 per cent of the egg masses of *Spodoptera* spp. (Alam, 1978). It was introduced into Israel in 1969 for the control of *Spodoptera littoralis*. Gerling (1972) and Schwartz and Gerling (1974) reported on the biology and Gerling and Schwartz (1974) on

[1] Present director of the Commonwealth Institute of Biological Control (CIBC).

the host selection of the parasite. WOJCIK et al. (1976) found 11 Noctuid species and one Pyralid to be hosts, among them five *Spodoptera* species, *Heliothis zea* and *Feltia subterranea*, which all occur in Nicaragua.

In 1976, 1977 and 1978 parasites were obtained by Dr. F. D. BENNETT from CIBC in Trinidad and introduced into Nicaragua. Releases were made in 1977 and 1978 in the South Interior of Nicaragua (FAO/UNDP, 1980) but only one recovery was made of a parasitized egg mass of *S. frugiperda* at Camoapa and one from *S. exigua* at la Calera, Managua. In addition to Nicaragua the rearing and release of *T. remus* has also been carried out for a short time in El Salvador. In Nicaragua one of the main problems of the multiplication of the parasite was the absence of a developed program for rearing the host on an artificial diet. The availability of host egg masses of *S. frugiperda* for parasite rearing mostly depended on field collections.

D. lineolata

The three larval and larval-pupal parasites of *D. lineolata* found in Nicaragua had low levels of parasitism (chapter 3.4., table 33). The introduction was considered of the braconid *Apanteles flavipes* Cam. and the tachinids *Lixophaga diatraeae* T.T., the Peruvian strain of *Paratheresia claripalpis* Wulp. and possibly *Metagonistylum minense* T.T., into Nicaragua.

Apanteles flavipes was introduced[1] into Nicaragua in 1977 and 1978. The rearing of the parasite failed in Nicaragua, because only diapausing larvae of *D. lineolata* were available in which *A. flavipes* did not develop. ALAM et al. (1971) assumed that *A. flavipes* could not become established in the USA because of its inability to reproduce in hibernating *Diatraea*. However FUCHS et al. (1979) reported at least temporarily establishment of *A. flavipes* on *D. saccharalis* on sugarcane and maize in Texas, USA. BENNETT (1978, pers. communic.) suggests that *A. flavipes* will adapt and enter diapause within the diapausing larvae of *D. lineolata*. He considers the parasite of sufficient promise to persevere with its introduction into Nicaragua until extensive releases have been made.

GAVIRIA (1977) reported from Columbia (Northern part of Cauca valley) that the succesful adaptation of a Peruvian strain of *P. claripalpis* coupled with the hybrid vigour obtained from spontaneous crosses between native and introduced flies, resulted in an increased parasitism of 152% compared to the original level of parasitism in 1970 when the program was started. BENNETT (1978, pers. communic.) recommended checking the host suitability of the Nicaraguan strain of *D. lineolata* for this tachinid as some races of *P. claripalpis* do not develop well on *D. lineolata*. MCPHERSON and HENSLEY (1976) quoted SCARAMUZZA (1945) that *Lixophaga diatraeae* was collected from *D. lineolata* in Cuba. According to PSCHORN-WALCHER and BENNETT (1970) *L. diatraeae* develops satisfactorily on *D. lineolata* in the laboratory.

The Amazone fly, *Metagonistylum minense*, however does not develop well on *D. lineolata* and should therefore not be recommended for introduction, unless

[1] By F. D. BENNETT from CIBC, Trinidad and by J. D. GAVIRIA from Ingenio Riopaila Ltda., Columbia.

laboratory trials show otherwise (BENNETT, 1978, pers. communic.).

In Barbados the biological control of *Diatraea saccharalis* in sugarcane has been attempted since 1930. In 40 years, 15 introductions of parasites took place. Only *L. diatraeae* (after prolonged efforts) and *A. flavipes* became permanently established. Due to unexpectedly high parasitism by the latter, borer infestation of the sugarcane joints diminished from 15% in 1966 to less than 6% in 1970 (ALAM et al., 1971). The experience with *Lixophaga* in Barbados demonstrates the merits of persevering with a program of biological control over a prolonged period of time.

As control methods other than biological for *D. lineolata* appear to be rather difficult, the introduction and establishment of parasites, such as *A. flavipes*, the Peruvian strain of *P. claripalpis* and *L. diatraeae* in Nicaragua might keep *D. lineolata* below the level of economic injury in maize.

5.2.2. *Parasite inundation*

Inundative releases of *Trichogramma minutum* and *Paratheresia claripalpis* for control of *Diatraea saccharalis* in maize in Peru increased parasitism from zero to 16 per cent (GONZALEZ, 1968). Augmentation of parasites, such as *Trichogramma* sp. or the above mentioned parasites of *D. lineolata* would not be very practical for Nicaragua. The bulk of maize production is carried out by small farmers, who have their fields scattered over the hill sides. This makes the release area very large and the related costs, of constantly rearing the hosts and parasites high. Besides parasitism may be ineffective due to the low maize (host)/area ratio and parasitism on alternative hosts in interjacent pastures and wild vegetation.

5.2.3. *Microbial control*

The application of microbial insecticides (entomopathogens) to control *S. frugiperda* in maize has been carried out by several research workers with varying success. *Bacillus thuringiensis* Berliner was used by REVELO (1973) to control *S. frugiperda* and *D. saccharalis* in maize in Columbia. The success depended on temperature, exposure to ultra-violet radiation, the age of the insect population and on the formulation of the product. In field trials the fungus *Beauveria bassiana* (Balsamo) Vuillemin was ineffective against *S. frugiperda* and very sensitive to adverse environmental conditions (REVELO, 1973). Trials with *B. thuringiensis* against *S. frugiperda* in maize in Nicaragua did not give satisfactory results (MEDRANO , 1978; OBANDO and VAN HUIS, 1977, unpublished report). These biological insecticides have certain drawbacks for the small farmer. Firstly, *B. thuringiensis* has to be stored at low temperatures (refrigerator, although some wettable powders are claimed to have high thermal stability). Secondly, the products have to be applied with a knapsack sprayer, increasing application costs.

In addition to these pathogens other biological control agents have been evaluated. LANDAZABAL et al. (1973) applied the nematode *Neoaplectana carpocapsae* (Hough) against *S. frugiperda* in maize in Columbia. Larval populations were reduced drastically but only under conditions of high relative humidity.

5.3. Host plant resistance

In 1974 a collaborative breeding project was organized between CIMMYT, El Salvador and Nicaragua to develop germ plasm resistant to corn stunt transmitted by the leafhopper *Dalbulus maidis* (CIMMYT, 1979).

Nicaragua participates in the CIMMYT procedure by undertaking the research to improve the maize populations and to develop new varieties. Evaluations and selections for insect and disease resistance is carried out by CIMMYT in germ plasm pools at different stages of improvement in Mexico (CIMMYT, 1979). Plant populations are artificially infested with larvae of *S. frugiperda*, *Heliothis zea*, *Diatraea saccharalis* and *D. grandiosella* from cultures reared on artificial diet. More efficient rearing techniques for *D. lineolata* are developed. In the international progeny trials (250 progenies) each population is tested at five sites in different parts of the world. One of the characteristics tested is resistance to diseases and insects. From the results experimental varieties are identified and tested at 30 to 40 sites all over the world. (International Experimental Variety Trials – IEVT). Afterwards elite varieties are tested at 626 sites in 84 countries (Elite Experimental Variety Trials – EEVT). Nicaragua collaborates in maize testing at the IEVT as well as in the EEVT stage. The national program decides whether an elite experimental variety justifies demonstration on farmer's fields. According to the CIMMYT procedure, seed material with identified insect or disease resistance is only selected, when its agronomic qualities such as grain yield, plant height, absence of lodging, are acceptable.

In Nicaragua a resistance breeding program was initiated in 1976, in which material left idle in the CIMMYT selection procedure, but with resistance against *S. frugiperda*, stem borers and *Heliothis zea*, was utilized to obtain an early variety resistant to all these pests (Arguello and Lacayo, 1977). The genetic base was the Nic-Synt-2 population. At the same time 10 inland short-season varieties were checked for insect resistance. Unfortunately the program had to be discontinued in 1978 due to dismissal of the scientists concerned, following a political strike.

6. INTEGRATION OF CONTROL STRATEGIES (A SUMMARY)

6.1. GENERAL

Agriculture in Nicaragua and many other countries of Latin America can be divided in two sections. On the one hand there is a limited number of farmers with large land units on the most fertile soils, who use high technological inputs to produce cotton, coffee and sugar for the export market. On the other hand there is a very large group of small farmers with small land units usually on marginal soils, subject to various forms of land tenancy, who live at subsistence level and produce, almost without the use of any modern inputs, maize, beans and sorghum for the consumption market (WARNKEN, 1975). Many of these foodgrain farmers lack production facilities such as credit, technical assistance and marketing (chapter 1.1.). Rural development plans have been designed to remove these restrictions and to assure a better participation of this group in the national economy. The extent to which this succeeds will greatly determine how well a program of integrated pest management (IPM) can be implemented. IPM should therefore not be undertaken as an isolated effort (OECD, 1977).

The traditional agronomic practices of the small farmer and the lack of inputs, such as new varieties, fertilizers and pesticides were generally held responsible for the low yields. Therefore research stations developed a series of technological improvements for implementation by the small farmer. However since the growing conditions and the crop management at the research stations differ markedly from those on the average small farm this approach easily leads to failures, as in the Pueblo project in Mexico (CIMMYT, 1974). It is now commonly accepted that the peasant's method of farming under his specific socio-economic conditions should be given full consideration before any changes are proposed (WHYTE, 1977; HILDEBRAND, 1976; PERRIN, 1977; LITSINGER et al., 1980).

Within an IPM program the various control efforts should be undertaken on the basis of adequate knowledge of the damage that may be caused by the major pest species. This will allow for the calculation of economic thresholds. The use of these thresholds also requires the development of reliable methods of sampling. The different components to be used in IPM programmes include the following: the maximum use of natural mortality factors, the application of cultural control measures, the use of resistant varieties, the application of biological control i.e. the introduction and establishment of exotic natural enemies, the use of selective pesticides or the selective application of broad-spectrum pesticides.

Maize is the most important foodcrop of the small farmer in Central America. In Nicaragua some 200,000 ha of maize are sown annually, mainly in the first growing period (May-August; second: August-November). In Central America a well-developed IPM program for the crop was absent, because the research, almost exclusively concerned the evaluation of insecticides. In 1974 a joint IPM project was started in foodgrains by FAO, UNDP and the Nicaraguan Agricultural Research Institute INTA. The author was the FAO entomologist for this project and collected the information for this publication from 1974 to 1979. To develop an IPM program for maize an experimental approach was followed, taking into consideration the above elements. Relevant literature has been extensively reviewed.

Only two insect pests of the noxious arthropods were constantly found in all parts of the country viz. the whorl defoliator *Spodoptera frugiperda* (J. E. Smith) and the maize stalk borer *Diatraea lineolata* (Wlk.). Several aspects of crop losses by these moth species were assessed at the research station La Calera, Managua. The ecology of these pests was studied at a small farm at St. Lucia, situated on the border of the Interior South and the Interior North, both important maize producing regions.

6.2. CROP LOSS ASSESSMENT AND ECONOMIC THRESHOLD

S. frugiperda

S. frugiperda is considered as one of the major pests of maize in Latin America (ORTEGA, 1974; CHIANG, 1977). In our experiments loss of yield amounted to between 30 and 60 per cent (chapter 4.1., 4.3., 5.1.). Although chemical treatment of the whorl not only controls *S. frugiperda*, but also to some extent *D. lineolata*, the results of several experiments (chapter 4.4. and 5.1.) indicated that the damage caused by *S. frugiperda* is more important and can therefore serve as the basis for establishing an overall economic threshold.

The percentage of whorls injured by *S. frugiperda* is generally taken as a criterion for the threshold (SILGUERO, 1976; CLAVIJO, 1978; SARMIENTO and CASANOVA, 1975; OBANDO, 1976; YOUNG and GROSS, 1975). In Central America an empirically established threshold of 20 per cent of injured whorls is generally accepted by the extension services. This level was confirmed experimentally (chapter 5.1.).

This threshold is generally considered valid from plant emergence until tasseling. The results of our experiments (chapter 4.3. and 5.1.) and those by others (ALVARADO, 1975a and 1977b; OBANDO, 1976) indicated that the yield increase achieved because *S. frugiperda* was controlled at an early growth stage of maize, was a result of the prevention of plant loss (tunneling larvae feed on the meristematic tissue of the bud and causes 'dead heart') and not because the yield per plant was higher. An artificial defoliation experiment (chapter 4.2.) proved that the plant suffered very little in the early stages from whorl injury. Defoliation experiments in maize designed for other purposes and carried out in other areas confirmed this result (BROWN and MOHAMED, 1972; HICKS et al., 1977; CLONINGER et al., 1974; CROOKSTON and HICKS, 1978; CONDE, 1976).

'Dead heart' can be caused not only by *S. frugiperda* but also by *D. lineolata* and *Erwinia* sp., a bacterial disease. Plant losses caused by these agents or by soil insects (chapter 2.2.), can be compensated for by using higher plant densities. Two to three weeks after plant emergence weak or injured plants can be thinned and removed from the field. Withholding chemical treatment during this early growth stage allows full scope for the action of natural mortality factors (chapter 6.3.).

After thinning, the economic threshold of 20 per cent of injured whorls should be used; climatical conditions should also be considered. During drought the control of *S. frugiperda* did not increase yields, probably because the increased transpiring leaf area of treated plants enhanced the moisture stress (chapter 4.3.).

An easy way for the small farmer to monitor the level of a pest attack in his field is by counting the number of injured whorls at five random sampling sites, each composed of 20 consecutive plants in a row, this figure can be compared with the economic threshold.

D. lineolata

Information on yield losses by *D. lineolata* in maize was not available. One of the main difficulties in assessing the crop loss is that the infestation of *S. frugiperda* largely coincides with that of the borer. The separation of both types of damage and their interaction is extremely difficult. An example of such an interaction is that the control of *S. frugiperda* may cause an increased infestation by *D. lineolata* (chapter 5.1.), possibly by oviposition of the borer on the enlarged leaf area of treated plants (oviposition on maize up to silking was proportional to the green leaf area of the plant; chapter 3.1.).

The damage was therefore assessed by artificially infesting maize plants in cages (about 40 per cage) (chapter 4.4.). Two independent statistical methods were used: an analysis of variance per plot (cage) and a multiple correlation and regression analysis per plant. The analysis on a per plant base was complicated by the effect of the plant variability on the survival of the larvae and the distribution of the larvae on the stalk. With both methods the loss of yield found was similar and ranged from 3 to 6 per cent per borer per plant for both the infestation at whorl and at silking stage. In the investigation into the importance of the feeding site, the plant appeared to be most sensitive to injury of the lowest internodes.

The injury by *D. lineolata* can be evaluated from maize stalks, the leaves of which are stripped at harvest, by counting the number of perforations or injured internodes. To estimate borer presence the stalk should be dissected and larvae, pupae and pupal skins counted. During the first growing period of 1978 extension workers sampled maize stalks at harvest for *D. lineolata* injury from fields in different parts of Nicaragua. The level of injury was generally low and the loss of yield in most fields was less than three per cent (chapter 4.4.).

In addition to the generally low levels of infestation it should be recognized that:

1. *D. lineolata* is either unknown to the farmer or is not considered by him to be a pest, because the insect, the injury or the damage is hardly perceptible, therefore his readiness to control this pest is certainly low;

2. the larva having left the whorl and penetrated into the stalk, is well-protected against insecticides, therefore chemical control will only be effective against early instar larvae;
3. the correct timing of insecticide applications is difficult because borer generations overlap;
4. an economic threshold has to be based on either the number of egg masses or on leaf injury; egg masses are small (an average of 2 eggs per mass, chapter 3.1.) and therefore difficult to monitor, whereas the injury is hardly distinguishable from that of *S. frugiperda* (chapter 2.2.);
5. because the main oviposition takes place at tasseling (chapter 3.1.), application of insecticides by spraying seems obvious. However these sprays are indiscriminate (chapter 6.4.), not effective (chapter 5.1.) and need expensive spraying equipment.

Therefore chemical control of the borer is generally not justified. The fact that insecticides used against *S. frugiperda* will also partly control *D. lineolata*, should not be a motive to apply them. However when pesticides are evaluated for the control of *S. frugiperda* their effect on *D. lineolata* should possibly be taken into account. Other, more appropriate control methods for the borer will be discussed in the next chapters.

6.3. NATURAL MORTALITY FACTORS

In the mainly unsprayed foodgrain ecosystems (chapter 1.1.) a rich beneficial fauna is present. For *S. frugiperda* a large number of predator species, 16 parasite species and 3 entomopathogen species were identified and for *D. lineolata* 4 parasite species and 4 pathogen species (table 33). However these natural enemies are often not able to keep the pests below the level of economic injury. This especially applies to *S. frugiperda*. Therefore technical means of control (pesticides in particular) are important. However, to conserve the populations of natural enemies chemical control should be judiciously used in Central America (QUEZADA, 1973), otherwise maize cultivation will become increasingly dependent on insecticides to boost production (JAVIER and PERALTA, 1975a, b).

During early plant development liquid insecticides are normally sprayed to control *S. frugiperda*, because the whorl is too small to apply granules or insecticide baits. These sprays however are indiscriminate and may severely reduce the predator and parasite populations which occur during an early growth stage. As such are of importance:
1. The braconid parasites (mainly *Rogas laphygmae* and *Chelonus insularis*) which may kill up to 30 per cent of the (collected) *S. frugiperda* larvae (chapter 3.4.). The parasites kill the host at about the fourth larval instar and thus prevent serious whorl injury. For this reason RYDER and PULGAR (1969) recommended that early applications of insecticides should be avoided.
2. The egg parasite *Trichogramma pretiosum* reduced the number of eggs of *D.*

lineolata by at least half (chapter 3.4.). An early application of insecticides will prevent the build-up of the parasite populations.

3. Spiders were most frequently found at the early growth stage of the maize crop. Several unidentified species were found that preyed on *S. frugiperda* larvae (chapter 3.2. and 3.3.).
4. The earwig *Doru taeniatum*, an insect commonly found on maize in Central America (PAINTER, 1955; ESTRADA, 1960), preys on the egg masses and first three larval instars of *S. frugiperda* (chapter 3.4.). In cage studies *S. frugiperda* infestations were reduced by half (chapter 3.4.). The earwig is most frequently found during early plant growth and populations are most numerous in the second growing period (chapter 3.2. and 3.3.). Another earwig species *Labidura riparia* was found to be abundant in maize fields in the Pacific plain. The predacious habits of the earwig on lepidopterous larvae have been described by a number of research workers (chapter 3.4.).

Withholding chemical treatments during early plant growth, as discussed in chapter 6.2., will preserve these natural enemies. In addition to these natural mortality factors, heavy rainfall reduces *S. frugiperda* populations of early instar larvae (chapter 3.4.).

After the midwhorl stage the most important natural causes of mortality of *S. frugiperda* are the tachinids (mainly *Lespesia archippivora*), the mermithid nematode *Hexamermis* sp. and several predator species (e.g. *Polystes* wasps). The parasites were able to parasitize up to 50 and 30 per cent respectively of the (collected) larvae (chapter 3.4.). As they kill the host in the last larval instar or in its pupal stage, damage is not prevented. Since the parasites reduce population growth of following generations they should be conserved as much as possible by the rational and selective use of pesticides.

6.4. PESTICIDES AND THEIR SELECTIVE USAGE

Selective chemical control reduces ecological disruption, takes into account the delicate socio-economic condition of the small farmer and minimizes the risk of poisoning. The number of insecticide applications against *S. frugiperda* can be kept low by avoiding treatments during early plant growth and at later stages of plant development by using the economic threshold of 20 per cent of injured whorls (chapter 6.2.). The insecticides should only be applied to the part of the plant that needs it, i.e. by directing the applications towards the whorl or by only treating the injured whorls. This last practice is favoured by the small farmer as it saves a considerable amount of insecticide, but it needs further investigation (chapter 5.1.).

The formulation under which the insecticides are used can be of great importance. The sprays of liquid insecticides are indiscriminate and may disrupt parasitism and predation. Granules or insecticide baits seem less harmful. Moreover they can be applied without expensive application equipment. Granules can easily be applied by means of a jar with a perforated lid. Insecticide-sawdust mixtures can also be applied by hand using plastic bags as gloves.

The lowest effective concentrations of preferably low toxic insecticides should be used. For example chlorpyrifos, when mixed with sawdust proved effective against *S. frugiperda* at one fifth of the concentration, that is commercially recommended (chapter 5.1.). Even a few granules of phoxim per whorl suffice. The traditional farmer's practice of applying soil to whorls injured by *S. frugiperda* proved ineffective as control measure (chapter 5.1.).

Carbofuran, a systemic insecticide and nematicide has been recommended for soil treatment to control *Dalbulus maidis*, a cicadellid which transmits corn stunt spiroplasma (ANAYA and DIAZ, 1974). This disease may cause much damage in the second growing period, particularly in the Pacific plain. Soil treatment with carbofuran has also been used to control early *S. frugiperda* infestations in maize. Although yield did increase, this could not be attributed to the control of *S. frugiperda* or *D. lineolata* (chapter 5.1.). DAYNARD et al. (1975) suggested that the cause of the higher yield be first investigated before carbofuran should be recommended. Recently carbofuran has been recommended to control *Phyllophaga* spp., a soil pest of beans (beans are either intercropped or grown in crop rotation with maize). However, it should be realized that the application of carbofuran to the soil annihilates *Hexamermis* sp., the parasitic nematode of *S. frugiperda*.

The biological control agents such as *Bacillus thuringiensis*, the fungus *Beauveria bassiana* and the nematode *Neoaplectana carpocapsae* have been used against *S. frugiperda* with varying success, the effectiveness is greatly dependent on environmental conditions (chapter 5.2.).

Generally in Central America the pesticide marketing system is defective: 'powders' without warning or instruction labels are sold in drugstores. An IPM program should consider this situation.

In rural development plans high yields were anticipated from new technological inputs, such as new varieties, fertilizer and pesticides. As these inputs have to be obtained with credit, they are a high socio-economic risk for the small farmer. Firstly because these inputs must be combined with the necessary supporting production factors (credit, technical assistance, etc.) which are either absent or insufficient, and secondly yields may be lost because of drought. Research is needed to ascertain how these inputs individually and in combination with each other affect the yield under small farmer's conditions. The relevance of such research is demonstrated by the fact that the application of NPK fertilizer without controlling *S. frugiperda* hardly stimulated yields, probably partly due to increased damage by *S. frugiperda* and *D. lineolata*. Chemical whorl protection alone resulted in a yield increase of 24 per cent, but in combination with NPK fertilizer the yield increased by 60 per cent (chapter 4.1.).

6.5. CULTURAL CONTROL

Cultural control is a very useful IPM component for the small farmer, it hardly requires extra expenses. In some cases encouragement of the normal routine, such as maize-bean intercropping or stubble destruction is sufficient. In other cases only small changes in the farmer's practice may reduce pest incidence. For some practices, such as synchronization of sowing dates or stalk and stubble destruction, a cooperative effort of a community is necessary to be effective.

Maize-bean intercropping is common practice in Latin America (FRANCIS et al., 1978). For this cropping system ALTIERI et al. (1978) reported a reduced infestation of *Diabrotica balteata*, a common pest in maize and beans in Columbia. In our studies (chapter 3.2.) *S. frugiperda* attacks on maize were reduced by 20 to 30 per cent with bean intercropping. The bean plants probably trapped wind-dispersed first instar larvae, preventing the larvae from infesting new maize plants. The optimal use of this control effect merits further investigation. In one of the maize varieties intercropped with beans *D. lineolata* injury was reduced by 30 to 60 per cent, probably because of a lower oviposition (chapter 3.1. and 3.2.). Bean intercropping significantly increased the incidence of spiders on maize. In addition to a reduced pest incidence in maize-bean intercropping systems a number of agronomic, socio-economic and nutritional benefits can be added (chapter 3.2.). Only monocultures were used in the demonstration plots for the small farmer, showing the 'technological packages' (chapter 1.). Therefore a revaluation of these 'packages' is needed.

ALTIERI et al. (1977) demonstrated that several grass weeds, mainly *Eleusine* sp. and *Leptochloa* sp., reduced the incidence of the leafhopper *Empoasca kraemeri* on beans in Columbia. *Eleusine indica* and *Digitaria* sp. were frequently occurring weeds in maize fields in Nicaragua. They may carry a large number of *S. frugiperda* larvae, which probably as first instar larvae, have been wind dispersed from maize. Oviposition by *S. frugiperda* on maize was higher in plots with weeds than in weeded plots (chapter 3.3.). The high number of larvae in weeds may be a potential threat to maize. As leaf contact between maize and weeds is probably necessary for migration of the larvae towards maize, this should be prevented by weeding in strips on both sides of the maize row and leaving a band of weeds between the row as scource of food. The larvae in weeds were heavily parasitized by *Lespesia archippivora*. We found no beneficial effects of weeds on the pest incidence in maize. Grain yield was considerably reduced (chapter 3.3.; NIETO et al., 1968). For these reasons regular and thorough weeding is to be recommended; maize-bean intercropping smothers the growing of weeds.

Destruction of maize and sorghum stalks after harvest is an important method of reducing populations of diapausing larvae (chapter 2.2.) in the dry season. Cattle feed on the stalks and the remnants are burned in April-May. The fire passes quickly over the field, if there are enough stalks and provided a strong wind is blowing; if there are less stalks they should be raked into heaps before burning. In this way 50 to 70 per cent of the diapausing larvae can be killed (VAN HUIS, 1977).

The sowing date largely depends on the climatic conditions. In the first growing period many farmers sow in dry soil and germination starts with the first rain. The few maize fields that were sown late generally suffered greater damage by *S. frugiperda*. Late sowing should be avoided.

6.6. Biological and varietal control

The introduction and establishment of biological control agents as well as the use of resistant varieties requires limited efforts from both the small farmer and the extension services and therefore are appropriate IPM components to lower the pest attack, particularly under Central American farming conditions.

The introduction of the egg parasite *Telenomus remus* to control *S. frugiperda* might be promising, notwithstanding the fact that releases made in Nicaragua from 1976 to 1978 did not result in the establishment of the parasite. This may be attributed to the low frequency of the releases (chapter 5.2.). For *D. lineolata* the introduction of the braconid *Apanteles flavipes* and the tachinids *Paratheresia claripalpis* (Peruvian strain) and *Lixophaga diatraeae* should be considered (chapter 5.2.). The introduction of parasites would be greatly facilitated by rearing the hosts on an artificial diet. When deciding on this method the availability of rearing facilities and trained personnel, which in Nicaragua was insufficient, should be carefully considered. These facilities can also be used for a program on resistance breeding.

Due to the fact that maize and sorghum fields are scattered over the hills the inundative releases of parasites, such as *Trichogramma* sp. against *D. lineolata*, seem inefficient (chapter 5.2.).

Breeding programmes for pest resistance in maize should aim primarily at varieties resistant or tolerant to *S. frugiperda*, but maize stalk borers and cob feeders should also be considered. The resistant material already identified but left idle in the CIMMYT selections should be used in national or Central American programmes (chapter 5.3.).

6.7. Development and implementation of integrated pest management

The pest problems in foodgrains throughout the Central American region are very similar. The development of a comprehensive IPM program is hampered by the limited financial and professional resources of the national research institutes. These constraints could be alleviated if Central American countries would cooperate by dividing research tasks (concerning IPM components or pest species) (see also FAO/UNEP, 1975).

The development of an IPM program does not necessarily need to be preceded by a large amount of local research (Brader, 1980). The cheapest way of obtaining a first set of control recommendations is by carefully evaluating the information that is available locally and abroad. In this way the guideline for IPM in foodgrains in Nicaragua was edited (MAG/FAO/PNUD, 1976), it fulfilled a need for the whole of Central America. However such guidelines should be revalued regularly to incorporate new research data or insights. In an IPM program the regular evaluation of progress will be an important feed-back mechanism to improve the strategy. For instance 80 per cent of the number of insecticide applications recommended by extensionists in Nicaragua during 1978 were unnecessary. This indicates the need for better training.

As shown in this publication factors such as cropping systems, weed management, fertilizer and irrigation affect the pest status. Therefore IPM should be a structural part of an overall crop strategy, in which all disciplines of agricultural research should cooperate.

Traditional control practices should be evaluated and an insight should be gained into agronomic practices, pest knowledge, risk perception and the socio-economic background of the peasant. Such information can be acquired by simple inquiries, conducted by census institutions or the extension service (LITSINGER et al., 1980). Because of the great differences between research stations and the average small farm with regard to soil type, cropping system, use of inputs and crop management, new and advanced techniques should be evaluated when applied by the small farmer in his field. If he adopts the technique this is the highest evaluation (WAUGH, 1975).

To serve the farmer with timely and relevant recommendations it must be known which pest attacks when, where and at which level. Therefore in Nicaragua in 1978 pest information from different parts of the country was regularly collected in a National Pest Warning and Recommendation System, managed by a national extension entomologist. Extension workers filled in phytosanitary reports on pest incidence; simple insect or injury counts were included. Based on such information research priorities can be adjusted. The outline of this approach is presented in diagram 1 (chapter 1.1.).

A prerequisite for both the development and the implementation of an IPM program for the small farmer is an effective cooperation between research and extension. This especially applies to those IPM components that require a great deal of participation from the extension service. Considering the fact that most maize-growing farmers live at a minimum subsistance level and face a magnitude of problems to raise their production, the research program on IPM should be regularly evaluated to prevent alienation from the realities of the small farmer's practice.

The research reported in this document was inspired by the needs of the small farmer and will hopefully contribute to his well-being.

ABSTRACT

Maize, the main food crop in Nicaragua, is produced by a large group of small landowners, who farm under constraints of land tenure, marginal soils, poor infrastructure and inadequate production services (credit, technical assistance, marketing). Rural development plans, designed to raise the peasant above his low subsistence level, encourage the use of new varieties, fertilizer and pesticides to increase the low yields. However, as pesticides can have severe health, socio-economical and ecological implications, particularly for the small farmer, they should be used judiciously. This is attempted by a program of integrated pest management.

Among the destructive maize insects two moth species, viz. the whorl defoliator *Spodoptera frugiperda* and the stalk borer *Diatraea lineolata*, are the most important, but a well-considered control strategy is lacking. An experimental approach and an extensive literature review aimed at developing an integrated pest management program, taking into consideration that the biophysical and socio-economical conditions, and the agronomic practices of the small farmer often differ greatly from those at research stations.

In various experiments *S. frugiperda* reduced yields by 30 to 60 per cent. However during the two to three weeks after emergence, plants proved to be almost insensitive to whorl injury by either *S. frugiperda* or artificial defoliation. The reason for the reported losses of yield as a result of damage at this stage of development is because plants are eliminated by larvae feeding on the meristematic tissue of the bud. This loss can be compensated for by sowing at higher densities and thinning the infested and least vigorous plants two to three weeks after emergence. Therefore chemical control during early plant development can generally be avoided, giving full scope to natural mortality factors. These are for *S. frugiperda* braconid parasites, mainly *Rogas laphygmae* and *Chelonus insularis*, the predacious earwig *Doru taeniatum* and heavy rainfall, and for *D. lineolata* the egg parasite *Trichogramma pretiosum*. During later growth stages of maize *S. frugiperda* is heavily attacked by tachinids, mainly *Lespesia archippivora*, the parasitic nematode *Hexamermis* sp. and several species of insect predators.

These natural enemies however, are often not able to keep the pest below the level of economic injury. Control measures should be taken when 20 per cent of the whorls are injured by *S. frugiperda*. To preserve the beneficial fauna, the spraying of liquid insecticides should be avoided and granules or insecticide baits (e.g. mixtures with sawdust) should be applied instead, at low concentrations, to the whorls or to the injured whorls only (the latter therapeutic method, favoured by the small farmer, seems promising). To preserve the parasitic nematode of *S. frugiperda* soil treatments with insecticides which are also nematicides should be prevented.

No information was available of the damage to maize by *D. lineolata*. The

assessment of field crop losses by the borer is complicated, as the infestation coincides with that of *S. frugiperda* and the separation of both types of damage is extremely difficult. The control of *S. frugiperda* for example, can cause a heavier attack of *D. lineolata*, possibly by oviposition of the moth on the enlarged leaf area of treated plants (oviposition by *D. lineolata* on maize up to silking, was proportional to the green leaf area). Therefore maize was artificially infested in cages. Results were statistically analysed by two independent methods: per cage and per plant. Yield losses ranged between three and six per cent per borer per plant. The plant was most sensitive to injury of the lowest internodes. Chemical control of *D. lineolata* seems not to be justified because 1. field infestation is generally low, 2. egg masses are small and too inconspicuous for easy pest scouting and 3. insecticide applications are mostly ineffective. Therefore other control methods need to be emphasized such as stalk and stubble burning in the dry season.

Droughts are frequent in Nicaragua and under this soil moisture stress the control of *S. frugiperda* did not increase yields. The application of NPK fertilizer stimulated the attack by *S. frugiperda* and *D. lineolata*. Yield was only increased by fertilizer use, when combined with chemical protection of the whorl.

Maize-bean intercropping is common practice in Latin America and has many agronomic and socio-economic advantages for the small farmer. It lowers the injury by both *S. frugiperda* and *D. lineolata* when compared with a monoculture. Less plants were colonized by first instar larvae of *S. frugiperda*, as the larvae, when dispersed by the wind, are probably trapped by bean plants; oviposition by *D. lineolata* is probably reduced.

Grass weeds, mainly *Digitaria* sp. and *Eleusine indica*, may contain high numbers of *S. frugiperda* larvae forming a potential threat to maize. Oviposition on maize was significantly larger in plots with weeds than in weeded plots.

The introduction of exotic parasites should be considered i.e. for *S. frugiperda* the egg parasite *Telenomus remus*, and for *D. lineolata* the braconid *Apanteles flavipes*, and the tachinids *Paratheresia claripalpis* (Peruvian strain) and *Lixophaga diatraeae*. In the Central American region a resistance breeding program in maize should be established, that concentrates on *S. frugiperda*, utilizing the identified resistant material of CIMMYT.

Also for the development of other integrated pest management methods the Central American countries could greatly benefit from an interinstitutional coordination of efforts. An integrated pest management program is best adapted to the small farmer's needs if it is a part of an interdisciplinary crop strategy and if research and extension closely cooperate.

RESUMEN

En Nicaragua el maíz, principal cultivo de consumo interno, es cultivado por un sector numeroso de pequeños agricultores bajo limitaciones de tenencia de tierra, suelos de baja productividad, infraestructura pobre y servicios agrícolas ineficáces (crédito, asistencia técnica y comercialización). En los proyectos de desarrollo rural, concebidos para elevar los niveles de subsistencia del campesinado, se ha promovido, además de la introducción de nuevas variedades, el uso de pesticidas y fertilizantes. Respecto de los pesticidas hay que observar que su uso puede tener serias consecuencias para la salud humana (intoxicaciones) y severas implicaciones socio-económicas y ecológicas. Todo esto indica que se les debe usar juiciosamente, lo cual forma parte de las tareas del manejo integrado de plagas. En la introducción y desarrollo de tecnologías se deben considerar los aspectos socio-económicos, las condiciones biofísicas y las prácticas agronómicas bajo las cuales produce el agricultor, ya que éstas son, muchas veces, muy diferentes de las condiciones de las estaciones experimentales.

Entre los insectos nocivos, dos especies de lepidópteros son los más importantes: el 'cogollero', *Spodoptera frugiperda*, y el 'barrenador' *Diatraea lineolata*. Sin embargo, no existe una estrategia bien planificada para su control. A fin de desarrollar un programa de manejo integrado de plagas en el cultivo del maíz de los pequeños agricultores, se realizaron diversos experimentos. La literatura sobre el tema fué también ampliamente revisada.

Los resultados de varios experimentos demuestran que el ataque de *S. frugiperda* redujo el rendimiento de 30 a 60 porciento. Sin embargo, las plantas a penas se mostraron sensibles al daño del cogollo causado tanto por *S. frugiperda*, como por su defoliación artificial antes desde la 2ª a la 3ª semana después de la emergencia. Las pérdidas en rendimiento durante ese período, que a menudo se reportan, se deben principalmente a la eliminación de plántulas por ataque de larvas que barrenan y destruyen el punto de crecimiento. Pérdidas que pueden ser compensadas aumentando la densidad de siembra y raleando las plantas atacadas y menos vigorosas desde la 2ª a la 3ª semana después de la emergencia; con lo cual se puede evitar el control químico durante el estadio de crecimiento temprano, dando así amplia oportunidad de acción a factores naturales de mortalidad. Estos factores de mortalidad son: para *S. frugiperda*, los parásitos bracónidos (principalmente *Rogas laphygmae* y *Chelonus insularis)*, la 'tijereta' depredadora *Doru taeniatum* y las lluvias intensas. Para *D. lineolata* es el parásito ovífago *Trichogramma pretiosum*. Durante estadios de crecimiento más tardíos de la planta, *S. frugiperda* es fuertemente atacada por parásitos tachínidos, principalmente *Lespesia archippivora*, el parásito nemátodo *Hexamermis* sp. y varias especies de depredadores.

Sin embargo, estos enemigos naturales no son capaces de mantener la plaga por debajo del nivel de daño económico. Las medidas de control se deben tomar cuando el 20 porciento de los cogollos están dañados por *S. frugiperda*. Para preservar la fauna benéfica se debe evitar la aspersión con pesticidas líquidos y,

en su lugar, aplicar insecticidas granulados o cebos de insecticidas (por ejemplo, mezclas con aserrín), dirigidos a los cogollos o solamente a los cogollos dañados (este último método, preferido por los agricultores, parece promisorio). Para preservar el nemátodo parásito de *S. frugiperda* se deben evitar las aplicaciones de pesticidas al suelo que tienen acción nematicida.

En la evaluación de pérdidas del cultivo en el campo, causadas por *D. lineolata*, interfieren los daños originados por *S. frugiperda*. Por ejemplo, el control de *S. frugiperda* puede intensificar el ataque de *D. lineolata*, debido posiblemente a la oviposición de la polilla en el área foliar incrementada de las plantas tratadas (la oviposición de *D. lineolata* en el maíz fué proporcional al área foliar verde, hasta la fase de crecimiento en que la planta poliniza). Por ello, se infestó maíz artificialmente en jaulas; los resultados fueron analizados estadisticamente por métodos independientes: por jaula y por planta. Las pérdidas en rendimiento variaron entre 3 y 6 porciento por barrenador, por planta. La planta fué más sensible al daño en los internudos inferiores.

El control químico de *D. lineolata* no parece justificado debido a que: 1. las infestaciones de campo son generalmente bajas, 2. las masas de huevos son pequeñas y poco visibles para un muestreo fácil, 3. las aplicaciones de insecticidas son, la mayoría de las veces, inefectivas. Por eso, es necesario enfatizar otros métodos de control; como es la destruccíon de rastrojos en la estación seca.

Las sequías son frecuentes en Nicaragua. Bajo estas condiciones de déficit de humedad del suelo, el control de *S. frugiperda* no aumentó el rendimiento. La fertilización completa (N-P-K) elevó el nivel de ataque de *S. frugiperda* y *D. lineolata*. El rendimiento se incrementó solamente cuando la fertilización fué acompañada de protección química del cogollo.

El sistema de cultivo maíz-frijol intercalados es una práctica muy común en Latino América y tiene muchas ventajas agronómicas y socio-económicas para el pequeño agricultor, respecto del monocultivo. Además, reduce los daños causados tanto por *S. frugiperda* como por *D. lineolata*. Así, para *S. frugiperda* el número de plantas colonizadas por larvas del primer estadio fue menor, debido probablemente a que al ser dispersadas las larvas por el viento son atrapadas por las plantas de frijol. En el caso de *D. lineolata* la oviposición pareció disminuir.

Las malezas de gramíneas, principalmente *Digitaria* sp. y *Eleusine indica*, pueden contener altas cantidades de larvas de *S. frugiperda*, constituyendo una amenaza potencial para el maíz. La oviposición de *S. frugiperda* en el maíz fué mucho más alta en las parcelas con malezas que en parcelas desmalezadas.

Se debe considerar la introducción de parásitos exóticos: el parásito ovífago *Telemonus remus* para *S. frugiperda* y el bracónido *Apanteles flavipes* y los tachínidos *Paratheresia claripalpis* (raza peruviana) y *Lixophaga diatraeae* para *D. lineolata*. En los países centroamericanos se debería intentar, en cooperación con el CIMMYT, el establecimiento de un programa de mejoramiento de maíz, para obtener variedades resistentes a *S. frugiperda*.

La coordinación inter-institutional de los esfuerzos de todos las países centroamericanos sería muy beneficiosa para el desarrollo eficaz de otros métodos de manejo integrado de plagas. Un programa de manejo integrado de plagas se adapta mejor a las necesidades de los pequeños agricultores cuando es parte de una estrategia interdisciplinaria de cultivo y si la investigación y la extensión cooperan estrechamente.

SAMENVATTING

Mais, het belangrijkste voedselgewas in Nicaragua, wordt geteeld door een grote groep van kleine boeren op percelen van gemiddeld twee ha marginale grond, terwijl nauwelijks gebruik gemaakt wordt van moderne technologie. Krediet en voorlichting kunnen moeilijk worden verkregen en de marktprijs is instabiel. Hierdoor leeft een groot deel van de plattelandsbevolking onder het bestaansminimum. Ontwikkelingsplannen worden gemaakt om deze groep beter te laten deelnemen aan de national economie. Het gebruik van nieuwe variëteiten, bemesting en insecticiden wordt gestimuleerd om de lage opbrengsten te verhogen. Bij het gebruik van insecticiden moet men speciaal wat de kleine boer betreft bedenken, dat het ernstige sociaal-economische en oecologische gevolgen kan hebben en dat het vergiftigingsrisico's met zich meebrengt. Deze problemen kunnen worden ondervangen, wanneer de insecticiden weloverwogen worden gebruikt. Dit wordt nagestreefd bij een geïntegreerde bestrijding van plagen.

Onder de schadelijke maisarthropoden zijn vooral twee lepidopteren van belang, nl. *Spodoptera frugiperda*, die de bladkrans (de nog niet volledig ontwikkelde bladeren aan de top van de plant) vreet, en de stengelboorder *Diatraea lineolata*. Aan de hand van een aantal experimenten en een uitgebreide literatuurstudie is getracht een geïntegreerd bestrijdingsschema te ontwerpen, rekening houdend met het feit dat de biofysische en de oecologische omstandigheden van de kleine boer evenals zijn teeltmaatregelen dikwijls zeer verschillend zijn van die van de onderzoekstations.

S. frugiperda heeft de opbrengsten in onze experimenten met 30 tot 60 procent verminderd. Het bleek dat de plant gedurende de eerste twee tot drie weken nauwelijks gevoelig is voor bladkransbeschadiging teweeggebracht door zowel *S. frugiperda* vreterij als door kunstmatige ontbladering. De gerapporteerde opbrengstverhogingen door chemische bestrijding van *S. frugiperda* gedurende deze periode zijn voornamelijk verkregen, doordat het verlies van planten wordt voorkomen (de groeipunt van de maisplant kan door inboring van *S. frugiperda* worden vernietigd). Het plantverlies kan worden gecompenseerd door het zaaien met een hogere plantdichtheid en door vervolgens, ongeveer twee tot drie weken na plantopkomst, de aangetaste en slecht groeiende planten uit te dunnen. Hierdoor kan het gebruik van insecticiden gedurende deze vroege groeiperiode worden vermeden, terwijl de natuurlijke mortaliteitsfaktoren ten volle worden benut. Voor *S. frugiperda* zijn dit braconide parasieten, met name *Rogas laphygmae* en *Chelonus insularis*, de predatoire oorwurm *Doru taeniatum* en regenval. Voor *D. lineolata* is de eiparasiet *Trichogramma pretiosum* de belangrijke mortaliteitsfaktor. In een later groeistadium van de plant worden *S. frugiperda* populaties gereduceerd door tachinide parasieten, met name *Lespesia archippivora*, de parasitaire nematode *Hexamermis* sp. en verschillende soorten predatoren.

Maar deze mortaliteitsfaktoren zijn meestal niet in staat de plaag beneden de economische schadedrempel te houden. Bestrijdingsmaatregelen dienen te wor-

den genomen wanneer twintig procent van de bladkransen zijn beschadigd door *S. frugiperda*. Om de natuurlijke vijanden te sparen, moeten bespuitingen met vloeibare insecticiden worden vermeden. In plaats daarvan kunnen granulaten of insecticiden gemengd met zaagsel in lage concentraties worden toegediend aan de bladkransen of alleen aan de beschadigde bladkransen. (Deze laatste therapeutische methode, die de voorkeur van de kleine boer heeft, lijkt veelbelovend). Om de parasitaire nematode van *S. frugiperda* in stand te houden moet het gebruik van bodeminsecticiden met nematicide werking worden voorkomen.

Over de schade die *D. lineolata* aan mais toebrengt was geen informatie beschikbaar. De moeilijkheid is dat in het veld de aantasting grotendeels samenvalt met die van *S. frugiperda* en het is moeilijk om de twee soorten schade te scheiden. Bij onderzoek is gebleken, dat bestrijding van *S. frugiperda* de aantasting van *D. lineolata* kan verhogen, mogelijk door ovipositie van de boorder op het vergrote bladoppervlak van behandelde planten. Ovipositie van de boorder bleek namelijk tot de bloei zeer nauw gecorreleerd met de grootte van het bladoppervlak. Om deze reden zijn maisplanten in grote gazen kooien kunstmatig besmet en de resulterende schade is geanalyseerd met behulp van twee onafhankelijke statistische methoden: per kooi en per plant. De laatste analyse bleek nogal gecompliceerd door het effekt van plantvariabiliteit op de boorder. Beide analyses gaven eenzelfde resultaat, namelijk drie tot zes procent opbrengstverlies per boorder per plant. De plant bleek het meest gevoelig voor beschadiging van de laagste internodiën.

Chemische bestrijding van *D. lineolata* lijkt niet gerechtvaardigd omdat: 1. het aantastingsnivo in het land over het algemeen laag is, 2. insecticide toedieningen meestal ineffektief zijn, 3. de eimassa's klein en onopvallend zijn en daardoor ongeschikt voor een gemakkelijke bemonstering. Andere bestrijdingsmethoden verdienen de voorkeur: zoals het verbranden van stoppels en stengels van mais en sorghum in het droge seizoen. Dit reduceert de populaties van diapause larven.

Een belangrijke beperkende faktor voor maisproduktie in Nicaragua is de onvoldoende regenval. Onder droogteomstandigheden bleek dat de chemische bestrijding van de bladkrans tegen *S. frugiperda* niet leidde tot opbrengstverhoging. Het gebruik van NPK kunstmest stimuleerde de aantasting van zowel *S. frugiperda* als *D. lineolata*. Bemesting gaf alleen opbrengstverhoging wanneer ze plaats vond bij planten met door insecticide beschermde bladkransen.

Bonen worden in Latijns Amerika dikwijls in rijen tussen de mais gezaaid. Dit plantsysteem biedt een aantal agronomische en sociaal-economische voordelen voor de kleine boer. In onze proeven verminderde het de aantasting van zowel *S. frugiperda* als *D. lineolata*. Voor *S. frugiperda* was verminderde kolonisatie van nieuwe maisplanten door eerste stadium larven die zich met de wind verspreiden verantwoordelijk; hoogstwaarschijnlijk doordat ze door de bonenplanten (geen waardplant) worden weggevangen. Wat betreft *D. lineolata* leek verminderde ovipositie verantwoordelijk.

Op veel voorkomende onkruidgrassen (met name *Digitaria* sp. en *Eleusine indica*) in maisvelden, kunnen hoge aantallen *S. frugiperda* larven voorkomen, die een potentiële plaag voor het maisgewas vormen. De ovipositie van *S. frugiperda* op mais in proefvakken met onkruiden was hoger dan op mais in gewiede proefvakken.

De introduktie van exotische parasieten kan worden overwogen: voor *S. frugiperda* de eiparasiet *Telenomus remus* en voor *D. lineolata* de braconide *Apanteles flavipes* en de tachiniden *Paratheresia claripalpis* (peruviaans ras) en *Lixophaga diatraeae*. Resistentieveredeling zal zich in Centraal Amerikaans verband moeten concentreren op *S. frugiperda*, waarbij gebruik gemaakt moet worden van het geïdentificeerde resistente materiaal van CIMMYT.

Ook bij het ontwikkelen van andere geïntegreerde bestrijdingsmethoden zouden de landen van Centraal Amerika veel baat kunnen hebben, wanneer hun inspanningen interinstitutioneel worden gecoördineerd. Een geïntegreerd bestrijdingsprogramma is het best aangepast aan de behoeften van de kleine boer, wanneer het een structureel onderdeel vormt van een interdisciplinaire teeltstrategie en wanneer onderzoek en voorlichting nauw samenwerken.

ACKNOWLEDGEMENTS

The data for this publication were collected from the joint project NIC/70/002 of the United Nations Organizations FAO and UNDP, together with the Nicaraguan Agricultural Research Institute INTA. The data processing, the writing up and the publishing of this paper were made possible by the Agricultural University of Wageningen. I am very much indebted to Prof. Dr. J. de Wilde for suggesting to me to publish my Nicaraguan data in the present form. His continuous interest in the progress of my work was a big stimulus. The discussions with Dr. L. Brader on integrated pest management in developing countries have been very instructive. His critical reading of the manuscript and many suggestions are gratefully acknowledged. In Nicaragua the personnel of the Department of Parasitology of INTA actively participated in the investigations. Excellent work was carried out by Agr. R. Obando, who accurately supervised a great number of the experiments. I am also grateful to the field technicians J. Morales, E. Perez, F. Estrada, A. Membreño, A. Gadea, A Budier and S. Rendero. I further want to express my thanks to Ir. C. Y. Schotman, Lic. L. Lacayo and the laboratory technicians J. Bodan and F. Jaime for their assistance in the studies of parasites. In the project my colleages Dr. R. Daxl, Drs. M. J. Sommeyer, Ir. C. Y. Schotman and Ing. F. Petersen are thanked for the excellent teamwork. The ecological studies in the Interior could only be realized by the hard work and sincere interest of the students E. den Belder, F. Meerman, R. S. Nauta, M. S. H. Thesingh and M. E. Vulto and the efficient cooperation of the farmer A. Mendoza. In addition many thanks are due to Mrs. A. C. Henriquez-Obando for the preparation of the insect material and to Dr. L. Knudson and the specialists of the Insect Identification and Beneficial Insect Introduction Institute, United States Department of Agriculture at Beltsville, Maryland for the identifications of the insects (the specialists are mentioned in the text, mainly page 16 and table 33). I received enormous help from Mr. M. Keuls, who made many suggestions for the analysis of the data and the presentation of the results. The support of the programmers of the computer centre of the Agricultural University is also acknowledged. For the critical reading of the manuscript I am very much indebted to Dr. Ir. G. W. Ankersmit. Parts of the manuscript were read by Dr. Ir. J. B. M. van Dinther, Dr. F. D. Bennett, Dr. R. Daxl, Prof. Dr. H. C. Chiang, Dr. Ir. R. Rabbinge, Dr. Ir. P. van Halteren and several research workers of the Department of Entomology of the Agricultural University. For all their suggestions and comments I would like to express my gratitude. Many thanks are due to Miss G. P. Bruyn for typing the manuscript, to Mr. S. G. Wever for making the drawings, to Mrs. S. Kerkhoven-Hodges for correcting the English, to Mrs. G. de Wilde-van Buul and Ir. P. Manzanares, respectively for correcting the Dutch and Spanish of the summaries.

Last but not least I am very grateful to my wife Corry and our children Marijn and Karen for their understanding and support.

REFERENCES[1]

ACOSTA, M. J. C., 1964. La chicharrita del maiz, *Delphax maidis* (Ashmead) (Homoptera: Delphacidae), en sembríos escalonados de maiz y su relación con los factores climáticos. Revta. Fac. Ing. Agron. Univ. Cent. Venez., **3**: 42–68.

AFIFY, A. M. and H. T. FARGHALY, 1970. Comparative laboratory studies on the effectiveness of *Labidura riparia* Pall. and *Coccinella undecimpunctata* Reiche, as predators of eggs and newly hatched larvae of *Spodoptera littoralis* (Boisd.). Bull. Soc. Entomol. Egypte, **54**: 277–282.

ALAM, M. M., 1978. Attempts at the biological control of major insect pests of maize in Barbados, W. I.. In: Proceeding of Symposium on maize and peanut, p. 127–135, Paramaribo.

ALAM, M. M., F. D. BENNETT and K. P. CARL, 1971. Biological control of *Diatraea saccharalis* (F.) in Barbados by *Apanteles flavipes* Cam. and *Lixophaga diatraeae* T.T.. Entomophaga, **16**: 151–158.

ALLISON, J. C. S., J. H. WILSON and J. H. WILLIAMS, 1975. Effect of partial defoliation during the vegetative phase on subsequent growth and grain yield of maize. Ann. Appl. Biol., **81**: 367–375.

ALMEIDA, W., 1978. Fundamentos toxicológicos en el uso de plaguicidas. Seminario regional sobre uso y manejo de plaguicidas en Centroamérica, Guatemala. 21 pp.

ALTIERI, M. A., C. A. FRANCIS, A VAN SCHOONHOVEN and J. D. DOLL, 1978. A review of insect prevalence in maize (*Zea mays* L.) and bean (*Phaseolus vulgaris* L.) polycultural systems. Field Crops Res., **1**: 33–49.

ALTIERI, M. A., A. VAN SCHOONHOVEN and J. DOLL, 1977. The ecological role of weeds in insect pest management systems: a review illustrated by bean (*Phaseolus vulgaris*) cropping systems. PANS, **23**: 195–205.

ALTIERI, M. A. and W. H. WHITCOMB, 1979. The potential use of weeds in the manipulation of beneficial insects. Hortic. Sci., **14**: 12–18.

ALVARADO, B., 1975a. Epoca y número de aplicaciones de varios insecticidas para el control del gusano cogollero del maiz en el estado de Quintana Roo. Meeting of the Entomological Society of America, New Orleans. 8 pp.

ALVARADO, B., 1975b. Control quimico del gusano cogollero del maíz, *Spodoptera frugiperda* (J. E. Smith), en Quintana Roo. Instituto Nacional de Investigaciones Agricolas, México. Inf. Téc. del Depto. de Entomologia, **2**(2): 49–60.

ALVARADO, B., 1977a. Determinación del parasitísmo natural de dípteros en larvas de cogollero, *Spodoptera frugiperda* (J. E. Smith), en Quintana Roo. Instituto Nacional de Investigaciones Agrícolas, México. Inf. Téc. del Depto. de Entomologia, **3**(1): 65–68.

ALVARADO, B., 1977b. Influencia del control químico del gusano cogollero, *Spodoptera frugiperda*, en el rendimiento de dos variedades de maiz a espeque en Santa Rosa, Quintana Roo. Instituto Nacional de Investigaciones Agricolas, México. Inf. Téc. del Depto. de Entomologia, **3**(1): 61–64.

ALVAREZ, J. F., 1977. Control de insectos en maiz. XXIII Reunión Anual del PCCMCA, Panamá. 10 pp.

AMMAR, E. D. and S. M. FARRAG, 1974. Studies on the behaviour and biology of the earwig *Labidura riparia* Pallas (Derm., Labiduridae). Z. Angew. Entomol., **75**: 189–196.

ANAYA, M. A. and A. DÍAZ, 1974. Determinación del efecto de Furadan 5% G y Dysiston 5% G en el control del vector del achaparramiento en maiz. SIADES (El Salvador), **3**(4): 110–115.

APPLE, J. W., 1971. Response of corn to granular insecticides applied to the row at planting. J. Econ. Entomol., **64**: 1208–1211.

ARBUTHNOT, K. D., R. R. WALTON and J. S. BROOKS, 1958. Reduction of corn yield by first-generation southwestern corn borers. J. Econ. Entomol., **51**: 747–749.

ARGÜELLO, R. and L. LACAYO, 1977. Obtención de variedades de maiz resistentes a *Spodoptera*

[1] Bibliographic abbreviations according to: International Series Cataloque Part 1: Cataloque (1978). International Council of Scientific Unions Abstracting Board, Paris. 521 pp.

frugiperda. Informe anual 1976, cultivo del maíz, p. 140–146. Instituto Nicaragüense de Tecnología Agropecuaria, Managua. 257 pp.

Argüello, R. and L. Pineda, 1976. Recomendaciones generales sobre el cultivo del maíz en Nicaragua. Ministerio de Agricultura y Ganadería. Programa de Investigación, División de Cultivos Anuales, Managua. 4 pp.

Barel, C. J. A., 1973. Studies on dispersal of *Adoxophyes orana* F.v.R. in relation to the population sterilization technique. Meded. Landbouwhogesch. Wageningen, 73-7. 107 pp.

Barraclough, S., 1978. Perspectivas de la crisis agrícola en América Latina. Estudios Rurales Latinoamericanos, **1**: 33–57.

Barry, D. and A. Q. Antonio, 1979. Leaf feeding ratings for evaluating insecticidal control of southwestern corn borer in artificially infested plots. J. Econ. Entomol., **72**:13–14.

BCN, 1976. Indicadores económicos, Vol. 2(3). Departamento de Estudios Económicos, Banco Central de Nicaragua, Managua. 134 pp.

BCN, 1978a. Informe anual 1977. Banco Central de Nicaragua, Managua. 237 pp.

BCN, 1978b, Boletín anual, año XVII, No. **53**, 1977. Departamento de Estudios Económicos, Banco Central de Nicaragua, Managua. 138 pp.

Beck, S. D., 1950. Nutrition of the european corn borer, *Pyrausta nubilalis* (Hbn.). II Some effects of diet on larval growth characteristics. Physiol. Zool., **23**: 353–361.

Beirne, B. P., 1967. Pest management. CRC Press, Cleveland, Ohio. 123 pp.

Bennett, F. D., 1969. Tachinid flies as biological control agents for sugar cane moth borers. In: Pests of sugar cane, J. R. Williams, J. R. Metcalfe, R. W. Mungomery, R. Mathes (Eds.), p. 117–148. Elsevier Publishing Co., Amsterdam. 568 pp.

BNN, 1978. Informe anual, 1977. Banco Nacional de Nicaragua, Managua. 55 pp.

BNN/INCEI/IAN/MAG, 1974. El cultivo del maíz en Nicaragua. Comisión Nacional Permanente para la coordinación de Asistencia Técnica Agropecuaria, Ministerio de Agricultura y Ganadería, Managua. 64 pp.

Bosch, R. van den and V. M. Stern, 1969. The effect of harvesting practices on insect populations in alfalfa. Proc. Tall Timber Conf. Ecological Animal Control by Habitat Management, Tallahassee, Fla., **1**: 47–54.

Bottger, G. T., 1951. Sugars and protein in the corn plant as related to nutrition of the european corn borer. J. Econ. Entomol., **44**: 40–44.

Box, H. E., 1949. Notes on the genus *Diatraea* Guilding (Lepid., Pyral.) (Parts IV and V). Rev. de Entomología, **20** (fasc. 1–3): 541–555.

Box, H. E., 1950. The geographical and ecological distribution of some neotropical species of *Diatraea* Guild. (Lep., Pyral.) and certain of their parasites. Proc. 8th Internat. Congress of Entomology, 1948, p. 351–357, Stockholm.

Brader, L., 1976. Fertilizers in regard to plant resistance to pests: their role in FAO's integrated pest control programme. In: Fertilizer use and plant health, p. 307–316. Proceedings of the 12th Colloquium of the International Potash Institute, Izmir, Turkey.

Brader, L., 1979. Integrated pest control in the developing world. Annu. Rev. Entomol., **24**: 225–254.

Brader, L., 1980. Transfer of integrated plant protection techniques to developing countries. In: Proceedings International Symposium of IOBC/WPRS on integrated control in Agriculture and Forestry, p. 389–392. October 1979, Vienna, 648 pp.

Brindle, A., 1971. A revison of the genus *Doru* Burr (Dermaptera, Forficulidae). Pap. Avulsos Zool. (Sao Paulo), **23**: 173–196.

Britton, W. E., 1923. Guide to the insects of Connecticut. In: State geological and natural history survey, H. H. Robinson (Ed.). Bulletin No. **47**, Hartford. 807 pp.

Brown, E. S., 1972. Armyworm control. PANS, **18**: 197–204.

Brown, E. S. and A. K. A. Mohamed, 1972. The relation between simulated armyworm damage and crop-loss in maize and sorghum. East Afr. Agric, For. J., **37**: 237–257.

Bruner, S. C., L. C. Scaramuzza and A. R. Otero, 1975. Catálogo de los insectos que atacan a las plantas económicas de Cuba. Academia de Ciencias de Cuba, Instituto de Zoología, La Habana. 399 pp.

Bryan, D. E., C. G. Jackson and R. Patana, 1968. Laboratory studies of *Lespesia archippivora* in four lepidopterous hosts. J. Econ. Entomol., **61**: 819–823.

Burkhardt, C. C., 1952. Feeding and pupating habits of the fall armyworm in corn. J. Econ. Entomol., **45**: 1035–1037.

Buschman, L. L., W. H. Whitcomb, R. C. Hemenway, D. L. Mays, N. Ru, N. C. Leppla and B. J. Smittle, 1977. Predators of velvetbean caterpillar eggs in Florida soybeans. Environ. Entomol., **6**: 403–407.

Butler, G. D., 1958a. Tachinid flies reared from lepidopterous larvae in Arizona, 1957. J. Econ. Entomol., **51**: 561–562.

Butler, G. D., 1958b. Braconid wasps reared from lepidopterous larvae in Arizona, 1957. Pan-Pac. Entomol., **34**: 221–223.

Cannon, W. N. and A. Ortega, 1966. Studies of *Ostrinia nubilalis* larvae (Lepidoptera: Pyraustidae) on corn plants supplied with various amounts of nitrogen and phosphorus. I. Survival. Ann. Entomol. Soc. Am., **59**: 631–638.

Cherian, J. C. and M. S. Kylasam, 1938. Proc. Ass. Econ. Biol., Coimbatore.

Chiang, H. C., 1959. A note on some mortality factors of the european corn borer, *Pyrausta nubilalis*. Ecology, **40**: 310–312.

Chiang, H. C., 1964. The effects of feeding site on the interaction of the european corn borer, *Ostrinia nubilalis* and its host, the field corn, *Zea mays*. Entomol. Exp. Appl., **7**: 144–148.

Chiang, H. C., 1977. Integrated control of maize insects in Latin America. Working paper. Seventh Session of the Panel of Experts on Integrated Pest Control, Rome. Food and Agriculture Organization of the United Nations. AGP: IPC/WP/9, Rome.

Chiang, H. C., L. K. Cutkomp and A. C. Hodson, 1954. The effects of the second generation european corn borer on field corn. J. Econ. Entomol., **47**: 1015–1020.

Chiang, H. C. and A. C. Hodson, 1950. Stalk breakage caused by european corn borer and its effect on the harvesting of field corn. J. Econ. Entomol., **43**: 415–422.

Chiang, H. C. and A. C. Hodson, 1952. Relation between egg mass abundance and fall populations of first-generation corn borer and justification for insecticidal control in field corn. J. Econ. Entomol., **45**: 320–323.

Chiang, H. C. and A. C. Hodson, 1959. Distribution of the first-generation egg masses of the european corn borer in corn fields. J. Econ. Entomol., **52**: 295–299.

Chiang, H. C. and F. G. Holdaway, 1959. Effect of *Pyrausta nubilalis* (Hbn.) on the growth of leaves and internodes of field corn. J. Econ. Entomol., **52**: 567–572.

Chiang, H. C. and F. G. Holdaway, 1960. Relative effectiveness of resistance of field corn to the european corn borer, *Pyrausta nubilalis*, in crop protection and in population control. J. Econ. Entomol., **53**: 918–924.

Chippendale, G. M. and G. P. V. Reddy, 1974. Dietary carbohydrates: role in feeding behaviour and growth of the southwestern corn borer, *Diatraea grandiosella*. J. Insect Physiol., **20**: 751–759.

CIMMYT, 1974. El plan Puebla. Siete años de experiencia: 1967–1973. Centro Internacional de Mejoramiento de Maíz y Trigo, El Batán, México. 127 pp.

CIMMYT, 1979. CIMMYT review 1979. Centro Internacional de Mejoramiento de Maíz y Trigo, El Batán, México.

Clavijo, A. S., 1978. Distribución espacial del gusano cogollero del maiz *Spodoptera frugiperda* (Smith) (Lepidóptera: Noctuidae). Revta. Fac. Ing. Agron. Univ. Cent. Venez., p. 93–99.

Cloninger, F. D., M. S. Zuber and R. D. Horrocks, 1974. Synchronization of flowering in corn (*Zea mays* L.) by clipping young plants. Agron. J., **66**: 270–272.

Collins, C. W., 1915. Dispersion of the gipsy-moth larvae by the wind. USDA Bull., **273**: 1–23.

Collins, C. W., 1917. Methods used in determining wind dispersion of the gipsy moth and some other insects. J. Econ. Entomol., **10**: 170–177.

Conde, E. E., 1976. Tolerancia de la planta de maíz a la disminución de su área foliar. Tésis, Universidad de San Carlos de Guatemala, Facultad de Agronomía, Guatemala. 32 pp.

Cooley, W. W. and P. R. Lohnes, 1971. Multivariate data analysis. John Wiley and Sons, New York. 364 pp.

Coria, R. R. and S. Delgado, 1973. Evaluación de insecticidas para el control del gusano cogollero del maiz en CD. Delicias, CHIH. Instituto Nacional de Investigaciones Agrícolas, México. Inf. Téc. del Depto. de Entomología, **1**(3): 80–85.

CORTÉS, R., 1977. Multi-control of cutworms and armyworms (Noctuidae) in alfalfa in the desert valleys of Lluta and Camarones, Arica. Est. Exp. Agron., Univ. de Chile, p. 79–85, Santiago.

CROOKSTON, R. K. and D. R. HICKS, 1978. Early defoliation affects corn grain yields. Crop Sci., **18**: 485–489.

DAMPTEY, H. B. and D. ASPINALL, 1976. Water deficit and inflorescence development in *Zea mays* L.. Ann. Bot. (London), **40**: 23–35.

DAVIS, F. M., G. E. SCOTT and W. P. WILLIAMS, 1978. Southwestern corn borer: effect of levels of first brood on maize. J. Econ. Entomol., **71**: 244–246.

DAYNARD, T. B., C. R. ELLIS, B. BOLWYN and R. L. MISENER, 1975. Effects of carbofuran on grain yield of corn. Can. J. Plant Sci., **55**: 637–639.

DAYNARD, T. B., J. W. TANNER and D. J. HUME, 1969. Contribution of stalk soluble carbohydrates to grain yield. Crop. Sci., **9**: 831–834.

DEMPSTER, J. P. and T. H. COAKER, 1974. Diversification of crop ecosystems as a means of controlling pests. In: Biology in pest and disease control, D. Price-Jones and M. E. Solomon (Eds.), p. 106–114. **13**th Symposium of British Ecological Society, Oxford. Blackwell, Oxford. 398 pp.

DENMEAD, O. T. and R. H. SHAW, 1960. The effects of soil moisture stress at different stages of growth on the development and yield of corn. Agron. J., **52**: 272–274.

DINTHER, J. B. M. VAN, 1955. *Laphygma frugiperda* S & A and *Mocis repanda* F. in Suriname. Entomol. Ber., **15**: 407–411.

DIPSA, 1976. Producción agropecuaria: comportamiento, perspectivas y política de producción del Plan de Desarrollo Rural de Nicaragua 1975–1980. Dirección de Planificación Sectorial Agropecuaria, Managua. 118 pp.

DIPSA, 1977a. Programa Nacional de Granos Básicos: tecnología disponible y posibilidades de mejorar la productividad. Dirección de Planificación Sectorial Agropecuaria, Managua. 212 pp.

DIPSA, 1977b. Informe sobre el estudio de comunidades rurales en la región Interior Central. En: Estudio de nivel de vida: ingresos, empleo y satisfacción de necesidades de la población rural de Nicaragua, primera fase. Dirección de Planificación Sectorial Agropecuaria, Managua. 40 pp.

DIPSA, 1977c. Zonas biofísicas homogéneas e infraestructura vial de Nicaragua. Dirección de Planificación Sectorial Agropecuaria, Managua. 174 pp.

DUNGAN, G. H. and H. W. GAUSMAN, 1951. Clipping corn plants to delay their development. Agron. J., **43**: 90–93.

DYAR, H. G., 1890. The number of moults of lepidopterous larvae. Psyche, **5**: 420–422.

DYAR, H. G. and C. HEINRICH, 1927. The American moths of the genus *Diatraea* and allies. Proc. U.S. Natl. Mus., **71**(19). 48 pp.

EASTIN, J. D. and C. Y. SULLIVAN, 1974. Yield considerations in selected cereals. In: Mechanisms of regulation of plant growth, R. L. Bieleski, A. R. Ferguson, M. M. Cresswell (Eds.), p. 871–877. Bulletin **12**. The Royal Society of New Zealand, Wellington.

EMDEN, H. F. VAN, 1965. The role of uncultivated land in the biology of crop pests and beneficial insects. Sci. Hortic., **17**: 121–136.

EMDEN, H. F. VAN, 1977. Insect pest management in multiple cropping systems - a strategy. In: Proceedings Symposium on cropping systems research and development for the Asian rice farmer, p. 325–343. International Rice Research Institute, Los Baños, Phillippines.

ESAU, K., 1965. Plant anatomy. John Wiley & Sons, Inc., New York. 767 pp.

ESTRADA, F. A., 1960. Lista preliminar de insectos asociados al maíz en Nicaragua. Turrialba, **10**: 68–73.

EVERETT, T. R., H. C. CHIANG and E. T. HIBBS, 1958. Some factors influencing populations of european corn borer (*Pyrausta nubilalis* (Hbn.)) in the North Central States. Univ. Minnesota Agr. Exp. Sta. Tech. Bull., No. **299**. 63 pp.

FALCON, L. A. and R. DAXL, 1973. Control integrado de plagas del algodonero. FAO/MAG/PNUD. Informe al gobierno de Nicaragua por el Programa de las Naciones Unidas para el Desarrollo (Junio 1970 a Junio 1973)(actualizado 1977), Managua. 57 pp.

FALCON, L. A. and R. F. SMITH, 1973. Guidelines for integrated control of cotton insect pests. Food and Agriculture Organization of the United Nations, AGPP: Misc/8 (revised, 1974), Rome. 92 pp.

FAO, 1978. FAO production yearbook, Vol. **31**. Food and Agriculture Organization of the United Nations, Rome. 291 pp.

FAO/UNDP, 1980. Control integrado de plagas agrícolas, Nicaragua. Resultados y recomendaciones del proyecto. Informe preparado para el Gobierno de Nicaragua por la Organización de las Naciones Unidas para la Agricultura y la Alimentación en su carácter de organismo ejecutivo del Programa de las Naciones Unidas para el Desarrollo. AG: DP/Nic/70/002, Informe Terminal, Roma. 92 pp.

FAO/UNEP, 1975. The development and implementation of integrated pest control in agriculture. Formulation of a Cooperative Global Programme. Food and Agriculture Organization of the United Nations. AGP: 1974/M/8, Rome.

FICHT, G.A., 1932. Some studies on the planting rate of corn in relation to oviposition, population and injury by the european corn borer. J. Econ. Entomol., **25**: 878–884.

FIGUEROA, A., 1976. Insectos hallados en malezas de Colombia. I Encuentro Regional sobre interacciones malezas-insectos-cultivos. Centro Internacional de Agricultura Tropical, Cali, Colombia. 22 pp.

FLANDERS, S. E., 1968. The validity of *Trichogramma pretiosum*. Ann. Entomol. Soc. Am., **61**: 1122–1124.

FRANCIS, C. A., C. A. FLOR and M. PRAGER, 1978. Effects of bean association on yields and yield components of maize. Crop Sci., **18**: 760–764.

FUCHS, T. W., F. R. HUFFMAN and J. W. SMITH, 1979. Introduction and establishment of *Apanteles flavipes* (Hym.: Braconidae) on *Diatraea saccharalis* (Lep.: Pyralidae) in Texas. Entomophaga, **24**: 109–114.

FYE, R. E. and R. L. CARRANZA, 1972. Movement of insect predators from grain sorghum to cotton. Environ. Entomol., **1**: 790–791.

GAMEZ, R., 1980. Rayado fino virus disease of maize in the American tropics. Tropical Pest Management, **26**: 26–33.

GARCÍA, J. B., 1977. Evaluación de insecticidas para el control de gusano cogollero *Spodoptera frugiperda* en sorgo. XXIII Reunión Anual del PCCMCA, Panamá. 8 pp.

GARCÍA, J. G. L., A. MACBRYDE, A. R. MOLINA and O. HERRERA-MACBRYDE, 1975. Prevalent weeds of Central America. International Plant Protection Center Oregon State University, Corvallis. 161 pp.

GAVIRIA, J. D., 1977. Evaluación del control biológico en la industria azucarera colombiana. Su utilización práctica en el ingenio Riopaila Ltda.. Seminario sobre el problema de los taladradores de la caña de azúcar *Diatraea* spp.. Barquisimeto, Venezuela. 26 pp.

GENUNG, W. G., M. J. JANES and V. E. GREEN, 1976. Insects and other dietary items of Maynard's red-wing blackbird in relation to agriculture. Fla Entomol., **59**: 309–316.

GERLING, D., 1972. The development biology of *Telenomus remus* Nixon (Hym. Scelionidae). Bull. Entomol. Res., **61**: 385–388.

GERLING, D. and A. SCHWARTZ, 1974. Host selection by *Telenomus remus*, a parasite of *Spodoptera littoralis* eggs. Entomol. Exp. Appl., **17**: 391–396.

GHIDIU, G. M., E. C. BERRY and P. DUBOSE, 1979. The relationship between entrance holes and stalk cavities caused by 1st-and 2nd- generation european corn borer in field corn. J. Econ. Entomol., **72**: 85–86.

GIRLING, D. J., 1978. The distribution and biology of *Eldana saccharina* Walker (Lepidoptera: Pyralidae) and its relationship to other stem-borers in Uganda. Bull. Entomol. Res., **68**: 471–488.

GONZÁLEZ, P., 1968. El *Diatraea saccharalis* Fabr. y su control integrado en maíz, arroz y caña de azúcar en los valles de Arequipa. Rev. Peru. Entomol., **11**: 9–17.

GUAGLIUMI, P., 1969. As cigarrinhas dos canaviais no Brasil. Perspectivas de uma luta biológica nos estados de Pernambuco e Alagoas. Bras. Açuc., **72**(3): 34–43.

GURNEY, A. B., 1972. Important recent name changes among earwigs of the genus *Doru* (Dermaptera, Forficulidae). USDA Coop. Econ. Ins. Rpt., **22**: 182–185.

GUTHRIE, W. D., W. A. RUSSELL, F. L. NEUMANN, G. L. REED and R. L. GRINDELAND, 1975. Yield losses in maize caused by different levels of infestation of second-brood european corn borers. Iowa State J. Res., **50**: 239–253.

HAGEMAN, R. H., D. FLESHER and A. GITTER, 1961. Diurnal variation and other light effects influencing the activity of nitrate reductase and nitrogen metabolism in corn. Crop Sci., 1:201–204.

HANWAY, J. J., 1966. How a corn plant develops. Iowa State Univ. Spec. Rep., No. **48**. Ames, Iowa. 13 pp.

HANWAY, J. J., 1969 Defoliation effects on different corn (*Zea mays*, L.) hybrids as influenced by plant population and stage of development. Agron. J., **61**: 534–538.

HARCOURT, D. G., 1966. Major factors in survival of the immature stages of *Pieris rapae* (L.). Can. Entomol., **98**: 653–662.

HARDING, J. A., T. A. BRINDLEY, C. CORLEY and W. G. LOVELY, 1971. Effect of corn row spacing and of plant populations on establishment and control of the european corn borer. J. Econ. Entomol., **64**: 1524–1527.

HARRIS, C. R., H. J. SVEC, S. A. TURNBULL and W. W. SANS, 1975. Laboratory and field studies on the effectiveness of some insecticides in controlling the armyworm. J. Econ. Entomol., **68**: 513–516.

HARWOOD, R. R., 1975. Farmer-oriented research aimed at crop intensification. In: Proceedings of the cropping systems workshop, p. 12–32. International Rice Research Institute, Los Baños, Philippines, 396 pp.

HEERDT, P. F. VAN, 1946. Eenige physiologische en oecologische problemen by *Forficula auricularia*. Proefschrift Rijksuniversiteit te Utrecht. N.V. Drukkerij P. den Boer, Utrecht. 126 pp.

HENSLEY, S. D. and K. D. ARBUTHNOT, 1957. Migration of larvae of southwestern corn borer on corn. J. Econ. Entomol., **50**: 103.

HICKS, D. R., W. W. NELSON and J. H. FORD, 1977. Defoliation effects on corn hybrids adapted to the Northern Corn Belt. Agron. J., **69**: 387–390.

HILDEBRAND, P. E., 1976. Generando tecnología para agricultores tradicionales: una metodologia multidisciplinaria. Socioeconomía rural, Instituto de Ciencia y Tecnologia Agrícolas, Guatemala. 25 pp.

HU, M. and B. SUN, 1979. Integrated control of european corn borer (*Ostrinia nubilalis* (Hübner)). In: Integrated control of major insect pests in China. Edited by Institute of Zoology, Academica Sinica, Peking. 467 pp.

HUFFAKER, C. B. and P. S. MESSENGER, 1964. The concept and significance of natural control. In: Biological control of insect pests and weeds, P. DeBach (Ed.), p. 74–117. Chapman and Hall Ltd., London. 844 pp.

HUIS, A. VAN, 1975. *Diatraea lineolata* (Wlk.): Diapause and spatial distribution in sorghum stubbles in Nicaragua. Project FAO/UNDP/Nic/ 70/002, Progress Report No. **1**, Managua. 12 pp.

HUIS, A. VAN, 1977. Duty travel report: Guatemala, El Salvador, Honduras, Costa Rica, Panama. Project FAO/UNDP/Nic/70/002, Report to FAO. Managua. 21 pp.

HYNES, H. B. N., 1942. Lepidopterous pests of maize in Trinidad. Trop. Agric. (Trinidad), **19**: 194–202.

ICA, 1974. Evaluación de insecticidas para el control del cogollero del maíz, *Spodoptera frugiperda*. Programa 'Entomologia', Informe Anual 1974, p. 51–55. Instituto Colombiana Agropecuario, Palmira. 82 pp.

INCEI, 1978. Boletin estadistico, Vol. **1** (1–12). Instituto Nacional de Comercio Exterior e Interior, Managua.

INTA, 1978. Memoria 1977. Instituto Nicaragüense de Tecnología Agropecuaria, Managua. 123 pp.

INVIERNO, 1977. Informe anual 1975–1976. Instituto de Bienestar Campesino, Managua. 82 pp.

IRRI, 1974. Annual report for 1973. International Rice Research Institute, Los Baños, Philippines. 266 pp.

JARVIS, J. L., T. R. EVERETT, T. A. BRINDLEY and F. F. DICKE, 1961. Evaluating the effects of european corn borer populations on corn yield. Iowa State J. Sci., **36**: 115–132.

JAVIER, G. and T. PERALTA, 1975a. Evaluación cuantitativa del control biológico en tres cultivos del valle Mantaro. Rev. Peru. Entomol., **18**: 69–71.

JAVIER, G. and T. PERALTA, 1975b. Tendencia del control biológico en tres sistemas de cultivo de maiz 'choclo'. Rev. Peru. Entomol., **18**: 72–76.

JIMÉNEZ, J. G. and J. L. CARRILLO, 1976. Incidencia de la fauna insectil en algodonero con maiz intercalado y en cultivo comercial en Ceballos, DGO. Resúmenes del informe de 1976 por centros de investigaciones agrícolas, p. 37–38. Instituto Nacional de Investigaciones Agrícolas, México.

JONES, W. J. and H. A. HUSTON, 1914. Composition of maize at various stages of its growth. Bull. Agr. Exp. Sta. Purdue Univ., **175**: 599–629.

KASS, D. C. L., 1978. Polyculture cropping systems: review and analysis. New York State College of agriculture and life sciences. A Statutory College of the State University, Cornell, Ithaca, New York. 69 pp.

KEVAN, D. K. M., 1943. The neotropical cornstalk borer, *Diatraea lineolata* Walk., and the sugar-cane moth borer, *D. saccharalis* (Fabr.), as maize pests in Trinidad, B.W.I., with notes from Grenada. Trop. Agric. (Trinidad), **20**: 167–174.

KEVAN, D. K. M., 1944. The bionomics of the neotropical corn stalk borer, *Diatraea lineolata* Wlk. (Lep., Pyral.) in Trinidad, B.W.I..Bull. Entomol. Res., **35**: 23–30.

KUMAZAWA, M., 1961. Studies on the vascular course in maize plant. Phytomorphology, **2**: 128–139.

LACAYO, L., 1977. Especies parasíticas de *Spodoptera frugiperda* (Smith), *Diatraea lineolata* (Wlk.) y *Trichoplusia ni* (Hbn.) en zonas de Managua y Masatepe. Tésis, Universidad Nacional de Nicaragua, León. Informe Anual 1976, cultivo del maiz, p. 162–200. Instituto Nicaragüense de Tecnología Agropecuaria, Managua. 257 pp.

LANDAZABAL, J., F. FERNÁNDEZ and A. FIGUEROA, 1973. Control biológico de *Spodoptera frugiperda* (J. E. Smith) con el nemátodo: *Neoaplectana carpocapsae* en maíz (*Zea mays*). Acta Agron. (Palmira), **23**(3,4): 41–70.

LAWSON, F. R., R. L. RABB, F. E. GUTHRIE and T. G. BOWERY, 1961. Studies of an integrated control system for hornworms on tobacco. J. Econ. Entomol., **54**: 93–97.

LEÓN, O. and P. H. GILES, 1976. Informe anual 1975. Sección de Productos Almacenados (SEP-RAL), Ministerio de Agricultura y Ganadería, Managua. 57 pp.

LEONARD, D. E., 1971. Air-borne dispersal of larvae of the gypsy moth and its influence on concepts of control. J. Econ. Entomol., **64**: 638–641.

LEUCK, D. B., 1972. Induced fall armyworm resistance in pearl millet. J. Econ. Entomol., **65**: 1608–1611.

LEUCK, D. B., B. R. WISEMAN and W. W. MCMILLIAN, 1974. Nutritional plant sprays: effect on fall armyworm feeding preferences. J. Econ. Entomol., **67**: 58–60.

LEVY, R. and D. H. HABECK, 1976. Descriptions of the larvae of *Spodoptera sunia* and *S. latisfascia* with a key to the mature *Spodoptera* larvae of the Eastern United States (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am., **69**: 585–588.

LEWIS, T., 1969. Factors affecting primary patterns of infestation. Ann. Appl. Biol., **63**: 315–317.

LITSINGER, J. A., M. D. LUMABAN, J. P. BANDONG, P. C. PANTUA, A. T. BARRION and R. F. APOSTOL, 1980. A methodology for determining insect control recommendations. IRRI Research Paper Series, No.**46**. 31 pp.

LITSINGER, J. A. and K. MOODY, 1976. Integrated pest management in multiple cropping systems. In: Multiple cropping, R. I. Papendick and P. A. Sanche (Eds.), p. 293–316. Proceedings of a Symposium held in Knoxville, Tennessee. Special Publication No. **27**, American Society of Agronomy, Madison, Wisconsin.

LOACH, C. J. DE, 1970. The effect of habitat diversity on predation. Proc. Tall Timbers Conf. Ecological Animal Control by Habitat Management, Tallahassee, Fla., **2**: 223–241.

LUCKMANN, W. H. and G. C. DECKER, 1952. A corn plant maturity index for use in european corn borer ecological and control investigations. J. Econ. Entomol., **45**: 226–232.

MAG/FAO/PNUD, 1976. Guía de control integrado de plagas de maíz, sorgo y frijol. Proyecto Control Integrado de Plagas, Managua. 58 pp.

MARTINEZ, E., 1977. Influencia de las malezas sobre la incidencia de plagas en el cultivo del maíz (*Zea mays* L.). Tésis, Escuela Nacional de Agricultura y Ganadería, Instituto Nicaragüense de Tecnología Agropecuaria, Managua. 50 pp.

MATTAS, R. E. and A. W. PAULI, 1964. Trends in nitrate reduction and nitrogen fractions in young corn (*Zea mays* L.). Plants during heat and moisture stress. Crop Sci., **4**: 181–184.

MCGUIRE, J. N. and B. S. CRANDALL, 1966. Reporte preliminar sobre evaluación de pérdidas causadas por plagas y enfermedades en los cultivos básicos de consumo interno en la región del OIRSA. Organización Internacional Regional de Sanidad Agropecuaria. San Salvador.

MCMILLIAN, W. W., M. C. BOWMAN, R. L. BURTON, K. J. STARKS and B. R. WISEMAN, 1969. Extract of chinaberry leaf as a feeding deterrent and growth retardant for larvae of the corn earworm and fall armyworm. J. Econ. Entomol., **62**: 708–710.

McPherson, R. M. and S. D. Hensley, 1976. Development of *Lixophaga diatraeae* (Tachinidae) on several lepidopterans. Environ. Entomol., **5**: 1146–1148.

Medina, R., 1976. Control químico del gusano cogollero del maíz, *Spodoptera frugiperda* (J. E. Smith) en Calera, Zac.. Resúmenes del informe de 1976 por centros de investigaciones agrícolas, p. 70–71. Instituto Nacional de Investigaciones Agrícolas, México.

Medrano, G., 1978. Evaluación de insecticides para el control del cogollero *Spodoptera frugiperda* (J. E. Smith) en maíz. Tésis, Escuela Nacional de Agricultura y Ganadería, Instituto Nicaragüense de Tecnología Agropecuaria, Managua. 35 pp.

Miller, M. C., 1971. Parasitism of the corn earworm, *Heliothis zea*, and the european corn borer, *Ostrinia nubilalis*, on corn in North Georgia. J. Ga. Entomol. Soc., **6**: 246–249.

Monteith, L. G., 1960. Influence of plants other than the food plants of their host in host-finding by tachinid parasites. Can. Entomol., **92**: 641–652.

Morrill, W. L. and G. L. Greene, 1973a. Distribution of fall armyworm larvae. 1. Regions of field corn plants infested by larvae. Environ. Entomol., **2**: 195–198.

Morrill, W. L. and G. L. Greene, 1973b. Distribution of fall armyworm larvae. 2. Influence of biology and behaviour of larvae on selection of feeding sites. Environ. Entomol., **2**: 415–418.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent, 1975. SPSS: Statistical Package for the Social Sciences. McGraw-Hill Book Company, New York. 675 pp.

Nieto, J., M. A. Brondo and J. T. González, 1968. Critical periods of the crop growth cycle for competition from weeds. PANS (C), **14**: 159–166.

Norton, G. H., 1975. Multiple cropping and pest control. An economic perspective. Meded. Fac. Landbouwwet., Rijksuniv. Gent, **40**: 219–228.

Notz, A., 1972. Parasitismo de Diptera e Hymenoptera sobre larvas de *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) recolectadas en maíz, Maracay, Venezuela. Revta. Fac. Ing. Agron. Univ. Cent. Venez., **6**(3): 5–16.

Oatman, E. R., G. R. Platner and D. González, 1970. Reproductive differentiation of *Trichogramma pretiosum*, *T. semifumatum*, *T. minutum*, and *T. evanescens*, with notes on the geographical distribution of *T. pretiosum* in the Southwestern United States and in Mexico (Hymenoptera: Trichogrammatidae). Ann. Entomol. Soc. Am., **63**: 633–635.

Obando, R., 1976. Cogollero: umbrales permisibles de daño foliar en maíz. XXII Reunión Anual del PCCMCA, San José. 14 pp.

OECD, 1977. Report of the steering group on pest control under the conditions of small farmer food crop production in developing countries. Organization for Economic Co-operation and Development, Paris. 86 pp.

Ogura, N., S. Yagi and M. Fukaya, 1971. Hormonal control of larval coloration in the common armyworm, *Leucania separata* Walker. Appl. Entomol. Zool., **6**: 93–95.

Orphanides, G. M., D. Gonzalez and B. R. Bartlett, 1971. Identification and evaluation of pink bollworm predators in Southern California. J. Econ. Entomol., **64**: 421–424.

Ortega, A., 1974. Maize diseases and insects. In: Proceedings world wide maize improvement in the 70's and the role for CIMMYT, **7**: 1–41. Centro Internacional de Mejoramiento de Maíz y Trigo, El Batán, México.

Painter, R. H., 1955. Insects on corn and teosinte in Guatemala. J. Econ. Entomol., **48**: 36–42.

Parisi, R. A., A. Ortega and R. Reyna, 1973. El daño de *Diatraea saccharalis* Fabricius (Lepidóptera: Pyralidae) en relación con la densidad de plantas, nivel de fertilidad e híbridos de maíz, en Argentina. Agrociencia, **13**: 43–63.

Patch, L. H., 1929. Some factors determining corn borer damage. J. Econ. Entomol., **22**: 174–183.

Patch, L. H., 1942. Height of corn as a factor in egg laying by the european corn borer moth in the one generation area. J. Agr. Res., **64**: 503–515.

Patch, L. H., 1943. Survival, weight, and location of european corn borers feeding on resistant and susceptible field corn. J. Agric. Res., **66**: 7–19.

Patch, L. H., 1947. Manual infestation of dent corn to study resistance to european corn borer. J. Econ. Entomol., **40**: 667–671.

Patch, L. H., G. W. Still, M. Schlosberg and G. T. Bottger, 1942. Factors determining the reduction in yield of field corn by the european corn borer. J. Agric. Res., **65**: 473–482.

PEARSON, E. S. and H. O. HARTLEY, 1954. Biometrika tables for statisticians, Volume I. University Press, Cambridge. 238 pp.

PEÑA, N. S., 1974. Ensayo sobre control químico del 'cogollero del maíz' en Tarapoto. Rev. Peru. Entomol., **17**: 123.

PENNY, L. H. and F. F. DICKE, 1959. European corn borer damage in resistant and susceptible dent corn hybrids. Agron. J., **51**: 323–326.

PERRIN, R. M., 1975. The role of the perennial stinging nettle, *Urtica dioica*, as a reservoir of beneficial natural enemies. Ann. Appl. Biol., **81**: 289–297.

PERRIN, R. M., 1977. Pest management in multiple cropping systems. Agro-ecosystem, **3**: 93–118.

PERRIN, R. M. and M. L. PHILLIPS, 1978. Some effects of mixed cropping on the population dynamics of insect pests. Entomol. Exp. Appl., **24**: 385–393.

PETERSON, G. D., J. SEQUEIRA and F. ESTRADA, 1969. Principios y problemas del control integrado de plagas del algodón en Nicaragua. Programa de Control Integrado de Plagas. Ministerio de Agricultura y Ganadería, Managua. 183 pp.

PINEDA, L., 1978. Apuntes generales sobre el cultivo del maíz en Nicaragua. Escuela Nacional de Agricultura y Ganadería, Instituto Nicaragüense de Tecnología Agropecuaria, Managua. 23 pp.

PSCHORN-WALCHER, H. and F. D. BENNETT, 1970. Host suitability experiments with three tachinid parasites of *Diatraea* spp. in Barbados and Trinidad, W. I.. Proc. Int. Soc. Sugar-Cane Technol., **13**: 1331–1341.

QUEZADA, J. R., 1973. Insecticide applications disrupt pupal parasitism of *Rothschildia aroma* populations in El Salvador. Environ. Entomol., **2**: 639–641.

RAMÍREZ, J. L., 1971. Combate del gusano cogollero del maíz *Spodoptera (Laphygma) frugiperda* (J. E. Smith) con insecticidas granulados bajo condiciones de temporal en Muna, Yucatán. Tésis, Universidad de Agricultura, Chapingo, México. 59 pp.

RANDOLPH, M. M. and P. M. WAGNER, 1966. Biology and control of the fall armyworm. Texas Agr. Exp. Sta. PR-**2431**. 6 pp.

RAROS, R. S., 1973. Prospects and problems of integrated pest control in multiple cropping. Saturday Seminar. International Rice Research Institute, Los Baños, Philippines. 20 pp.

REVELO, M. A., 1973. Efectos del *Bacillus thuringiensis* sobre algunas plagas lepidópteras del maíz bajo condiciones tropicales. Revista ICA (Colombia), **8**(4): 429–503.

ROGERS, R. R. and J. C. OWENS, 1974. Relationship of carbofuran treatment to agronomic traits in maize. J. Econ. Entomol., **67**: 557.

ROOT, R. B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards *(Brassica oleracea)*. Ecol. Monogr., **43**: 95–124.

RUTHENBERG, H., 1971. Farming systems in the tropics. Clarendon Press, Oxford, 302 pp. (revised, 1980).

RYDER, W. D., 1968. Reduced incidence of damage of the fall armyworm *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera, Noctuidae) in alternating eight-row strips of maize and sunflower compared with maize alone. Rev. Cubana Cienc. Agric., **2**: 233–243.

RYDER, W. D., M. NEYRA and O. CHONG, 1968. Grain sorghum insects in Cuba, and some effects of DDT high-volume emulsion sprays on their abundance and on yield. Rev. Cubana Cienc. Agric., **2**: 245–252.

RYDER, W. D. and N. PULGAR, 1969. A note on parasitism of the fall armyworm *Spodoptera frugiperda* on maize. Rev. Cubana Cienc. Agric., **3**: 267–271.

SAÉNZ, L. and F. SEQUEIRA, 1972. Especies parasíticas del gusano cogollero, *Spodoptera frugiperda* (J. E. Smith) y del barrenador del tallo del maíz, *Diatraea lineolata* (Wlk.), encontradas en los diferentes campos experimentales del PMMYSN. XVIII Reunión Anual del PCCMCA, Managua. 6 pp.

SANDHU, G. S., B. SINGH and M. S. DHOORIA, 1975. Effect of rain on the population of *Oligonychus indicus* (Hirst) (Acarina: Tetranychidae) on different varieties of maize *(Zea mays* L.) in the Punjab, India. Int. J. Acar., **1**(2): 10–13.

SARMIENTO, J. and J. CASANOVA, 1975. Busqueda de límites de aplicación en el control del 'cogollero del maíz', *Spodoptera frugiperda* S & A. Rev. Peru. Entomol., **18**: 104–107.

SCARAMUZZA, L. C., 1945. Biological control of the sugarcane borer in Cuba by means of the fly *Lixophaga*. Mems. Asoc. Téc. Azuc. Cuba, **19**: 11–16.

SCHELTES, P., 1978. Ecological and physiological aspects of aestivation-diapause in the larvae of two pyralid stalk borers of maize in Kenya. Thesis, Agricultural University of Wageningen. Pudoc, Wageningen. 110 pp.

SCHLINGER, E. I., R. VAN DEN BOSCH and E. J. DIETRICK, 1959. Biological notes on the predaceous earwig *Labidura riparia* (Pallas), a recent immigrant to California (Dermaptera: Labiduridae). J. Econ. Entomol., **52**: 247–249.

SCHWARTZ, A. and D. GERLING, 1974. Adult biology of *Telenomus remus* (Hymenoptera: Scelionidae) under laboratory conditions. Entomophaga, **19**: 483–492.

SCOTT, G. E. and F. M. DAVIS, 1974. Effect of southwestern corn borer feeding on maize. Agron. J., **66**: 773–774.

SCOTT, G. E., F. F. DICKE and L. H. PENNY, 1965. Effects of first brood european corn borers on single crosses grown at different nitrogen and plant population levels. Crop Sci., **5**: 261–263.

SCOTT, G. E., W. D. GUTHRIE and G. R. PESHO, 1967. Effect of second-brood european corn borer infestation on 45 single-cross corn hybrids. Crop Sci., **7**: 229–230.

SIECA/FAO, 1974. Perspectivas para el desarrollo y la integración de la agricultura en Centroamérica. Vol. I. El grupo asesor de la FAO para la integración económica centroamericana. Organización de las Naciones Unidas para la Agricultura y la Alimentación, Guatemala. 281 pp.

SIFUENTES, J. A., 1976. Plagas del maíz en México. Algunas consideraciones sobre su control. Instituto Nacional de Investigaciones Agrícolas, SAG. Folleto de divulgación No. **58**, México. 21 pp.

SILGUERO, J. F., 1976. Determinación del tamaño de muestra y método de muestreo para evaluar infestaciones de gusano cogollero *Spodoptera frugiperda* (J. E. Smith). **XI** Congreso Nacional de Entomología, México. 18 pp.

SMITH, J. G., 1976a. Influence of crop background on aphids and other phytophagous insects on brussels sprouts. Ann. Appl. Biol., **83**: 1–13.

SMITH, J. G., 1976b. Influence of crop background on natural enemies of aphids on brussels sprouts. Ann. Appl. Biol., **83**: 15–29.

SOUTHWOOD, T. R. E., 1966. Ecological methods. Chapman and Hall, London. 391 pp.

SOZA, R. F., A. VIOLIC and V. CLAURE, 1975. Defoliación para forraje en maíz. **XXI** Reunión Anual del PCCMCA, El Salvador. 12 pp.

STERN, V. M., 1969 Interplanting alfalfa in cotton to control *Lygus* bugs and other insect pests. Proc. Tall Timber Conf. on Ecological Animal Control by Habitat Management, Tallahassee, Fla., **1**: 55–69.

STEWART, K. W. and R. R. WALTON, 1964. Oviposition and establishment of the southwestern corn borer on corn. J. Econ. Entomol., **57**: 628–631.

TAHVANAINEN, J. O. and R. B. ROOT, 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). Oecologia, **10**: 321–346.

TAYLOR, L. F., J. W. APPLE and K. C. BERGER, 1952. Response of certain insects to plants grown on varying fertility levels. J. Econ. Entomol., **45**: 843–848.

THOMPSON, W. R. and F. J. SIMMONDS, 1965. A catalogue of the parasites and predators of insect pests. Section **4**. Host predator catalogue. Comm. Wealth Agr. Bureau. 198 pp.

TINGLE, F. C., T. R. ASHLEY and E. R. MITCHELL, 1978. Parasites of *Spodoptera exigua, S. eridania* (Lep.: Noctuidae) and *Herpetogramma bipunctalis* (Lep.: Pyralidae) collected from *Amaranthus hybridus* in field corn. Entomophaga, **23**: 343–347.

TURNER, N. and R. L. BEARD, 1950. Effect of stage of growth of field corn inbreds on oviposition and survival of the european corn borer. J. Econ. Entomol., **43**: 17–22.

TYSOWSKY, M. and T. GALLO, 1977. Ovicidal activity of Ambush, a synthetic pyrethroid insecticide, on corn earworm, fall armyworm, and cabage looper. Fla. Entomol., **60**: 287–290.

UNASEC, 1974. Resumen de la situación y diagnóstico del sector agropecuario de Nicaragua, capítulo **VIII**. Comité Nacional Agropecuario, Unidad de Análisis Sectorial, Managua. 231 pp.

USUA, E. J., 1973. Induction of diapause in the maize stemborer, *Busseola fusca*. Entomol. Exp. Appl., **16**: 322–328.

VALENCIA, H., H. VELASCO and J. A. SIFUENTES, 1972. Evaluación de la efectividad de diversos insecticidas contra el gusano cogollero del maíz en el trópico. Agric. Téc. Mex., **3**: 157–158.

VAUGHAN, M., 1962. Especies parasíticas del gusano cogollero del maíz, *Laphygma frugiperda* (J. E. Smith) encontradas en 'La Calera' de Agosto de 1957 a Julio 1958. VIII Reunión Anual del PCCMCA, San José. 5 pp.

VAUGHAN, M., 1975. *Spodoptera* species of economic importance for cotton in Nicaragua. Armyworm study workshop. International Centre of Insect Physiology and Ecology (ICIPE), the East African Agriculture and Forestry Organization (EAAFRO) and the Centre for Overseas Pest Research (COPR), Nairobi. 40 pp.

VERSTEEG, M. N. and D. MALDONADO, 1978. Increased profitability using low doses of herbicide with supplementary weeding in smallholdings. PANS, **24**: 327–332.

WADDILL, V. H., 1978. Sexual differences in foraging on corn of adult *Labidura riparia* (Derm.: Labiduridae). Entomophaga, **23**: 339–342.

WARNKEN, P. F., 1975. The agricultural development of Nicaragua, an analysis of the production sector. International Series 1, Special Report **168**, Agricultural Experiment Station, University of Missouri, Columbia. 162 pp.

WAUGH, R. K., 1975. Four years of history. Instituto de Ciencia y Tecnología Agrícolas, Guatemala. 51 pp.

WHYTE, W. F., 1977. Towards a new strategy for research and development in agriculture; helping small farmers in developing countries. Desarrollo Rural en las Américas, **9**(1,2): 51–61.

WISEMAN, B. R., D. B. LEUCK and W. W. MCMILLIAN, 1973. Effects of fertilizers on resistance of antigua corn to fall armyworm and corn earworm. Fla. Entomol., **56**: 1–7.

WISEMAN, B. R. and W. W. MCMILLIAN, 1969. Competition and survival among the corn earworm, the tobacco budworm, and the fall armyworm. J. Econ. Entomol., **62**: 734–735.

WISEMAN, B. R., R. H. PAINTER and C. E. WASSOM, 1966. Detecting corn seedling differences in the greenhouse by visual classification of damage by the fall armyworm. J. Econ. Entomol., **59**: 1211–1214.

WOJCIK, B., W. H. WHITCOMB and D. H. HABECK, 1976. Host range testing of *Telenomus remus* (Hymenoptera: Scelionidae). Fla. Entomol., **59**: 195–198.

YAGI, S., 1980. Hormonal control of larval coloration associated with phase variation in the armyworm, *Spodoptera exempta*. Seventh Annual Report 1979, p. 13–14. The International Centre of Insect Physiology and Ecology, Nairobi.

YATES, F., 1937. The design and analysis of factorial experiments. Techn. Commun. No. **35**. Imperial Bureau of Soil Science, Harpenden, England. 95 pp.

YOUNG, J. R. and H. R. GROSS, 1975. Insect control in summer-planted sweet and field corn in South Georgia. Meeting of the Entomological Society of America. New Orleans. 3 pp.

ZANDSTRA, B. H. and P. S. MOTOOKA, 1978. Beneficial effects of weeds in pest management – a review. PANS, **24**: 333–338.

ZEPP, D. B. and A. J. KEASTER, 1977. Effects of corn plant densities on the girdling behavior of the southwestern corn borer. J. Econ. Entomol., **70**: 678–680.

APPENDIX

APPENDIX 1. Artificial defoliation of the whorl in four equitemporal periods (T_1–T_4) and four maize cultivars (C_1–C_4). The effect on yield and plant development of maize. Analysis of variance: F-values, significancies and means. (Exp. G)

Source of variation	df	Grain yield per									
		plot				plant				Total	
		C_1	C_2	C_3	C_4	C_1	C_2	C_3	C_4	C_1	C_2
Block	3	1.63	2.74^{+}	.47	.87	.24	3.24^{+}	.45	.59	2.35	1.18
Treatment	4	21.35^{**}	11.5^{**}	11.5^{**}	17.5^{**}	5.75^{**}	1.14	7.19^{**}	10.7^{**}	2.90^{+}	5.95^{**}
Defoliation Periods (T)											
Linear (T_L)	1	3.00	10.9^{**}	13.2^{**}	62.8^{**}	2.01	.93	13.3^{**}	29.9^{**}	.01	3.64^{+}
Quadratic (T_Q)	1	30.3^{**}	10.5^{**}	2.58	.69	6.42^{*}	.00	.19	1.04	6.10^{*}	12.4^{**}
Cubic (T_C)	1	6.25^{*}	7.44^{*}	1.08	.02	4.39^{+}	.47	.00	.34	.01	5.02^{*}
Control – $T_1T_2T_3T_4$	1	45.8^{**}	17.1^{**}	29.2^{**}	6.60^{*}	10.2^{**}	3.17	15.3^{**}	11.4^{**}	5.50^{*}	2.77
T_1T_2–T_3T_4	1	7.11^{*}	17.4^{**}	13.8^{**}	49.3^{**}	4.86^{*}	1.36	10.7^{**}	26.5^{**}	.01	7.33^{*}
T_1–T_2	1	8.19^{*}	2.57	2.64	10.2^{**}	.84	.01	2.11	.41	2.97	2.81
T_3–T_4	1	24.3^{**}	8.82^{*}	.42	4.07^{+}	7.13^{*}	.02	.69	4.33^{+}	3.14	10.9^{**}
T_2–T_1	1	8.52^{*}	13.2^{**}	4.56^{+}	5.56^{*}	5.93^{*}	.91	1.36	5.21^{*}	.01	7.44^{*}
Control – T_1	1	8.87^{*}	.98	4.62^{+}	4.20^{+}	1.66	1.11	1.48	.28	.92	.23
S^2max/S^2min[2]			1.49				1.64				1.40
Pooled error	48		28.91 × 10^4				15.08 × 10				54.57
Variation Coefficient	12	13.9	13.3	15.6	18.9	17.5	17.1	20.4	21.9	13.5	13.0
			kg ha^{-1}				gram				
Grand mean		4288	4502	3840	3158	70.1	72.0	60.2	56.2	60.9	63.1
Control		42	25	37	22	25	13	36	33	14	10
T_1		13	15	14	49	9	1	18	25	5	14
T_2		–15	0	–4	6	–2	2	–3	15	–11	–1
T_3		–44	–34	–27	–25	–33	–9	–20	–20	–13	–27
T_4		4	–6	–20	–52	1	–7	–31	–53	5	4
Standard error		7	6	7	8	8	8	12	11	6	6

[1] Against pooled error.
[2] The pooled error mean square may be used when the ratio between the maximum (S^2max) and minimum (S^2min) sum of squares is non-significant (i.e. $S^2max/S^2min = 4.79, p \leqslant .05$; PEARSON and HARTLEY, 1954).

Number of plants						Ear size								Plant height			
		Broken and lodged				length				diameter							
C_3	C_4	C_1	C_2	C_3	C_4	C_1	C_2	C_3	C_4	C_1	C_2	C_3	C_4	C_1	C_2	C_3	C_4
F-value[1]																	
.43	1.30	1.90	4.54*	3.58*	1.11	.29	3.90*	2.65	2.85+	1.23	2.09	.59	1.47	.45	2.53	2.50	.81
2.16	2.76+	25.5**	10.8**	20.2**	2.27	16.8**	6.77**	8.12**	37.6**	17.8**	6.78**	9.61**	15.4**	8.44**	4.74*	2.64	6.21**
1.50	4.43+	13.9**	30.2**	62.4**	.00	24.3**	21.1**	28.1**	101.**	9.51**	11.2**	24.3**	38.7**	1.33	.20	.11	7.67*
3.99+	4.55+	37.1**	.83	1.03	4.54+	11.9**	.12	.76	37.6**	23.3**	2.20	.05	12.9**	19.1**	6.39*	6.84*	.06
3.14	.42	50.1**	11.0**	3.63+	.35	17.0**	3.55+	.02	3.81+	27.5**	8.52*	2.09	.58	2.25	2.39	2.74	.02
.00	1.66	1.00	1.29	13.9**	4.17+	13.9**	2.28	3.57+	79.0**	10.8**	5.21*	12.0**	9.51**	11.1**	10.0**	.84	17.1**
.09	2.53	42.2**	40.9**	62.7**	.09	39.0**	24.5**	23.1**	65.9**	26.0**	18.5**	25.6**	27.3**	2.90	.09	.19	5.83**
.01	6.68*	1.01	1.01	.33	1.32	1.93	.00	4.89*	.01	1.15	.07	.65	.01	6.29*	.45	.48	.62
8.52*	.19	57.9**	.08	4.04+	3.48	12.2**	.26	.95	76.5**	33.1**	3.37+	.23	24.9**	13.5**	8.43*	9.02*	1.30
1.67	.00	62.3**	23.8**	18.5**	.33	29.9**	10.5**	3.25+	1.76	35.4**	14.7**	8.59*	1.55	3.19+	1.76	2.15	.55
.02	8.25*	4.04+	.74	.02	5.27*	.00	.32	1.71	.47	.07	.02	.30	.40	.60	4.24+	.05	4.08+
			3.10				2.31				1.83				3.25		
			60.67×10^{-1}				33.70×10^{-2}				26.14×10^{-4}				14.09×10		
12.6	14.6	34.7	28.2	32.4	70.4	3.79	4.00	3.87	3.86	3.67	3.77	3.82	3.98	5.21	5.64	6.24	6.38
means																	
number per ha ($\times 10^3$)											centimetre						
65.1	56.4	7.89	9.72	8.44	3.89	15.3	14.5	15.0	15.1	4.41	4.29	4.23	4.06	228.	211.	190.	186.
percentage deviation from grand mean																	
−0	−8	−15	−15	−54	−64	6	3	3	5	5	4	6	6	8	8	3	12
−1	21	−65	−31	−57	49	6	4	7	7	5	3	5	4	5	−0	1	3
−1	−6	−40	−51	−44	−7	3	4	1	6	2	3	2	4	−4	−3	−1	−1
−12	−6	153	46	55	−35	−12	−5	−4	3	−13	−7	−6	0	−11	−8	−8	−5
14	−1	−33	51	100	57	−3	−6	−7	−21	1	−3	−7	−14	2	3	5	−9
6	7	14	15	17	21	2	3	1	1	2	2	2	2	3	3	2	4

APPENDIX 2. Various chemical control methods. The effects on yield and plant development of the maize cultivar Salco and on the injury by *S. frugiperda* and *D. lineolata*. Analysis of variance: F-values, significancies and means. (See TABLE 56 for the specifications of tested contrast A – O) (Exp. K I).

Source of variation	df	Grain yield per: plot	Grain yield per: plant	Number of plants: Total	Number of plants: Lost	Plant height[1]	*S. frugiperda* Percentage (100 x) injured whorls (arcsin $\sqrt{x}$) at date (d)[2]: d<15	15<d<30	d>30	*D. lineolata* Number per plant: Injured inter-nodes	Perfo-rations	Number of injured plants
							F-values					
Blocks	7	7.94**	11.8**	.73	1.03	9.64**	1.99+	2.37*	.96	25.0**	30.6**	26.3**
After whorl prot.:	(A)	2.10	1.23	.58	.62	9.42**	7.94**	10.6**	.00	168.**	199.**	178.**
	(B)	1.93	1.30	.26	.10	.55	5.15*	4.33*	.01	126.**	140.**	125.**
Outer blocks	(C)	51.2**	77.2**	2.32	.00	17.6**	1.28	1.85	.27	2.48	10.3**	1.58
A × C		.07	.12	.08	3.99+	14.7**	.12	2.15	1.47	.00	.67	.53
Treatments	10	6.35**	4.06**	2.94**	2.74**	1.42	1.39	29.5**	23.4**	4.79**	7.05**	5.66**
Carbofuran	(D)	8.25**	5.74*	3.60+	3.46+	.97	4.96*	11.5**	.00	12.0**	13.5**	15.5**
Economic thresholds												
Thr∞ – Thr_{50}, Thr_{20}	(E)	6.14*	.56	13.8**	6.08*	2.54	.02	25.9**	77.5**	1.10	2.09	.44
Thr∞ – Thr_{50}	(F)	.47	.36	8.45**	4.84*	1.56	.00	2.53	46.0**	.51	1.31	.02
Thr∞ – Thr_{20} (Linear)	(G)	13.0**	3.62+	12.4**	3.21+	2.29	.04	52.1**	71.6**	1.21	1.85	1.00
Thr_{50} – Thr∞, Thr_{20} (Quadr.)	(H)	1.67	3.21+	1.76	1.36	.32	.01	5.42*	8.70**	.03	.29	.16
Thr_{50} – Thr_{20}	(J)	8.56**	6.26*	.37	.02	.07	.03	31.6**	2.81+	.15	.04	.72
Interactions (D × (E to J))												
D × E		.23	.06	.12	.50	.59	.16	4.55*	1.48	2.24	.49	.16
D × F		.65	.10	.05	1.34	.05	.24	4.80*	5.06*	1.59	.24	.21
D × G		.00	-.01	.68	.00	1.23	.04	2.26	.02	1.77	.51	.05
D × H		.19	.00	1.17	.25	1.32	.00	.22	10.8**	.65	.30	.00
D × J		.60	.05	1.09	1.18	.77	.08	.47	5.73*	.00	.06	.05
Programmed applications (control included)												
Linear	(K)	12.5**	5.83*	13.6**	11.1**	11.1**	3.83+	57.7**	108.**	1.89	4.87*	8.91**
Quadratic	(L)	.46	.57	.11	.09	.02	.12	.01	.04	3.72+	5.82*	2.11
Cubic	(M)	.02	.04	.05	.21	1.17	3.38+	4.04*	25.8**	.55	.23	3.05+
Other treatments												
Control – Me, Chl	(N)	34.7**	19.3**	16.4**	11.7**	3.48+	5.16*	65.2**	91.1**	1.35	2.78	7.60**
Me – Chl	(O)	.40	1.03	.61	1.63	.34	.31	14.4**	6.09*	21.3**	36.8**	20.7**
Error: V.C.	70	23.6	21.9	12.2	43.5	5.86	22.1	21.6	36.5	28.0	30.3	17.3
Total	87											

means

		Grain yield per ha (kg)	Grain yield per plant (gram)	Number of plants per ha: Total	Number of plants per ha: Lost	Plant height[1] (cm)	*S. frugiperda* Percentage[3] injured whorls at date (d)[2]: d<15	15<d<30	d>30	*D. lineolata* Number per plant: Injured inter-nodes	Number per plant: Perfo-rations	Number of injured plants per ha ($\times 10^3$)
Grand mean		1183	22.5	52.8	15.6	124.	8.34	13.3	10.0	1.38	2.36	14.8
Block Number	Protection after whorl stage	percentage deviation from grand mean					percentage[3]			percentage deviation from grand mean		
1	+	34	37	−2	19	−10	8	9	9	−31	−32	−23
2	+	−3	−6	3	−8	−5	9	12	10	−30	−43	−19
3	+	−13	−16	3	−11	2	7	12	11	−41	−47	−24
4	+	−4	−4	0	14	6	6	12	10	−52	−60	−33
5	−	−12	−15	3	−4	5	9	14	7	41	45	23
6	−	−20	−23	2	7	2	9	17	9	33	39	23
7	−	−11	−7	−4	3	−2	9	14	15	33	30	22
8	−	29	34	−5	−20	2	10	15	10	47	68	31
Standard error		7	7	4	13	2	2.0[4]	2.4[4]	3.6[4]	9	9	5
Economic thresholds												
Control (C)	(T_1)	−30	−18	−15	51	−5	11	22	35	8	16	11
Thr_{50}	(T_2)	−31	−25	−4	−1	−2	10	23	6	13	9	13
Thr_{20}	(T_3)	0	−5	3	18	1	10	10	8	10	9	7
Carbofuran at sowing												
Control (C_c)	(T_4)	−15	−6	−7	11	−2	8	35	29	−3	−8	−5
Thr_{50}	(T_5)	−2	−8	7	−5	1	8	25	14	−22	−25	−9
Thr_{20}	(T_6)	16	10	5	−19	−1	8	14	5	−27	−29	−13
Programmed applications												
at date[2] : 15	(T_7)	−12	−6	−8	27	1	8	11	34	28	36	22
15+30	(T_8)	3	5	1	−11	1	10	10	2	12	18	−1
10+15+30	(T_9)	10	6	6	−25	6	6	3	2	−7	−14	−8
Other treatments												
mefosfolan (date[2]: 15 + 30)	(T_{10})	27	18	8	−7	−1	8	8	5	26	40	11
chlorpyrifos (weekly)	(T_{11})	34	29	4	−39	1	6	2	1	−38	−52	−28
Standard error		8	8	4	15	2	2.3[4]	2.9[4]	4.2[4]	10	11	6

[1] Average of samplings 38, 42 and 45 days after plant emergence.
[2] Date = days after plant emergence.
[3] Backtransformed.
[4] Arcsin $\sqrt{x}$.

CURRICULUM VITAE

De auteur is op 25 mei 1946 te Wormerveer geboren. Na het behalen van het MULO-B diploma in 1962, heeft hij de Rijks Hogere Tuinbouwschool te Utrecht van 1962 tot 1966 doorlopen. Zijn militaire dienstplicht heeft hij vervuld van 1966 tot 1967. Aansluitend is hij zijn studie aan de Landbouwhogeschool te Wageningen begonnen met als verzwaard hoofdvak entomologie en als verzwaard keuzevak zoölogie (populatiedynamica); ingenieursonderzoek is in Ivoorkust en Kenya verricht. In 1974 heeft hij zijn studie beëindigd en heeft hij vervolgens in een projekt van geïntegreerde bestrijding van landbouwplagen in Nicaragua gewerkt, aanvankelijk als assistent-deskundige en later als deskundige entomologie van de Voedsel en Landbouw Organisatie van de Verenigde Naties (FAO). In deze periode, tot april 1979, zijn de gegevens voor dit proefschrift verzameld en in 1979 en 1980 zijn ze uitgewerkt op de Landbouwhogeschool te Wageningen.