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► **To cite this version:**

Pierre Anglade, Jacques Stockel, I.W.G.O. Cooperators. Intraspecific sex-pheromone variability in the European corn borer, *Ostrinia nubilalis* Hbn. (Lepidoptera, Pyralidae). *Agronomie, EDP Sciences*, 1984, 4 (2), pp.183-187. hal-00884625

HAL Id: hal-00884625

<https://hal.archives-ouvertes.fr/hal-00884625>

Submitted on 1 Jan 1984

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Intraspecific sex-pheromone variability in the European corn borer, *Ostrinia nubilalis* Hbn. (Lepidoptera, Pyralidae)

Pierre ANGLADE, Jacques STOCKEL & I.W.G.O. COOPERATORS (1)

I.N.R.A., Station de Zoologie, Centre de Recherches de Bordeaux, F 33140 Pont-de-la-Maye

SUMMARY

Following the first survey of intraspecific pheromone variability in *Ostrinia nubilalis* Hbn (ECB) in Europe and North America (KLUN & COOPERATORS, 1975), the sex attraction responses of male populations of ECB to 3 ratios of the Z : E isomers (97 : 3, 35 : 65, 3 : 97) of the 11-tetradecenyl acetate were studied at 28 locations in Europe, 3 in Egypt and one in the Hebei province of the People's Republic of China, during the 1978-1981 period, as a part of the cooperative program of I.W.G.O. (International Working Group on *Ostrinia*). In the palearctic region, the ECB populations exhibited pheromone polymorphism. The Z phenotype was the only one observed in 13 localities, mainly with low levels of capture. In other places, the two phenotypes Z and E were in sympatry, very often with the presence of their presumed hybrid Z × E, responding to the 35 : 65 Z : E mixture. The survey confirms the great prevalence of the Z phenotype in corn fields all over the world. The E phenotype was prevalent only in 5 locations in northern Italy and southern Switzerland.

Additional key words : *Polymorphism, 11-tetradecenyl acetate, China, Egypt, Europe.*

RÉSUMÉ

Variabilité intraspécifique de la pyrale du maïs (O. nubilalis Hbn.) pour sa phéromone sexuelle.

Après une première enquête sur la variabilité phéromonale intraspécifique de la pyrale du maïs, *Ostrinia nubilalis* Hbn., en Europe et en Amérique du Nord (KLUN & COOPERATORS, 1975), les réponses des populations de mâles de pyrale à l'attraction sexuelle de 3 mélanges des isomères Z et E du 11-tétradécényl acétate dans les proportions Z/E 97/3, 35/65, 3/97, ont été étudiées en 28 lieux d'Europe, 3 en Egypte et un dans la province d'Hebei en République populaire de Chine, durant la période 1978-1981 en tant que partie du programme coopératif de l'I.W.G.O. (Groupe de travail international sur *Ostrinia*). Dans la région paléarctique, les populations de pyrale manifestent un polymorphisme pour leur phéromone sexuelle. Si le phénotype Z est le seul observé en 13 lieux, caractérisés en général par de faibles captures, dans les autres lieux, les 2 phénotypes Z et E sont sympatriques, très souvent avec la présence de leur hybride présumé Z × E répondant au mélange Z/E 35/65. L'enquête confirme la grande prédominance du phénotype Z dans les cultures de maïs dans le monde entier. Le phénotype E n'est prédominant que dans 5 localités du Nord de l'Italie et du Sud de la Suisse.

Mots clés additionnels : *Polymorphisme, 11-tétradécényl acétate, Chine, Egypte, Europe.*

(1) I.W.G.O. COOPERATORS :

W. AWADALLAH	Plant Protection Research Institute, Cairo, Egypt.
F. BACA	Institut za kukuruz, Zemun, Yugoslavia.
H. BERGER	Bundesanstalt für Pflanzenschutz, Wien, Austria.
F. BISCHOF	Regierungspräsidium, Karlsruhe, Federal Republic of Germany.
R. BUCHI	Eidg. Forsch. Landw. Pflanzenbau, Zurich-Reckenholz, Switzerland.
S. CAVICCHI	Universita degli studi, Bologna, Italy.
F. COPPOLINO	Istituto Cerealicoltura, Bergamo, Italy.
L. GERGINOV	Maize Research Institute, Kneja, Bulgaria.
CZ. KANIA	WSR College Agriculture, Wroclaw, Poland.
S. MAINI	Universita degli studi, Bologna, Italy.
D. MUSTEA	Academia de Stiinta agricole, Turda, Romania.
M. MYSLICKY	WSR College Agriculture, Wroclaw, Poland.
B. NAGY	Novenyvedelmi Kutato Intezet, Budapest, Hungary.
B. OHNESORGE	Universität Hohenheim, Stuttgart, Federal Republic of Germany.
G. ROTUNDO	Universita degli studi, Portici, Napoli, Italy.
D. ZHOU	Institute of Plant Protection, Chinese Ac. Agric. Sci., Beijing, People's Republic of China.

I. INTRODUCTION

The sex pheromone communication system of the European Corn Borer (ECB), *Ostrinia nubilalis* Hbn., is dependent on the balance of the Z and E geometric isomers of the major component of the pheromone, the 11-tetradecenyl acetate (11-tda) (KLUN *et al.*, 1973). In the United States, where the species was introduced seventy years ago, the males of the Corn Belt respond to the mixture of Z-11-tda with traces of E isomer (KLUN & ROBINSON, 1971), but the males of the Northeastern States respond to the opposite blend, a mixture of E-11-tda with traces of the Z isomer (ROELOFS *et al.*, 1972). In these 2 areas, the isomeric compositions of the natural pheromone of the females was found to be respectively 97:3 Z:E and 4:96 Z:E (KOCHANSKY *et al.*, 1975). In France, first surveys (ANGLADE, 1974) have shown that males respond almost exclusively to the 97:3 Z:E mixture. In a 2-year survey in North America and Europe, KLUN & COOPERATORS (1975), using 5 isomer formulations in 31 locations, have found that in most cases males were attracted to the 97:3 Z:E blend and responded preferentially to the 3:97 Z:E blend in only 3 locations, in Italy and in the North-Eastern States (New York and Pennsylvania); they also found that in areas where the 2 types Z and E are in sympatry (Austria, Central France, New Jersey, Pennsylvania), a significant number of males were attracted to the 1:1 mixture and they hypothesized that these males were hybrids between the 2 types.

Genetic studies in the laboratory (KLUN & MAINI, 1979) demonstrated that the geometric composition of the female ECB sex pheromone is controlled by simple mendelian inheritance involving a single pair of alleles with incomplete dominance. The female *AA* secretes a mixture approximately 3:97 Z:E, the *aa* one approximately 97:3 Z:E and the hybrids *Aa* an isomer mixture of about 35:65 Z:E. The males seem to respond more intensely to the isomer ratio secreted by sibling females and male hybrids especially respond preferentially to the 35:65 Z:E isomer combination. However, each male type may also respond to all isomer blends, in different proportions.

The three different forms were detected in feral populations in New Jersey and Italy, showing that opposite forms hybridize in nature, as a result of aggregation by environmental stimuli (SHOWERS *et al.*, 1976) and that they serve as a bridge for gene flow between their parent genotypes (KLUN & MAINI, 1979). Based on the wide distribution of the Z form and the presence of the E form in a small number of more restricted areas, the hypothesis was made that the large scale cultivation of corn might exert selection pressure in favour of the Z form (ANGLADE, 1977).

We report here the results obtained by the members of the International Working Group on *Ostrinia* (I.W.G.O.) for 4 years (1978, 1979, 1981 and 1982) mainly in Europe, but also in Egypt and in the People's Republic of China (1981) during a survey of sex attraction response specificities of populations of ECB males. This study was scheduled in order to enlarge the field of the 1973-74 survey (KLUN & COOPERATORS, 1975), and to verify the stability of its results, especially in the areas where the ECB exhibits pheromone polymorphism. Additional results from China and Switzerland are also included in the present paper, with the permission of the authors.

II. MATERIALS AND METHODS

For the I.W.G.O. program, the insect traps and chemicals were generally supplied by the "I.N.R.A. Station de Zoologie, Bordeaux". The traps were straight prism cartons "I.N.R.A." design (STOCKEL, 1977) with a sticky sheet on the bottom (STOCKEL, 1981b).

The chemicals (Z and E isomers of 11-tda) were synthesized by the "I.N.R.A. Médiateurs chimiques" Laboratory at Brovessy. The stereochemically pure isomers were used to prepare formulations of 11-tda in hexane solution with 3 ratios Z:E 97:3, 3:97 and 35:65. The last of these has been demonstrated as the pheromone component of the hybrid Z × E.

Rubber septa (Ets LEUNE, Orsay, France) were treated by topical application with each blend. We used 100 µg 11-tda for one septum which was demonstrated to be the best amount of pheromone bait for *O. nubilalis* (STOCKEL, 1981a) with an addition of 1 000 µg tetradecyl acetate which has a synergic effect on male captures (STOCKEL, 1980). The rubber septa were prepared just before they were mailed to the participants, who placed them after receipt into cold storage until they were deployed in the fields.

In each of the 4 years, sex-trapping material was mailed to each of the 12 participating countries. The number of sex trapping locations was fixed each year by each cooperator depending upon the local situation (fig. 1). Each sex trapping location involved 3 traps with 3 lots of rubber plugs corresponding to the 3 pheromone blends.

In order to make the results of different countries comparable, some guidelines were followed: the sex traps were placed at least 50 m from each other at the perimeter of the cornfield. The sex traps were positioned on stakes at a level with the growing host plants. The insects were counted twice a week for about 2 months. Changes of bait were made every two weeks and the sticky sheets were replaced when necessary (about once every 3 weeks).

In Bologna, Italy, during the second ECB flight, in 1979 and 1980, virgin female traps were set up with females obtained from laboratory rearing (MAINI *et al.*, 1978) of the two strains Iowa (Z), New York (E) and the F1 E × Z.

III. RESULTS

The results of the study are summarized in table 1. During the 4 years, results were obtained from 32 different locations in 12 countries in Europe, Near East (Egypt) and Far East (the Hebei province, China) (fig. 1).

On 26 occasions out of the 49 place and year combinations, the 2 phenotypes Z and E were in sympatry. Very often (23/26), the males also responded to the 35:65 Z:E mixture, as Z × E hybrids. In the other cases, homogeneous responsiveness to the 97:3 Z:E 11-tda was observed, mainly in places and years which gave low levels of captures, the three localities in Egypt and one in Germany excepted.

The Z phenotype, responding to the 97:3 Z:E 11-tda, was prevalent everywhere, except in 5 localities in Europe where the E phenotype, responding to the 3:97 Z:E was prevalent: Bergamo, Bologna, Pistoia (Italy), Berganzona and Gordola (Switzerland).

The percentages of captures of males responding to the 35:65 Z:E seemed to be higher in the places where the E phenotype was prevalent (Bologna, from 31 to 61%, Pistoia 29%, Berganzona 22 and 20%, Gordola 14%)



Figure 1
Distribution map of the trapping locations for ECB.

Carte de la distribution des lieux de piégeage de la pyrale du maïs.

than in the opposite situations where the Z phenotype was prevalent (from 2% at Kneja, Bulgaria, to 13% at Levesville, France).

The percentages of males caught by virgin females of different pheromone phenotypes in Bologna were similar to those caught by the synthetic mixtures.

IV. DISCUSSION

The present evaluation of the relative percentages of the three pheromone phenotypes Z, E and Z × E in the different populations of the ECB in the participating countries might be more or less biased for 2 reasons: the males of this polyphagous species were trapped only in the vicinity of corn fields and we lack information on feral populations in areas where corn is not cultivated. Secondly, the sizes of trapped samples showed great variation, from 5 to 2 084 males between places and years.

Nevertheless, on the basis of the two I.W.G.O. surveys in Europe, and of similar conclusions drawn from a recent trapping experiment at 15 locations in 11 provinces of the P.R. of China (W.C.C.B.R.G. *et al.*, 1982), it seems established, in answer to the question "ECB: pheromone polymorphism or sibling species?" (CARDÉ *et al.*, 1978),

that the ECB populations of the palearctic area exhibit pheromone polymorphism. The apparently pure Z population observed may be generally related to low levels of capture where the chances of trapping the rare phenotypes are very low.

The presence of Z × E hybrids was detected on many occasions, with higher percentages in Italy and Switzerland where the ratios of the 2 parental phenotypes were better balanced (Z : E 1 : 4) than in other places where Z is prevalent (E : Z 1 : 10). With such a balanced Z : E ratio, the chances of mating between the 2 parental phenotypes were greater, giving higher frequencies of hybrids (Z × E : 0.23/0.05). The observed frequencies of hybrids were lower than the expected values according to a hypothesis of panmixis (0.38 and 0.18 respectively). The difference between observed and expected values was smaller in the Italian-Swiss area, where the E phenotype is prevalent. This leads to the hypothesis that the degree of homogamy would be lower for E, which is in agreement with the percentages of precopulatory responses obtained for the opposite pheromone by KLUN & MAINI (1979), for phenotype E from New York (9%) and for phenotype Z from Iowa (3%).

The possibilities of mating among the three phenotypes are dependent not only on the presence of suitable places of "rendez-vous" as a consequence of attraction of both sexes

TABLEAU 1

Distribution of the captures of ECB males in sex-traps baited with the 3 different mixtures of the Z and E-11-ida isomers, in 49 location-year combinations in Europe, Egypt and China, in the I.W.G.O. program 1978-1981.

Répartition des captures de mâles de la pyrale du maïs dans les pièges appâtés par les 3 différents mélanges des isomères cis (Z) et trans (E) du 11 ida, dans 49 combinaisons lieux-années en Europe, Egypte et Chine, au cours du programme I.W.G.O. 1978-1981.

Countries	Locations	Years	Trapping periods	Trapped males Total	Trapped males by isomer mixture in %			
					Z : E 97 : 3	Z : E 35 : 65	Z : E 3 : 97	
Austria	Fuchsenbigl	1981	26/6	29/7	14	100	0	0
	Zelting	1981	9/6	4/8	76	84	9	7
Bulgaria	Kneja	1981	11/6	18/8	42	98	2	0
China	Zhangjiakou ⁽¹⁾	1980	1/8	13/8	253	95	2	3
	Zhangjiakou	1981	16/7	31/8	33	88	9	3
Egypt	Alexandria	1981	3/6	15/9	331	100	0	0
	Saft Khaled	1981	3/6	15/9	146	100	0	0
	Sakha	1981	3/6	15/9	210	100	0	0
France	Levesville	1978	23/6	18/8	191	74	13	13
	Levesville	1979	25/6	17/8	375	92	6	2
	Orsonville	1979	25/6	17/8	203	96	2	2
	Vouillé	1981	16/6	4/9	176	100	0	0
	St Laurent	1981	30/6	1/9	38	55	8	37
	Bischwir	1981	9/6	14/8	67	98	2	0
Germany	Bickenbach	1981	16/6	28/7	169	100	0	0
	Karlsruhe	1981	27/6	10/7	29	100	0	0
	Stuttgart	1981	25/6	6/8	36	100	0	0
Hungary	Velence	1978	11/7	18/8	20	90	0	10
	Mikepercs	1978	4/7	12/9	64	100	0	0
	Mikepercs	1979	2/7	7/9	32	100	0	0
	Tanakadj	1979	7/7	7/9	18	94	0	6
	Tanakadj	1981	6/7	1/9	37	100	0	0
	Seregelyes	1981	1/7	30/9	30	100	0	0
Italy	Bologna	1978	26/7	30/8	229	7	58	35
	Bologna	1979	22/5	24/8	369	11	31	58
	Bologna ⁽²⁾	1979	4/6	17/9	2 084	5	37	58
	Bologna ⁽²⁾	1980	21/8	5/9	304	5	61	34
	Bologna	1981	26/5	20/8	569	10	45	45
	Bergamo	1981	15/6	28/8	120	21	33	46
	Pistoia	1981	2/7	25/8	66	35	29	36
	Salerno	1981	2/7	31/8	97	92	4	4
Poland	Brnik	1978	27/6	7/8	13	61	8	31
	Brnik	1981	15/6	20/7	11	100	0	0
	Groraj	1978	30/6	10/8	5	80	0	20
	Kobierzyce	1978	23/6	1/7	16	100	0	0
	Kobierzyce	1979	19/6	12/7	37	100	0	0
	Kobierzyce	1981	25/6	30/8	8	100	0	0
	Borusowa	1981	13/6	3/8	29	100	0	0
	Turda	1979	11/6	24/7	112	92	7	1
Romania	Turda	1980	16/7	18/8	152	100	0	0
	Turda	1981	25/6	20/8	212	100	0	0
	Turda	1981	25/6	20/8	212	100	0	0
Switzerland	Berganzona ⁽³⁾	1976	13/8	27/8	36	6	22	72
	Berganzona ⁽³⁾	1977	5/8	21/9	40	10	20	70
	Gordola ⁽³⁾	1977	5/8	21/9	22	36	14	50
Yugoslavia	Zemun	1978	27/6	5/9	43	93	0	7
	Zemun	1979	7/6	20/8	87	85	12	3
	Zemun	1981	22/6	27/8	94	94	0	6
	Osijek	1979	6/6	17/7	18	100	0	0
	Osijek	1981	22/6	20/8	70	97	0	3

(1) Results of the cooperative program U.S.A.-P.R.C.

Résultats obtenus dans un programme en coopération entre les Etats-Unis d'Amérique et la République Populaire de Chine.

(2) Results of trapping by virgin females, Z, Z × E and E (see text).

Résultats de piégeage par des femelles vierges de type Z, Z × E et E (voir texte).

(3) For these additional results of a bilateral I.N.R.A.-Switzerland cooperation, the intermediate mixture is Z : E 50 : 50 instead of 35 : 65.

Dans ces résultats supplémentaires d'une coopération bilatérale I.N.R.A.-Suisse, le mélange intermédiaire est Z : E 50 : 50 au lieu de 35 : 65.

to the same environmental stimuli but also on these precopulatory responses governed by the isomer blends of the pheromone.

Environmental (climatic and trophic) conditions might exert a selection pressure in favour of one particular phenotype. It is surprising to observe that conditions favouring the E phenotype occur only in a restricted area in Europe (Northern Italy, Southern Switzerland) and in the north eastern states in USA (as a result of a population introduced from Italy). In the other observed locations, which are mainly in areas of intensive cultivation of corn, the environmental conditions favour the Z phenotype.

In a given place, variations from year to year in the responses of the males can be detected. A decrease of the total captures of E and Z × E phenotypes has been observed in recent years at Kobierzyce, Poland and Turda, Romania (Kobierzyce : 6 % in 1973, 2 % in 1974 and 0 % in 1978, 1979, 1981 ; Turda : 3 % in 1973, 7 % in 1979, 0 % in 1980, 1981). The same trend was also observed at Levesville, France (31 % in 1974, 26 % in 1978, 8 % in 1979). These variations might be in correlation with variations in the environmental conditions selectively favouring one of the phenotypes. A striking example of these variations in the captures of males was observed in a locality of southwest-

ern France (Z : E 97 : 3 15, 52, 92 % ; Z : E 35 : 65 29, 18, 6 % ; Z : E 3 : 97, 56, 30, 2 % respectively during the years 1980, 1981, 1982) (STOCKEL & DE LA MESSELIÈRE, 1983).

More advanced investigations, including the trapping of males, the study of their responses in the laboratory and the analysis of the secretion of the females, related to analysis of genetic distance (HARRISON & VAWTER, 1977 ; CIANCHI *et al.*, 1980), should be conducted in the different countries in order to test the hypotheses presented in this paper and to follow the variations in the frequencies of genes influencing the production of the different sex-pheromone components of the European corn borer.

Reçu le 14 juin 1983.

Accepté le 20 septembre 1983.

ACKNOWLEDGEMENTS

The authors thank Ch. BRIAN (I.N.R.A., Bordeaux), for his advice in the field of genetics, Prof. H. C. CHIANG (Univ. of Minnesota), and Dr. S. MAINI (Univ. of Bologna) for their valuable criticism in reading the manuscript.

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