Variation in the European corn borer, *Ostrinia nubilalis*, and allies (Lepidoptera, Pyralidae)

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Abstract

The population structure of the European corn borer, Ostrinia nubilalis, *and allies has been studied since the 20-s. The aim of the paper is to describe the known data on the population variability in borers, including i) variation in morphology of male midtibiae; ii) biological properties of* Ostrinia *races and "biospecies", with special reference to larval ability to survive on different host plants; iii) formation of reproductive isolation in the genus* Ostrinia*; iv) peculiarities of genetic structure of allopatric and sympatric populations; v) geographic distribution of populations with specific morphology and biology. Besides, the ecological factors supposed to be responsible for the variation in borers and principles of evolution in the genus* Ostrinia *are discussed as well as probable trends for further investigations.*

Introduction

Problems of population variability in insects have drawn the attention of many researchers (e. g. 20, 60, 122; see also 65), in view of its importance for theory as well as for practical applications.

As early as in the 20-40-s it was found that some populations of the European corn borer (ECB), *Ostrinia nubilalis* (Hübner), varied in many biological characteristics (8, 103, etc.). Although the ECB ecology had been studied very intensively (see reviews: 10, 13, 14, 40, 59, 108), problems of its biodiversity have been poorly discussed. So, the task of the present paper is to summarise the data obtained on population variability in the ECB and its allies, to discuss the factors affecting its population structure and evolution, and to trace the possible directions for further investigations.

Today the known materials on variability of *Ostrinia* representatives are extremely various; these are, firstly, remarkable data on the capacity of the EBC populations to change adaptively their voltinism very fast. This was seen

very clearly in North America after the pest introduction during World War I (109). Secondly, the EBC has proved to be a conspicuous species inasmuch as it exists in the form of two races specialized in sex pheromone composition produced by females (e. g. 67). Thirdly, numerous data, mainly obtained in east Europe, have confirmed the strong specificity of biological populations infesting different host plants, namely, maize and some dicotyledonous (dicots) plants such as wormwood, hemp, and thistle (e. g. 63, 77). Finally fourth, a number of sibling species were identified in the genus *Ostrinia*, and at least some of them are of unclear taxonomic status so far (91). Consequently, the EBC and its allies are extremely interesting even though they manifest the most different types of population variability.

It is quite correct to assume that the EBC fed originally on wormwood and hop, which are plants of European origin (92). As a pest of millet the ECB was registered officially since 1806 (21). Maize infestation by the ECB was first detected in Europe during the second half of the 19th century (100), i. e. more than 350 years after the maize introduction in Europe.

Being indistinguishable from the very related species, the ECB was known in the Russian Empire under the name *Botys* (*Pyralis*) *silacealis* as an important pest of hop, hemp, and millet long before the maize introduction in the country (120). The damage to maize by the ECB was first reported from Odessa (south - west Ukraine) in 1879 (64). At the early beginning of the 20th century the ECB caused damage to maize in Bessarabia and the Odessa District only (the far south-western part of the Russian Empire) (123), but since 1908 the insect started to infest maize in east Ukraine as well (117). At the Don River region the first record of maize injury started to be known in 1915 (24). Most likely the ECB had shifted to maize feeding first somewhere in West Europe before a somewhat specialized pest population penetrated into Russia; it is interesting to note that all outbreaks for the first time mentioned in Russia form an almost strict westward succession (25).

Data on population variability in *Ostrinia*

Voltinism

Some excellent reviews were published (e. g. 10, 109), so we may restrict our attention only to general ideas about effects of variation in voltinism as well as variations in temperature and photoperiodicity on the EBC populations. The EBC larvae overwinter in diapause condition induced by photoperiod reduction and lowering temperature (10). The end of the diapause is affected by a photoperiodic reaction (82) as well as a raising of temperatures and drop-liquid water (81). Insect photo- and thermoperiodic reactions, being the action of sex-linked genes and modification exposure to surroundings (44, 85, 98), can be easily selected (111). A relationship between the thermo- and the photoperiodic reaction is evidently a function of environmental conditions where the EBC population has been living.

It is known that originally the EBC was only present in the territories of Massachusetts, New York and Ontario, now it is widespread throughout 40 US states and 8 Canadian provinces (94). To inhabit such a wide area, the EBC populations should have developed adaptations permitting them to effectively exploit thermal resources of distinct climatic zones (11); as a result three ecotypes, such as, northern (univoltine), central (bivoltine), and southern (polyvoltine) were formed, showing considerable dissimilarity between one another in their reactions to photo- and thermoperiods (110).

The spread of the EBC in Russia is determined by temperature, wetting conditions, and host plants; this is also the case in the other countries (74, 108). The northern border of distribution of the EBC and its allies feeding on dicots in the European part of the Former Soviet Union (FSU) is European Russia, Ukraine, Byelorussia, the Baltic States, it passes through Estonia, the southern part of the St. Petersburg District, Novgorod, Tver, Yaroslavl, Kostroma, the Nizhny Novgorod Districts, the southern part of Kirov District, Udmurtia, and

Bashkiria (74). Contrary to the populations which feed on dicots, the maize inhabiting populations of the ECB are presently restricted to the north to Kiev and the Belgorod Districts. Besides, the northward line of demarcation, where at least a partial second generation develops, is located at about 250 km to the north of the populations which feeds on dicots (a tentative line passes over the northern part of the Odessa District, Dnepropetrovsk, and Volgograd) as compared to populations which feed on maize (the southern part of the Odessa District, Kherson, Rostov). The differences in border distributions and life histories seem to reflect some features of adaptations to exploit relatively late host plants (35).

Morphology and genetics

According to Mutuura & Munroe (91) the genus *Ostrinia* includes at least 20 species clustered into three groups. The first group consists of only one, the most primitive species *O. penitalis* (Grote) (4). The second one joins nine species which are multifarious in appearance or which are phyletically related, among which *O. obumbratalis* (Lederer) infesting maize occasionally (3) and *O. kasmirica* (Moore) being known in India as a pest of *Cnicus wallichii* (2). The most advanced, third group involves the ECB and its near relatives; all of them are characterised by a trilobed uncus in the males. *O. kasmirica* seems to be the closest species to this group in appearance, but it differs in structure of the male genitalia.

Based on a different morphology in the male midtibiae, Mutuura & Munroe (91) separated the species group with trilobed uncus into three subgroups. The authors included in the first subgroup only the forms with display so called "small" tibiae, namely, the Asian corn borer, *O. furnacalis* (Guénée), the EBC, *O. nubilalis*, *O. orientalis* Mutuura & Munroe, and *O. dorsivittata* (Moore); the second one united only two forms having "medium-sized" midtibiae in the males, namely, the naryn borer, *O. narynensis* Mutuura & Munroe, and the Kurentsov borer, *O. kurentzovi* auct. id.; the third subgroup joined species with

"large" male midtibiae, namely, the brush-legged borer, *O. scapulalis* (Walker), *O. zealis* (Guénée), *O. zaguliaevi* Mutuura & Munroe, and *O. putzufangensis* auct. id. (91). In some cases the male midtibiae morphology of borers is very original. It is, for example, *O. scapulalis* which is one of the easiest to distinguish from the ECB and the other allies on the basis of a distinctive structure of "large" midtibiae being characterised by high stability and low variability of all elements in their very complex construction (25). The morphological habitus of the "medium-size" tibiae of *O. narynensis* and of *O. kurentzovi* is characterised by a high variability both between and within individuals. Although a typical "medium-size" tibia shows a quite original habitus determined mainly by the presence of a deep invagination in the tibia, only a minor part of the individuals could be uniquely defined due to their polymorphism; as a result, a well-marked morphological boundary could not be shown between *O. nubilalis* and *O. narynensis* as representatives of the first (with "small tibiae") and the second (with "medium-size" tibiae) subgroups respectively (25).

Using hybrids in the analysis it was proved that a deep invagination in the "medium-size" tibia inherits as a recessive and sex-linked character named *invagination* (*i*) (25). Although the "large" midtibia of *O. scapulalis* has a very complicated morphological structure, it inherits as a single dominant autosomal character named *Massive tibia* (*Mt*) (25). Gene *i* is a hypostatic *Mt* and is actually present in the *O. scapulalis* genotype; so the typical male with "small" tibiae can be genetically described as $Mt^+Mt^+i^+i^+$, the one with "medium-size" tibiae as Mt^+Mt^+ii (deep invagination presents), and the last with "large" tibiae as *MtMtii*. Morphological realization of *Mt* in the ECB gene medium was studied and some changes were detected in "large" tibiae morphology in backcrossed males (25). Results of genetic analysis rigorously proved the idea that a borer with "medium-size" tibiae was an immediate progenitor of *O. scapulalis* for no other reason than that the latter carries "medium-size" tibiae genes (25).

It is assumed that the extraordinary complexity of the male midtibiae morphology in the course of evolution has an important, but now unknown, function in sex behaviour which could possibly involve a primitive species, viz. *O. nubilalis*. If the new data on reproductive biology in the ECB such as (105) are accepted, the complexity of sex communication in *O. nubilalis* and allies will become apparent. It is obvious that the systematics of *Ostrinia* species with trilobed uncus is far from being perfect. For example, differences between *O. narynensis* and *O. kurentzovi* are too small to consider them as distinct species (25); *O. nubilalis* populations feeding on dicots in dry localities of European Russia are so specialized that they have been considered as a separate species, namely, *O. persica*, rather than a subspecies (32, 34, 38). Difficulties in systematics are clearly enhanced by the existence of numerous populations with polymorphism on the genes controlling the male midtibiae morphology. For example, at the Krasnodar area the ECB populations feeding on monocotyledonous (monocots) hosts, viz. maize, live in sympatry with those feeding on dicots populations of the so called hemp borer, conventionally labelled *O. nubilalis* x *O. narynensis* (previously designed as *O.* sp. aff. *narynensis* in earlier publications, e. g. 25); in populations of *O. nubilalis* x *O. narynensis* frequency of *i* was evaluated in the range 0.29 to 0.35 which means that only about 5% of males is expected to carry the typical "medium-size" midtibiae and is easy to distinguish from *O. nubilalis* individuals (25). From the biological point of view (taking into account host plant specificity and reproductive isolation) the hemp borer is as distinct from the maize inhabiting ECB as the other morphologically "good" species of the genus such as *O. scapulalis*.

Host plant relations

Although the ECB has been usually considered as a remarkably polyphagous species (15, 74, etc.), in some cases the host plant specialization was well indicated (5, 62, 63, 77, 403, 116, 121). Even in the 30-40-s different explanations for the phenomenon of host plant specialization in the ECB

populations were proposed in Soviet literature (74, 76, 119). Long-term observations and experiments permitted to infer that at least in east Europe variation in the range of infested host plants depends principally on the genetic dissimilarity of the insects manifesting specific inherited preferences for egg-laying and nutrition, whereas the influence of weather/climatic conditions or food conditioning were of minor importance (25, 31, 33). Insect collections made at different sites of Russia and the neighbouring states of the FSU (Ukraine, Byelorussia, the Baltic states, Kazakhstan) gave the possibility to divide the host plants which made possible a complete larval development of *Ostrinia* ssp. into three groups, namely, 1) monocots (maize, *Zea mays*, panicled small cereals, primarily millet, *Panicum miliaceum* and sorghum, *Sorghum* spp.), 2) dicots (wormwood, *Artemisia vulgaris*; ruderal and cultured hemp, *Cannabis sativa*; common clotbur, *Xanthium strumarium*; iva, or great ragweed, *Cyclachaena xanthifolia*; common ragweed, *Ambrosia artemisifolia*; wild and cultured hop, *Humulus lupulus*; bur beggar-ticks, *Bidens tripartita*, and some others of infrequent occurrence), and 3) the Canadian thistle, *Cirsium arvense*. The plants belonging to the first group have been infested by borers with "small" male midtibiae alone (for example, by *O. nubilalis* in Europe and by *O. furnacalis* in the Far East). Those of the second group have been infested by either borers with typical "small" midtibiae at one zone (thus, by *O. nubilalis* on the west of Ukraine), or, in the other zones, by populations in which improved types of male midtibiae predominated, such as i) the "medium-size" type (restricted zones of central Ukraine, namely, Zhitomir, Vinnitsa, the Belaya Tserkov Districts), ii) the "large" type (expanded zones including central and east Ukraine, west and central parts of European Russia, including among other, Moscow, Bryansk, Belgorod, Orel, and the Nizhny Novgorod Districts) and, iii) a mixtures of two or three different types of midtibiae (thus, in Lithuania, some Districts of Byelorussia, St. Petersburg, wide territories of North Caucasus) (25, 27, 34). If the thistle is found to be infested outside the maize fields it is *O. kasmirica* that feeds on the host (25, 28).

Borer populations have been seen to perform strong host plant specialization when inhabiting dicots and maize in North Caucasus, the central part of European Russia, and Ukraine. It was shown in particular that 1) host plant specialization is first guaranteed by female choosing of plants when searching for egg-laying (25); 2) a strong insect choosing of its "own" a host plant could be seen even though it grew immediately adjacent to an "alien" host plant (29); 3) increased survival of larvae feeding on their "own" host plants and decreased survival of those feeding on "alien" host plants was easily verified by artificial infestation techniques (25, 26); 4). Marked differences in larval survival have come to light when artificial infestation was carried out during the early stages of plant development as leaf whorl in maize (25, 26); 5). Variation in the ability of larvae to survive is determined by their distinctions in either physiology or behaviour (30); 6). Sympatric populations adapted to different types of host plants can also differ in other inherited characters such as i) periods of adult emergence which results in differences in voltinism, ii) levels of fecundity in females, iii) the availability of a rearing medium for larvae to develop on, iv) a number of metabolic features in adults and preimaginal stages, and of chief importance v) sex behaviour differences giving rise to premating reproductive isolation which will be discussed below (25, 31, etc.); 7). The number of differences between populations adapted to dicots and to maize is practically unaffected by the male midtibiae morphology of those feeding on dicots, i. e. by their formal systematic position; to put it differently, "maize" and "dicots" *O. nubilalis* populations at west Ukraine are as much biologically dissimilar as *O. nubilalis* on maize and *O. scapulalis* on dicots at east Ukraine or central Russia (25, 31, etc).

Host plant specialization in *Ostrinia* populations seems to be characteristic not only for Russia and its neighbouring states. There are a number of publications which favours the idea that food specialization in the ECB should also exist in the other parts of Europe, specifically in France (103), Hungary (92, 107), Poland (62), and Romania (AN FROLOV, unpublished data).

On the other hand no sign of host plant specialization was revealed in some regions of the FSU, in particular in Transcaucasia (22). Thus, larval survival of "maize" population from Azerbaijan (east Transcaucasia) was as low as that of "dicots" populations from North Caucasus when feeding on maize under artificial infestation (26). The southern regions of the borers range, among others Uzbekistan (25), Yugoslavia (87), and probably Bulgaria (97) are the zones where host plant specialization on monocots and dicots has not been detected yet.

Distinctions of different *Ostrinia* species in host plant ranges were recorded in east Asia, namely in Japan, China and Korea, as well (57, 61, 88, 95, 106), but in general much more thorough investigations must be carried out to describe the peculiarities of host plant specialization of borers in these regions.

Sex pheromones

The ECB is one of the few insect species which displays intraspecific polymorphism in the composition of its sex pheromone (SP) (71, 101, etc.); this phenomenon can encourage the study of the perception mechanisms in insects (e. g. 126). Experiments of synthetic SP in North America, Europe, North Africa, and China showed that in the majority of regions what is known as a *cis*-race of the ECB predominates with the females releasing SP with about 97% *cis*-11-tetradecenyl acetate + 3% *trans*-11-tetradecenyl acetate, whereas in north Italy, south Switzerland, and the state of New York, the so-called *trans*-race of the ECB prevails with the females releasing an opposite SP composition (about 98% *trans*-11-tetradecenyl acetate + 2 *cis*-11-tetradecenyl acetate) (7, 67). Races are capable to coexist, this has been clearly shown in North America (16, 23, 102, etc.), in Europe (7) including Russia and its neighbouring newly independant states (25); moreover, polymorphism within populations of *cis*/*trans* SP responding/releasing genotypes is not uncommon (e. g. 96). In some cases pheromone strains were found to differ in host plant relations (e. g. 80), but it is obvious that the evolution of the strains was not

primarily associated with a host plant specialization. Ratio of geometrical isomers in SP constitution of females is governed by a single autosomal gene (69); the latter seems to constitute a complementary genetic system in concert with at least certain genes controlling male reactions to SP (68), although, at first glance, hereditary control of the male reaction is more complicated: it was reported to be accomplished by either autosomal or sex-linked genes (41, 42, 55). The central nervous system seems to be essential in governing the specific behavioural reactions of males to SP blends (18). Specificity of a SP blend releasing in the ECB races is primarily connected with reductase, responsible for specific conversion of a corresponding precursor (127). In some cases premating reproductive isolation was observed when populations belonging to either of two races were crossed in laboratory conditions (84), whereas in other cases no failure was detected in interracial mating (69). The isolation was also sometimes detected in nature by using electrophoretic approach (17, 56); on the other hand the distinctions in the SP structure appeared to be almost without action on the occurrence of an isolating effect (12, 43). When mating of insects belonging to ethologically isolated populations genuinely occurred, it gives rise to a properly developed and quite viable progeny (e. g. 84). Although the taxonomic nature of the pheromone strains in the ECB was an urgent problem in the 70-80-s, we suppose it will never be understood properly until pheromone strains will be regarded as a part of an quite complicated system of insect adaptations.

As was found in data gathered worldwide, insects attracted by the *cis*-race SP were dominant in the major part of European Russia, although curious exceptions have been recorded (25). Thus, in the hemp growing zone of Ukraine (the Sumy District and the Dnieper river left-bank part of the Cherkassy District) SP-baited traps caught much more males of *O. scapulalis* than of *O. nubilalis*, with the biggest attraction of SP specific for the *trans*-race; in the maize producing zone of Ukraine (as in the Dnieper river right-bank part of the Cherkassy District) SP-baited traps caught males of *O. nubilalis* only and not of *O. scapulalis*, although the latter is abundant in either

hemp or in maize cultivation zones of the country on dicots, but presumably the population densities are different. *O. nubilalis* is known to infest millet in both the two zones of the country but maize is infested in the zone of its traditional cultivation exclusively. Thereafter, the ECB SP-baited traps attracted males neither at the Primorsky area (Far East) nor in Uzbekistan (Middle Asia) and very few if any in Azerbaijan in spite of heavy maize damage and insect abundance in all the above-mentioned territories. It is worth noting that in Georgia (neighbour Azerbaijan Transcaucasian country) *O. nubilalis* was very efficiently attracted by the SP-baited trap (25).

It is argued that east Asia is inhabited by *O. furnacalis* rather than *O. nubilalis* (91): the SP experiments made afterwards in China corroborating this idea (e. g. 6). The taxonomic status of the borer living in Uzbekistan and in Azerbaijan was not clear until recently. Mutuura & Munroe (91) described a subspecies *O. nubilalis persica* with an indication that further investigations are required which may promote its taxonomic position to the point of being a separate species. The last suggestion of (91) seems to be very true despite that only a slight if any morphological distinctions from *O. nubilalis* were mentioned.

Reproductive isolation

Reproductive isolation barriers include both preventing mating (premating mechanisms) and reducing its success (postmating mechanisms) (90). Among premating mechanisms ethological ones are of crucial importance. To assess the differences between host specialized populations a great number of investigations was conducted to evaluate a range of reproductive isolation manifested in laboratory conditions (25). As a result the following conclusions were reached. 1) Insects inhabiting dicots could as a rule mate freely without any effect of male midtibiae morphology, i. e. their affiliation to the same or to distinct species. 2) The ECB populations infesting maize in Ukraine, central European Russia, and North Caucasus (i. e. in temperate European Zones) are

strictly ethologically isolated from the populations injuring dicots, namely *O. nubilalis, O. scapulalis, O. narynensis*, or *O. persica.* 3) Insects infesting maize in the southern regions of the FSU (*O. nubilalis* from Georgia and *O. persica* from Uzbekistan or Azerbaijan) were able to mate freely with those feeding on dicots, but failed to mate effectively with the ECB populations infesting maize in the northern regions of their distribution including Ukraine, central Russia and North Caucasus.

The data obtained suggested that in the *Ostrinia* group a tight relation exists between host plant specialization and premating isolation of the borer populations. In that way, the specialization and reproductive isolation arose evidently in the ECB populations which larvae feed on maize occurring most of the time within the leaf whorl. As far as ethological isolation is concerned, it appears that within the *O. nubilalis* species group the variability between the main components of their SP, as the only factor, is not necessary and sufficient for implantation or failure of different borers to heterogametic mates. This opinion could be supported, for example, by the following fact. "Maize" populations of the ECB both from central Ukraine and Yugoslavia have been actively attracted by a SP specific for *cis*-race of the ECB. Nevertheless a reliable ethological isolation was recorded when these populations were mated in laboratory; at the same time a Yugoslavian population was able to mate freely with populations adapted to dicots from central Ukraine and Russia, i. e. those isolated reproductively from "maize" populations of the same geographical origin (25).

Distinctive postcopulative mechanisms of sex isolation among borers with trilobed male uncus were not observed when crossing in laboratory (25). Success of interspecific crosses within the *O. nubilalis* species group was proved also in Japan by (89). The reliable degree of postcopulative isolation (the absence of spermatophorous transference or the reduction of hybrid viability) in the genus *Ostrinia* appears only when crossing species belonging to too widely diverged species groups. Thus, in spite of substantial ethological

isolation it was possible to obtain only a few viable F_1 *O. nubilalis* x *O. kasmirica* eggs which consisted of only males (28). Although mating of primitive *O. obumbratalis* and *O. penitalis* with *O. nubilalis* was observed in a few cases, the spermatophorous was unable to be transferred (47). It seems that the transition to exploitation of new host plants, which require need for serious modifications in physiology and behaviour, was connected with the obligatory formation of sex isolation barriers. Besides, it is apparent that during the course of evolution the mechanisms of premating isolation had originated first, those of postmating isolation were developed later as an accessory result of increasing divergence. Both are however coupled with a retention of the chromosome number ($n = 30$) (50).

Geographic distribution and population structure in east Europe

An examination of the population structure over many years in east Europe of borers inhabiting dicots, in which specific concentrations of genes and conditioning characteristic features of male midtibiae *(i* and *Mt)* are maintained, permitted to draw some conclusions of fundamental importance for understanding the evolution of *Ostrinia* (27, 34). Samples of larvae were brought from 66 localities of the European part (in central Russia, North Caucasus, the Volga regions, Ukraine, Byelorussia, Lithuania, Azerbaijan) and 5 localities of the Asian part of the FSU (West Siberia, Uzbekistan, south-east Kazakhstan, Far East) with a survey of some of these localities over a period of 3-10 years. As a result wide zones with a practically monotypic population composition were found as follows: 1) west zone (west Ukraine and west Byelorussia inhabited by $Mt^+Mt^+i^+i^+$ the genotype appeared phenotypically as *O. nubilalis*, 2) central zone (central Russia and east Ukraine occupied by Mt^+Mt^+ii the genotype phenotypically as *O. scapulalis),* and 3) east zone (middle and lower Volga, and Azerbaijan populated by $Mt^+Mt^+i^+i^+$ the genotype being affiliated on the basis of very specific biological features as *O. persica*). Aside from the zones mentioned above, a restricted one was detected in central Ukraine (Zhitomir and Vinnitsa Districts, partly Kiev District) where

Mt was estimated on a frequency of near 0 and *i* - close to 1 (i. e. *O. narynensis* phenotypically). Borders between the zones of distribution of the borers with specific genetic structure were clearly seen: changes of gene frequencies from almost 0 to near 1 were observed in spaces of about 50-60 km. At the borders between the zones occupied by monotypic populations, polytypic populations usually occurred, where specific frequencies of genes, determining the characteristic features of male midtibiae types, maintained, as a rule in accord with Hurdy-Weinberg equilibria. To illustrate this, there were 1) the so called hemp borer *O. nubilalis* x *O. narynensis* in the Krasnodar area and in north-west of Russia, in Byelorussia and Lithuania being polymorphic by "small" and "medium-size" midtibiae, 2) populations of *O. narynensis* x *O. scapulalis* in central Ukraine having both "medium-size" and "large" tibiae, 3) populations most probably originated from *O. scapulalis* x *O. persica* in Rostov District and in Crimea manifesting the enormous variability in "small", "medium-size" and "large" type of tibiae.

The long-term observations over the some populations (34) along with the records from museum collections (73, 91) testified that the borders between the areas occupied by borers characterised with specific genetic structure were almost fixed in space for a long time.

It is significant that polymorphism in borers with a trilobed uncus was documented for both Kazakhstan and the Far East (25). There is some evidence (e. g. 89) in favour of not infrequent polymorphism in *Ostrinia* populations inhabiting also east and south-east Asia.

Taking into account peculiarities of borer variability, FROLOV (27, 34) came up with a proposal to consider *O. nubilalis*, *O. persica*, *O. narynensis* and *O. scapulalis* as a group of semispecies being combined into a superspecies *O. nubilalis* s. l. If this is accepted, the existent nomenclature would remain intact, and transition polymorphic populations could be described by composite names such as *O. nubilalis* x *O. narynensis*. One can suppose that *O. furnacalis*

is a member of this superspecies too; this idea can be supported by the result of allozyme differentiation analysis among *O. furnacalis* and *O. nubilalis* (124), as well as of specificity in the SP biosynthesis (127).

All which is mentioned above indicates that the variability of borer populations, even if complicated, is regularly structured. The comprehension of the existence and subsistence of population variability in the *O. nubilalis* species group will never be achieved if it is not in the context of adaptiogenesis.

Ecological factors responsible for variation

In accordance with Liebig's low the adaptive evolution is primarily directed towards compensation of a limiting effect of the most important ecological factor. According to Haldane's dilemma, the limiting link evolution must be like a relay, with the mutations that cancel the limiting effect being always highly adaptive. It is true that heat, water, and food are the most critical factors for all living beings including insects, and it is not surprising that these factors are most likely to have a direct bearing on the evolution of complex population structures in borers with a trilobed uncus.

Temperature

Among the numerous factors that have affected the ECB development, the temperature is one of paramount importance (10). Completion of the entire ECB generation would require 600-715 days-degrees (DD) accumulated (10, 74). Spread of the different populations varies in its heat resources, i. e. in over years DD means providing the development of only certain number of generations per year. Reduction of day length serves as a reliable predictor of the onset of the cold period in the near future: thanks to photoperiodic reaction insects make appropriate preparations for diapausing; in addition, temperature decrease during the larval development is conducive to diapausing (10). One

can often find regional distinctions in developmental periods even though neighbour ECB populations are concerned with (83, 93).

Wetting Conditions

It is well known that the ECB is a hygrophilous species. Its geographic distribution and population dynamics depends on the amount of water available for pupation of overwintered larvae, development of eggs and early larval instars, and, especially, reproduction (e. g. 19, 66, 74, 78, 79, 104, 112).

O. nubilalis ☐   O. narynensis ▦
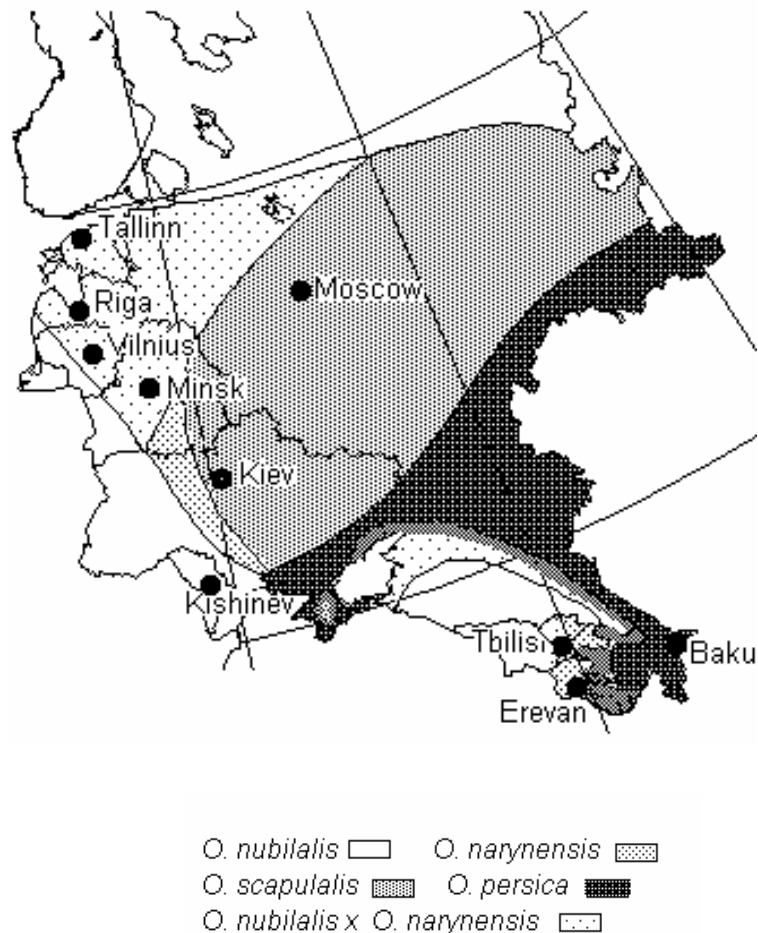O. scapulalis ▦   O. persica ■
O. nubilalis x O. narynensis ⬚

Figure 1. Schematic map of distribution of the European corn borer and allies feeding on dicotyledonous host plants at the European part of the Former Soviet Union.

Regular mapping of borers feeding on dicots, differed by their genetic population structures and correspondingly by the morphology of male midtibiae was observed in European part of the FSU and was in accordance with the data on humidity (34). On the basis of the average precipitation an easy prediction of the genetic structure of populations infesting dicots is possible: in zones, where the precipitation in June, is no less than 77 mm, *O. nubilalis* occurs, where it is between 51 and 76 mm *O. narynensis* and *O. scapulalis* (the first is more hygrophilous than the second) live, and where precipitation is no more than 50 mm *O. persica* is found. The suitability of the model was tested in an independent number of points with known climatic characteristics and borer population structures. Accordingly the schematic map was created which describes geographical distribution of known morpho-biological types of borers inhabiting dicots in the European part of the FSU (figure 1; see also 34).

Populations with a polymorphic structure are located in zones where intermediate wetting occurs. Therefore in spite of the very probable differences in the composition of the SP produced by females, the borers with trilobed uncus are able to form hybrid populations at the borders of their ranges. The jump-like changes of population structure of borers appear to follow the continuous and gradual changes in mean humidity. Apparently hybrid populations may be considered as an integral part of the strategy of space exploitation by borers infesting dicots as their original hosts (32, 34).

In the FSU larvae of the ECB were identified on dicots in very humid zones only, such as west Ukraine and Byelorussia, west Georgia, the foothills of North Caucasus, and the coast of the Black Sea. On maize this species was collected in dryer parts as well, such as central and east Ukraine, the central parts of Russia, and the steppe regions of North Caucasus. Within the latter territories morphologically distinctive populations of the ECB on maize and of *O. narynensis*, *O. scapulalis*, or different heterogeneous populations on dicots, have become sympatric (32, 34). Therefore, the ECB populations that shifted to

cereal feeding have become more widely distributed than the ECB populations restricted to dicots (35).

In general the evolution in the genus *Ostrinia* was supposed to be directed towards developing the adaptations which promoted insect expansion into more arid niches. For example, comparing of climate characteristics of the areas occupied by *O. furnacalis* and *O. nubilalis* shows that the former is much more hygrophilous than the latter. There is an unusually high variation in the average levels of precipitation specified for different localities in east Asia; this fact is likely to be of the utmost significance for the enormous variability of *Ostrinia* representatives having mapped there (32).

The ratio of pheromone strains in the ECB populations is observed to fluctuate in space and time (7, 114, 115, etc). The evolution of pheromone strains in *O. nubilalis* may be thought of as having occurred in the case of *O. nubilalis*, *O. narynensis*, *O. scapulalis*, and *O. persica* evolved as adaptations to climates which are variable in humidity. It seems that the evolution of a more hygrophilous *trans*-race was associated with wetted slopes of mountain systems such as the Alps, the Carpathians, or the Caucasus, this in opposition to the less hygrophilous *cis*-race adapting to the sea climate of West Europe (32).

Host Plant Resistance

Populations of *O. nubilalis* that shifted to maize, show many specific adaptations including behavioural reproductive isolation. This is an example of adaptations found in *Ostrinia* spp. which are seem to be connected with overcoming immunological barriers in their host plants (25, 31).

It is known that feeding of the 1-st and 2-nd instar larvae is the critical period in the ECB ontogenesis. The parts of a plant on which the insects feed vary with the stage of maize growth. Before tasseling, the larvae have to feed

on whorled leaves, and in this case their death rate, even on susceptible plant genotypes, can reach 75% and more (49). After tasseling the 1-st and 2-nd instar larvae gain access to more valuable food such as tassel spikelets, leaf sheaths and collars, ear husks and silks, and pollen grits; this results in a decline of insect mortality to somewhat a minimum (e. g. 51, 52). The resistance of maize to the ECB leaf feeding is known to be mainly conditioned by the action of secondary plant substances, with cyclic hydroxamates, such as 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), playing an important role among them (9, 54, 72); besides that, other factors of resistance are in operation (1, 118). The older the maize plant becomes the less relative content of hydroxamates is usually present, and after tasseling their action on larvae breaks down (53, 70). The content of DIMBOA seems to be correlated with the affluence of pathogens in places where local maize varieties had been established (99); it is clear that the selective value of antibiotic resistance of maize to pathogens must be effective just at the early developmental stages, because tolerance has not advanced adequately. The maize genotypes resistant to leaf feeding occur frequently in selection materials (e. g. 36, 48), whereas collar-sheath resistant genotypes are few and far between (45).

Compared to dicots, maize represents a valuable source for the ECB feeding, since 1) the expenditures for host searching due to abundance of resources available are diminished; 2) high food quality after tasseling is ensured (e. g. 79, 86); 3) comfortable surroundings for adults are provided due to higher humidity inside the field (35). So leaf feeding resistance may be one obstacle that prevents maize utilisation by the ECB as a mutual host plant together with dicots.

The fact that populations that feed on maize develop later compared to those feeding on dicots has been known long ago to be apparently related to temporal optimization of egg-laying owing to relative delaying in maize development (25, 92, 121). It is apparent that if thermic resources are limited, the natural selection is essential to reach some optimization of the ECB phenology: on the

one hand the development of larvae on maize should be carried over as later stages as possible to avoid leaf whorl feeding and enhance consequently insect survival, but on the other hand plants should be infested in time to complete insect life cycle before cold weather arrives (33). So when the ECB populations on the north are taken into account, the larger part of the larvae on maize are forced to feed on whorled leaves. In the view of the fact that maize leaf feeding is necessary for special physiological and ethological adaptations, the latter requires the host range restriction and reproductive isolation which develops in populations when they feed on maize. In the southern regions where heat resources are not often a limiting factor, the ECB populations can infest maize after tasseling following the strategy of escaping detrimental effects of leaf feeding resistance. In such a case the ECB distinctive polyphagous feature remain unchanged and no reproductive isolation occurs.

Therefore, at least two strategies of host plant exploitation by borers can be distinguished: 1) host species-generalized but host stages-specialized and 2) host species-specialized but host stages-generalized strategies. This means that in zones of favourable abiotic conditions insect populations feed on a wide range of host plants and at those stages when antibiotic resistance of plants is low, which usually happens after the vegetative stage is finished. It is obvious that this strategy is primary. The other strategy can be seen in more rigorous climates where insects have to begin feeding on plants early in the ontogenesis when antibiotic barriers are highly effective. This strategy is followed by the "maize" populations of the *O. nubilalis* from the European part of the FSU (31). In the light of these theoretical and empirical relations finding of sex isolation between borer populations have to be regarded as the first sign of their probable specialization through host plant exploitation strategies.

Variation and population dynamics

It is completely obvious that the survival of borers depends strongly on their diapausing in time; manipulation of the ECB larval diapause could possibly be a potential mechanism for pest management on maize (111).

The above mentioned data could suggest that the humidity influences the borer population's dynamics mainly during the periods of moth flight. It is truly known that the sexual activity and reproduction of the ECB moths is determined by the presence of drop-liquid water (19, 112). Furthermore, it was demonstrated in east Europe that overwintered ECB moths strongly manifest an aggregation behaviour directed to a search of "action" sites strongly protected by wood shelter belts from the prevalent winds (39).

It is common knowledge that host plant resistance in maize has a profound impact on ECB population dynamics; it does take an active part in the control of the ECB mainly during first generation development (46).

Alternatively, it is important to discuss the life table analysis experience that enables one to estimate quantitatively the effects of population dynamics factors. In the case of the ECB life tables should provide valuable information due to the fact that in general adult dispersal of *Ostrinia* representatives seems to be quite restricted (125), although some direct movements of moths could be detected also (113).

Three-year life table data showed that in the Krasnodar area the most distinct decrease in the ECB population density on maize is determined by 1) mortality of the early instar larvae of the 1-st generation during the beginning of their feeding within the maize leaf whorl (70-90% of the population decrease), and 2) death and/or dispersal activity of adults of the 2-nd (overwintered) generation when in search of plants at suitable stages of their development (74-89% of decrease) (37). In the Belgorod District (one generation zone of Russia) both the above-mentioned factors appeared to be in operation (37), while in Quebec (one generation zone of Canada) only the latter

factor was proved to be of prime importance and the former of less importance in the ECB population dynamics (58). Although the process of increase or decrease of borer populations may be in some areas of Russia due to the effects of density-dependent factors, such as larval parasites, the overall level of borer mortality from the biotic factors is of less and inconstant value through insect generations in comparison to the above mentioned two density-independent factors (37).

The above data on biological variability in the genus *Ostrinia* suggests a close relationship between the race formation as a microevolutionary event and the effects of the population dynamics factors as an ecological process. Race formation, as a relatively fast evolutionary event, is associated with changes in a rather small part of genome (75). In this connection it is not surprising that the phenomena of race formation have been making their appearance in the critical periods of the borer life cycle, when insect mortality peaked persistently and any mutation of even minuscule elevation of insect survival should be picked up by natural selection.

General remarks and considerations for the future

All above-mentioned materials strongly suggest that the process of race formation in the ECB and its allies is a matter not only of exceptional interest, but also of concern to general biology. Biotypes, including races, ecotypes, and semispecies, in *Ostrinia* have supplied some new ideas as "food for thought" on such topics as species concepts and its criteria, causes of origin of reproductive isolation and mechanisms of its maintenance, the role of SP in reproductive isolation support, nature of "tension" (hybrid) zones, the generalized properties of biological races in insects, and so on (33).

Although considerable progress has been made in recent years towards the comprehension of regularities in the evolutionary process of the genus *Ostrinia*, many questions remain to be answered. Only the first layer of

knowledge about the population biology of *Ostrinia* was opened at the moment, and one would expect remarkable findings in the near future.

In any case, valuable information on intimate aspects of population biology of *Ostrinia* can be gained, for example, from the performance of detailed biotaxonomic analysis of the enormous variability of *Ostrinia* populations in east and south-east Asia as was pointed out by Mutuura & Munroe (91) as early as in 1970. It is also necessary to underline that to make the picture complete, it is necessary to assess carefully insect biodiversity using the system of criteria proved to be informative; planning of works and analysing of results may be facilitated if one will take into consideration the well-defined effects of wetting. The thorough investigation of biology and ecology of *O. persica* as well as the clarification of its taxonomic position seems to be particularly interesting both for European and west Asian entomology and plant protection. As for *O. nubilalis s. s.,* little is known about its populations occupying distinct from maize cereals, notably cultured and wild small cereals, e. g. millet and cocksfoot panicum, *Echinochloa crus-galli*. Despite their low density nowadays these populations are doubtless important for the reconstruction of really protracted and complicated process of turning the ECB into the pest of agricultural crops in the historical past. It is of value also to clarify the extent to which the Far Eastern borer, *O. orientalis*, is genetically different from the ECB. It is not improbable that this morphologically indistinguishable from the ECB species, which has never been found on maize, is actually a part of feeding on dicots populations of *O. nubilalis s. l.*

Being critical for both the theory and the practice, the question of the diversity of borer populations in their strategies of host plant exploitation, is obviously in need of further intensive studying, first of all in different zones of insect inhabitancy in Eurasia. Besides, it would be most intriguing to trace probable microevolutionary changes in the strategies of ECB populations having occupied huge territories of North America for a relatively short period after the pest introduction into new surroundings.

The further progress in studying of *Ostrinia* biodiversity is evidently meaningless without identification of SP compositions of the closest ECB species. One might imagine exciting prospects of sex communication analysis in the systems of tension zones constituted by *O. nubilalis* and its allies. Besides *O. nubilalis*, *O. furnacalis* is today the only species of the genus, which SP was identified.

It would important to determine the real function of "evolutionary luxurious" sex modifications found in the male midtibiae of some borer species; if one knows the functioning of some organ in a high specialized species, it will be as easy as possible to find and estimate its role in a non-specialized one.

Both the ECB and its allies are widely distributed all over the world. It is obvious that prosperity of the ECB and allies is due in many respects to the evolution of adaptations to the local environments. Hence realizing the nature and variability of insect adaptations is hardly probable without close co-operation of national scientists joining their forces under the mutual program such as the International Working Group on *Ostrinia* and Other Maize Pests (IWGO) of IOBC.

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