POPULATION DYNAMICS OF *OSTRINIA NUBILALIS*: SPECIFICITY IN KEY FACTORS FOR ONE- AND TWO-GENERATION ZONES OF RUSSIA

ABSTRACT

Ecological factors critical for the European corn borer, *Ostrinia nubilalis* (Hbn.), (Lepidoptera: Pyralidae) were studied intensively, but their actual influence on population dynamics was not sufficiently understood yet. During 1994-1998 life tables were arranged for two local populations inhabiting eastern part of the Krasnodar Territory (two-generation zone) and southern part of the Belgorod Province (one-generation zone). By using graphic K-factor analysis (Varley, Gradwell, 1960) and regression component analysis (Harcourt, 1966) it was established that at the Krasnodar Territory a key factor performs during I-II instar larval feeding of the 1st generation, while in the Belgorod Province it operates during the period of moth activity. Just as density-independence, so density-dependence in operation of key factors was displayed. It is supposed that the behavioural responses of I-II instar larvae to aggregation may play an important role for density-dependent population decline. The density-dependence of egg realisation by females most likely based also on behavioural reactions of adults leaving overpopulated places.

Key words: European corn borer, *Ostrinia nubilalis*, population dynamics, Russia

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INTRODUCTION

Ecological factors critical for the European corn borer (ECB), *Ostrinia nubilalis* (Hbn.), (Lepidoptera: Pyralidae) were studied quite intensively (Shchoegolev, 1934; Kozhanchikov, 1935; Sparks et al., 1967; Barlow, 1971; Chiang, Hodson, 1972; Hudon, LeRoux, 1986, Kornoєor, Kayapinar, 1988, etc.), but their actual influence on population dynamics was not sufficiently understood yet. Wide growing of genetically engineered maize could occur in the very near future demanding to study the ECB population dynamics just now before significant alterations happen. Furthermore, the ECB population dynamics has been properly investigated only in North America, while the pest being of the European origin. Up to date, thorough analysis of the ECB population dynamics has never been fulfilled in Europe.

The Krasnodar Territory and the Belgorod Province are the main zones of grain and seed production of maize in Russia. Both regions are characterised by climatic conditions favourable for the ECB propagation. However, these regions differ in surroundings critical for the ECB ecology. Thus, in the former zone two annual generations develop and a trace of the 3rd generation appears almost each year, while in the latter only one generation develops per year. Besides, at the Krasnodar Territory maize had long-standing grown for grain and seed production, contrary to the Belgorod Province where it had almost exclusively cultivated for silage even about 20 years ago. In so doing, the ECB is known at the Krasnodar Territory as a prime pest of maize since the first quarter of the 20th century, whereas in the Belgorod Province the insect became attacking maize seriously only about 10-15 years ago. Furthermore, the ECB at the Krasnodar Territory is capable to infest actively sorghum aside maize in contrast with the Belgorod Province where the insect is able to develop on millet.

Final goal of the work is to construct an appropriate model for the ECB population dynamics in its homeland territories, including southern (Krasnodar) and northern (Belgorod) parts of the Russian "Corn Belt". First results of the study obtained in 1994-1995 were presented at the 18th IWGO Conference held in Romania (Frolov et al., 1995). The present paper reports on life-table analysis of the ECB population fluctuations during 1994-1998 with the aim to detect key factors responsible for the insect population dynamics. The study is going to be continued and during the next stage we will assess quantitatively effects of density-dependence and density-independence as well as to start investigation of a factor responsible for cyclicity in population dynamics of the pest at the Krasnodar Territory.

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MATERIALS AND METHODS

The ecological study plots were located within the scientific crop rotations of the Kuban Experimental Station (KES) of the All-Russian Institute for Plant Industry, located at eastern part of the Krasnodar Territory, and the Belgorod State Agricultural Academy (BSAA), located at southern part of the Belgorod Province. All the usual tillage cultural practices were used including cultivation, herbicide treatments, and mechanised cultivation, mowing and threshing at harvest. During 1994-1998 we made counts of insect densities on crops actively infested by the ECB, namely, maize (KES, BSAA) and sorghum (KES). Other host plants of the ECB, including millet (BSAA) or panicle cereal weeds (KES) usually occupied spaces much less than 5% of those occupied by maize, and thus were excluded of observation.

The samples were periodically collected to estimate insect densities and related mortality factors. Direct sampling was performed during certain time intervals when the specific stage of insect development (egg, larva, pupa, adult) prevailing on 0.02-22 ha fields (6-21 fields at KES and 2-4 in BSAA each year). The total number of surveys was 21-23 at KES and 12-14 in BSAA. Randomised sample units chosen were 0.1-1 m^2 plots for overwintering larvae in remnants, 1-3 m^2 plots for attacking plants larvae, and 0.8-5 m^2 plots for egg counts; the number of sample units on each field varied to assess statistically significant estimates (usually of 10-50 plots per field). All insect numbers were calculated per 1000 m^2 of maize sowing.

Spatially fixed plots were used to count egg densities. Each egg cluster found on foliage was marked and a hand lens was used to count the number of eggs as either hatched successfully, parasitised, predated, dislodged, or dead due to fail to develop embryo (infertility) or larval inability to hatch (possibly from desiccation). Each plot was examined for 6-8 times in 5-7 day intervals during the period of moth flight. To estimate the whole number of eggs laid we summed up the numbers of eggs found during each successive examination of a plot.

The summer larvae and pupae (in case of KES) were sampled on random plots usually twice by 5-10 days after finishing of egg laying. The leaf and stalk damage was used only as a good visual clue to locate presence of insects. The estimate of adult density was obtained from the number of pupal cases. To estimate female fecundity, insects were kept under insectary conditions. The total decrease in adult numbers during their egg laying was assessed indirectly on the basis of difference between actual and expected numbers of oviposited eggs.

For the Krasnodar population insect numbers were estimated for the following age intervals of the 1st generation: 1. total eggs (eggs laid either on maize or sorghum), 2. maize eggs (eggs laid on maize), 3. I-II instar larvae, 4. III-V instar larvae, 5. pupae, 6. adults, 7. females (= adults with sex ratio of 1:1), 8. normal females (= adults with sex ratio of 1:1 and 450 eggs deposited per one gravid female), and 9. ovipositing females (the number of eggs of the next generation divided on one-half of the mean number of eggs deposited per one gravid female, that is in this case — on 225). During the development of the 2nd generation insect numbers were estimated for the following age intervals: 1. total eggs, 2. maize eggs, 3. I-II instar larvae, 4. III-V instar larvae, 5. diapausing larvae before harvest, 6. diapausing larvae after harvest before hibernation, 7. overwintered larvae, 8. pupae, 9. adults, 10. females, 11. normal females, and 12. ovipositing females. For the Belgorod population insect numbers were estimated for the following age intervals: 1. eggs, 2. I-II instar larvae, 3. III-V instar larvae, 4. diapausing larvae before harvest, 5. diapausing larvae after harvest before hibernation, 6. newly overwintered larvae (April), 7. overwintered larvae before pupation (June), 8. pupae, 9. adults, 10. females, 11. normal females (the average level of fecundity was assumed 360 eggs deposited per one gravid female), and 12. ovipositing females.

Density drop for each age interval was assessed by $K = \log N_t - \log N_{t+1}$, population trend index, $I = \frac{N_{t+1}}{N_t} \times 100$, was calculated after R. Morris (1957), where N_t and N_{t+1} = insect densities before and after an action of mortality factor. Key factor analysis (Varley, Gradwell, 1970) and component regression analysis (Harcourt, 1969) were used to detect age intervals with the most significant insect mortality.

RESULTS AND DISCUSSION

Analysis of age and total mortality in two European corn borer populations

More than 10-fold fluctuations in total egg numbers were observed for the Krasnodar population during 1994-1998: from 6.9 m^{-2} to 109.0 m^{-2} (1st generation) and from 12.3 m^{-2} to 191.2 m^{-2} (2nd generation). Fluctuations in egg numbers of the Belgorod population were significant as well and varied from 15.5 m^{-2} to 70.8 m^{-2}. Changes in insect densities during specific age intervals are presented for both populations (fig. 1, 2).

Fluctuations in age mortalities along with a fluctuation in total mortality were presented also both for the Krasnodar (fig. 3, 4) and the Belgorod population (fig. 5) with a view to perform K-factor analysis.

It is obvious that the age interval of I-II instar larvae is a critical period in population dynamics of the Krasnodar population during the development of the 1st generation. The early instar larval mortality in the shape of curve of k follows the same fluctuating course as K (total mortality) (fig. 3). Besides, the late instar larval mortality influenced significantly the total mortality during the period of population depression (1994-1995), but was of minor importance when the insect density increased. Fluctuations in k-values for the other age intervals (eggs, pupae, adults) seemed to have low impact on total K.

As far as the 2nd generation is concerned, neither mortality factor is capable to vary through a sufficient range of magnitude to affect fluctuating course as K (fig. 4).

An adult mortality (normal females) influenced most significantly population dynamics of the Belgorod population (fig. 5).

The component regression analysis substantiates that the early instar survival is a critical factor for the Krasnodar population dynamics during the 1st generation development (table 1). Despite a high correlation and t-value significance, both the mortality of laid on maize eggs and the mortality of I-II instar larvae seem to affect the total mortality of insects during the 2nd generation less than some other mortalities, e. g. during harvest, overwintering, or egg laying (table 2). All it means that the mortality of I-II instar larvae should consider after Morris (1959) as the only principal key factor affecting population dynamics of the pest at the Krasnodar Territory.

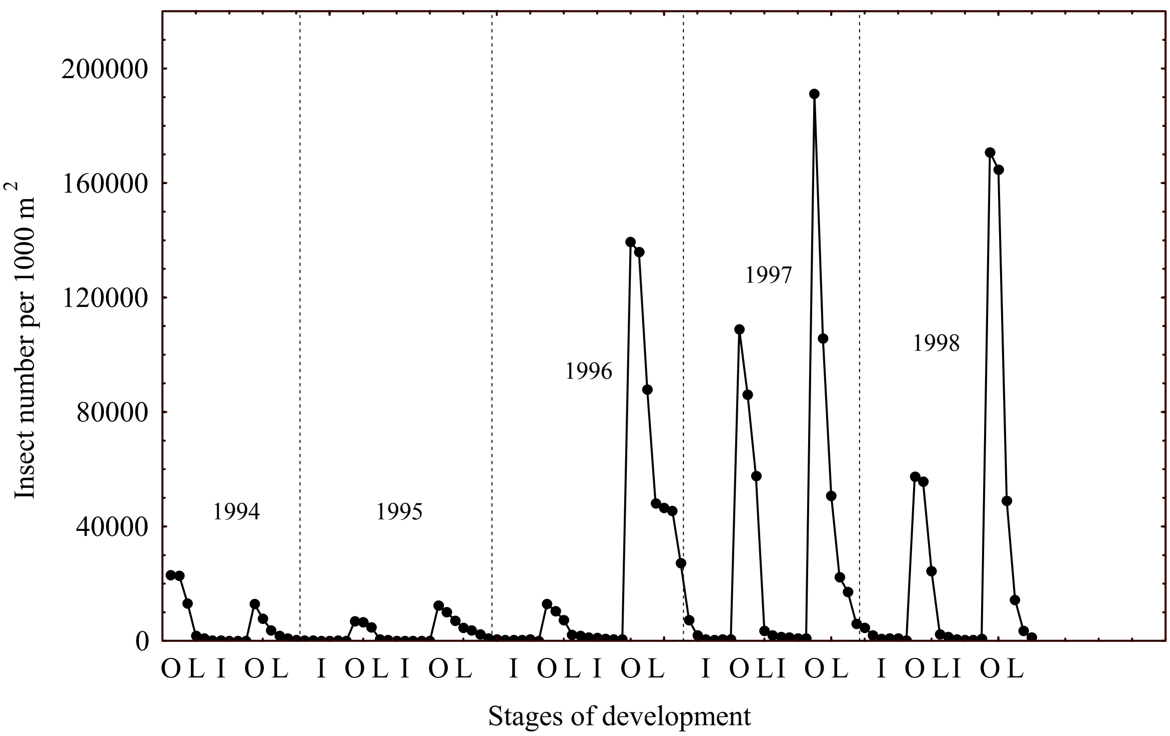

Figure 1. Population dynamics of the ECB at KES during 1994-1998. Letters O, L, I mark densities of total eggs, III-V instar larvae, and adults correspondingly.

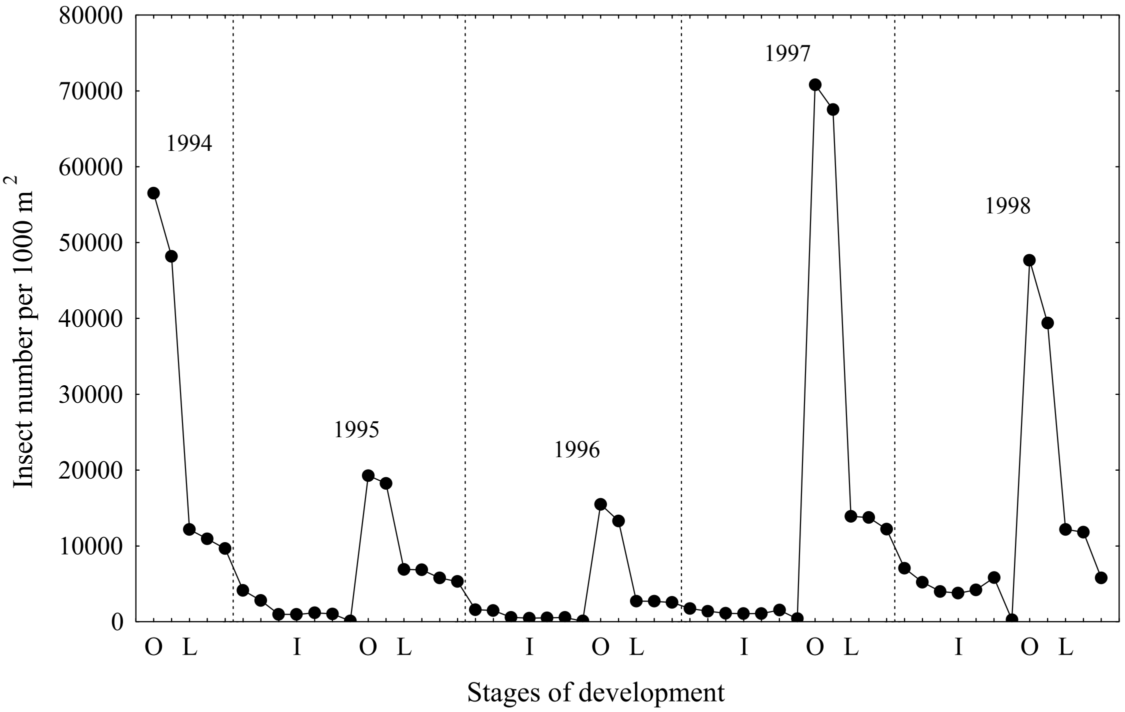

Figure 2. Population dynamics of the ECB in BSAA during 1994-1998. See legend of fig. 1 for explanation of O, L, and I.

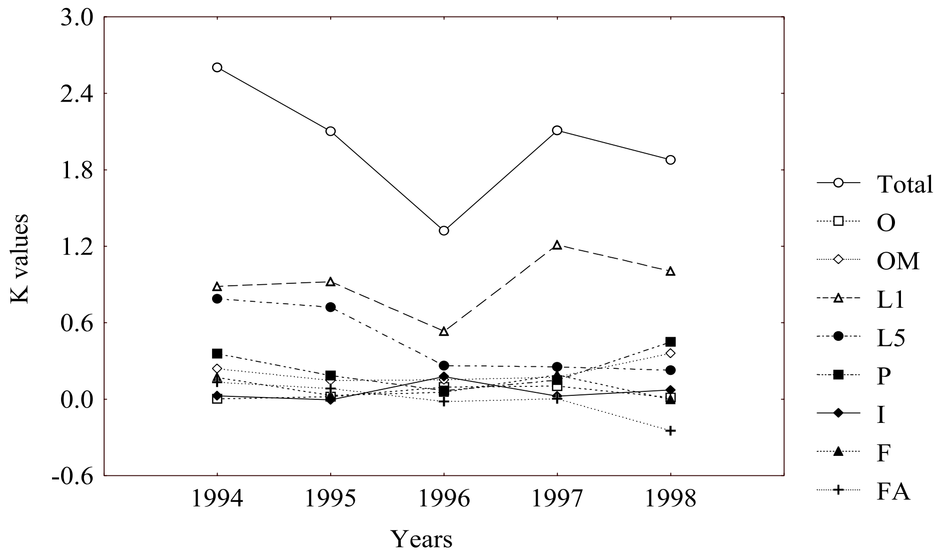

Figure 3. Curves of age and total mortalities of the ECB during the 1st generation at KES in 1994-1998. Age intervals: O – total eggs, OM – eggs laid on maize, L1 – I-II instar larvae, L5 – III-V instar larvae, P – pupae, I – adults, F – females, FA – normal females. Total – total K for a generation.

Table 1. Means, variances, correlation coefficients, and t-tests of significance of age survivals and population trend indices during the 1st and 2nd generation at KES (1994-1998)

Survival estimate	Mean	Variance	$r_{(Y.X)}$	$r^2_{(Y.X)}$	t	p_a
		1st generation				
Population trend index	3.564	4.105				
Total eggs	0.903	0.097	-0.572	0.328	-1.209	0.313
Maize eggs	0.620	0.115	0.313	0.098	0.570	0.608
I-II instar larvae	0.141	0.090	0.910	0.828	3.798	0.032
III-V instar larvae	0.410	0.214	0.496	0.246	0.988	0.396
Pupae	0.602	0.205	0.652	0.426	1.491	0.233
Adults	0.883	0.135	-0.931	0.866	-4.410	0.022
Females	0.828	0.160	0.330	0.109	0.606	0.587
Normal females	1.073	0.408	0.147	0.022	0.257	0.814
		2nd generation				
Population trend index	0.667	0.324				
Total eggs	0.737	0.196	0.756	0.572	1.635	0.244
Maize eggs	0.582	0.115	0.957	0.916	4.665	0.043
I-II instar larvae	0.529	0.087	0.993	0.987	12.215	0.007
III-V instar larvae	0.674	0.223	-0.180	0.032	-0.259	0.820
Diapausing larvae before harvest	0.466	0.106	0.364	0.132	0.552	0.636
Diapausing larvae after harvest before hibernation	0.498	0.240	-0.253	0.064	-0.370	0.747
Overwintered larvae	0.561	0.279	0.018	0.0003	0.026	0.982
Pupae	0.626	0.314	0.383	0.147	0.587	0.616
Adults	1.012	0.173	-0.015	0.0002	-0.022	0.984
Females	1.129	0.116	0.737	0.543	1.542	0.263
Normal females	0.405	0.378	0.030	0.0009	0.042	0.970

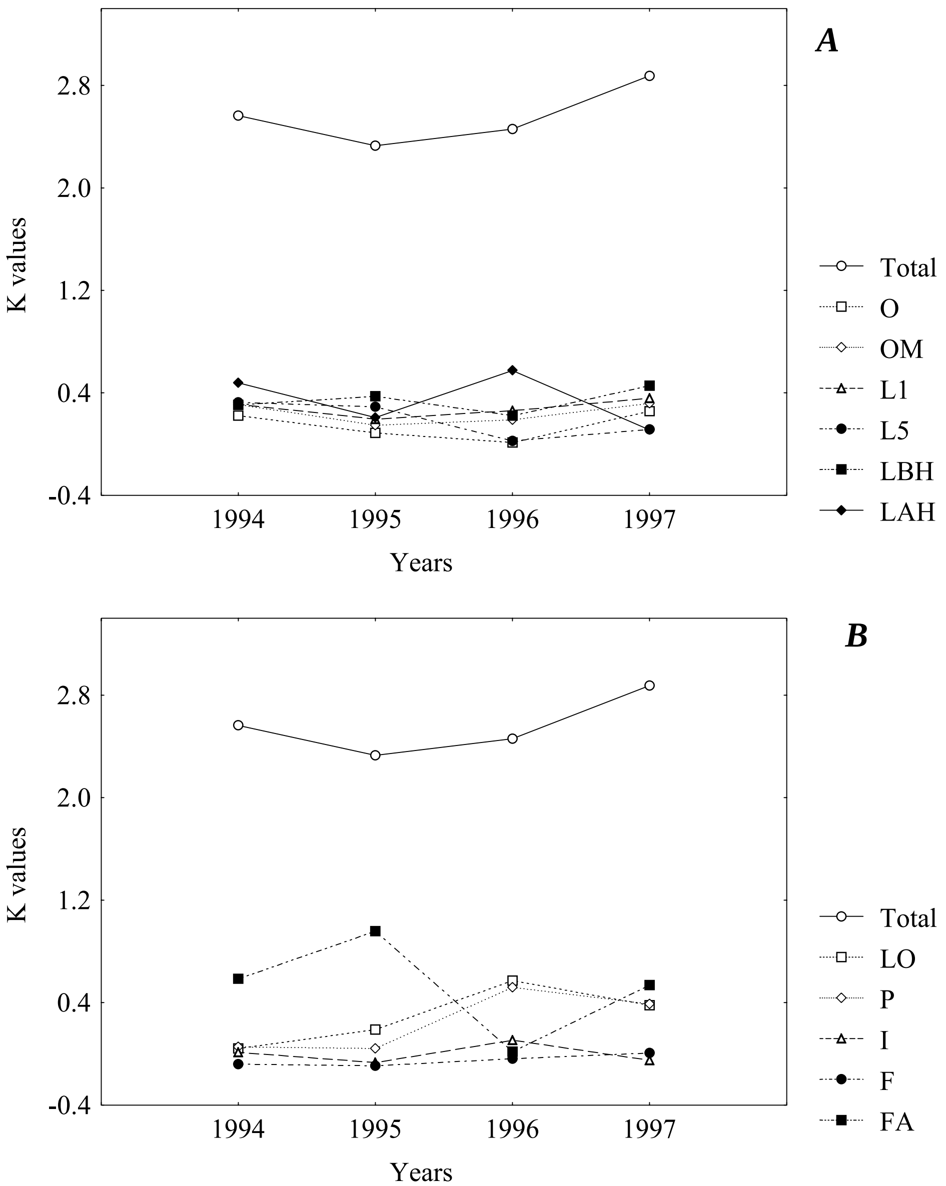

Figure 4. Curves of age and total mortalities of the ECB during the 2nd generation at KES in 1994-1998. ***A*** (before hibernation): O – total eggs, OM – eggs laid on maize, L1 – I-II instar larvae, L5 – III-V instar larvae, LBH – larvae before harvest, LAH – larvae after harvest, before hibernation; ***B*** (after hibernation): LO – overwintered larvae, P – pupae, I – adults, F – females, FA – normal females. Total – total K for a generation.

In spite of a high correlation and t-test significance, the larval mortality of the Belgorod population during harvest appeared to influence the total mortality less than some other factors, such as the larval death during hibernation or before pupation in April – June. The adult mortality (normal females) is the only factor, which affects a population dynamics dramatically (table 2).

It is important to mention that at the Krasnodar Territory the ECB population numbers declined seriously during the oviposition by overwintered (= 2nd generation) adults as well (table 1). For the Belgorod a population death of early instar larvae is detected being rather high too (table 2).

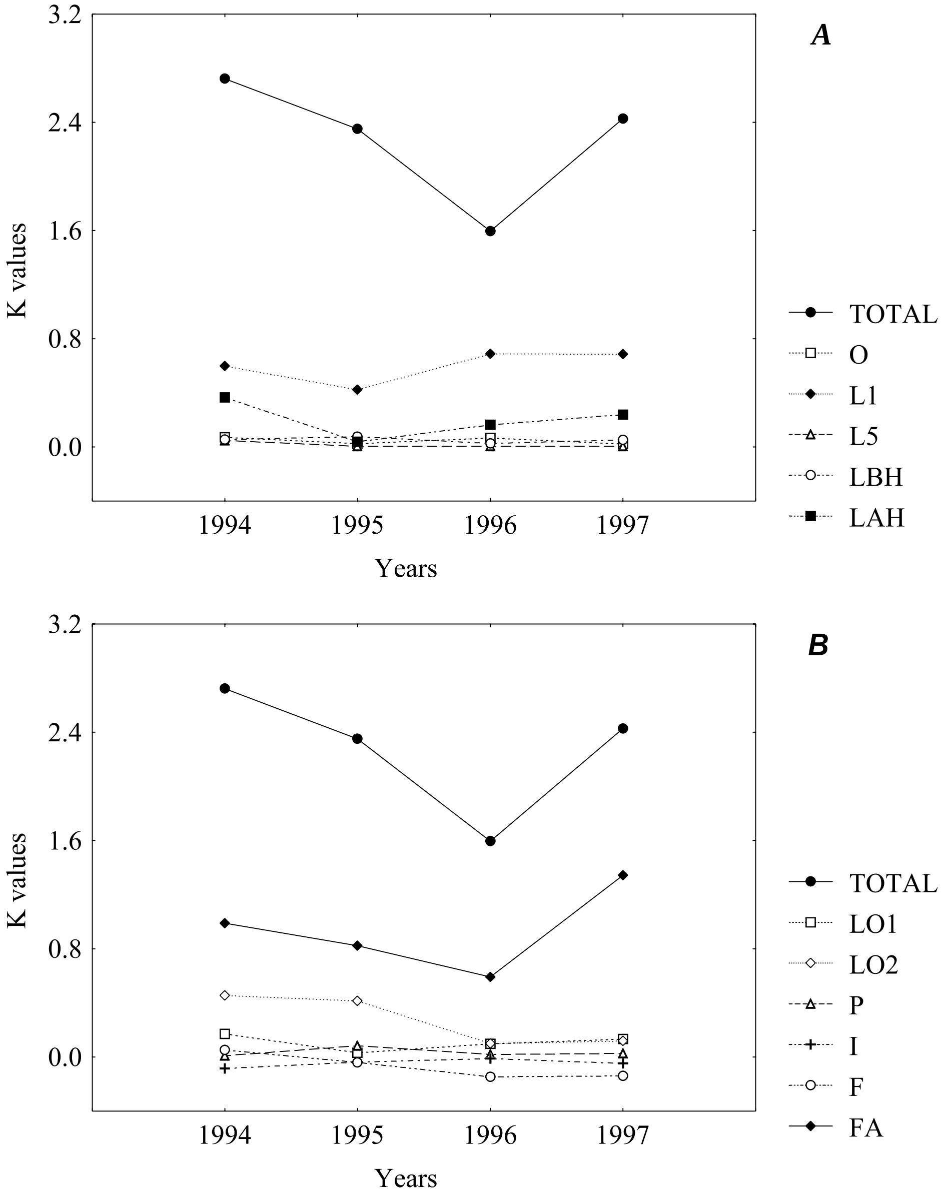

Figure 5. Curves of age and total mortality of the ECB in BSAA in 1994-1997. ***A*** (before hibernation): O – eggs, L1 – I-II instar larvae, L5 – III-V instar larvae, LBH – larvae before harvest, LAH – larvae after harvest, before hibernation; ***B*** (after hibernation): LO1 – newly overwintered larvae in April, LO2 – overwintered larvae before pupation in June, P – pupae, I – adults, F – females, FA – normal females. Total – total K for a generation.

In other words, insect numbers of both populations decreased most significantly during the same age intervals (= critical periods in general cycle), as follows: 1) the early instar larval feeding within the maize leaf whorl, and 2) the activity of overwintered adults when egg laying. However, graphic K-factor analysis and regression component analysis have proved their specific role in regional population dynamics: the former factor determines total mortality level at the Krasnodar Territory, the latter one – in the Belgorod Province.

Table 2. Means, variances, correlation coefficients, and t-tests of significance of age survivals and population trend index at BSAA (1994-1997)

Survival estimate	Mean	Variance	$r_{(Y.X)}$	$r^2_{(Y.X)}$	t	p_a
Population trend index (I)	1.598	1.994				
Maize eggs	0.903	0.054	-0.453	0.205	-0.719	0.547
I-II instar larvae	0.261	0.082	-0.403	0.163	-0.623	0.597
III-V instar larvae	0.966	0.045	0.403	0.163	0.623	0.597
Diapausing larvae before harvest	0.888	0.040	0.827	0.683	2.078	0.173
Diapausing larvae after harvest before hibernation	0.494	0.179	0.702	0.492	1.393	0.298
Overwintered larvae (April)	0.787	0.110	0.167	0.028	0.242	0.831
Overwintered larvae before pupation (June)	0.575	0.238	0.646	0.417	1.196	0.354
Pupae	0.926	0.068	0.209	0.044	0.302	0.791
Adults	1.112	0.078	-0.794	0.630	-1.840	0.206
Females	1.192	0.245	0.612	0.374	1.094	0.388
Normal females	0.139	0.894	0.883	0.780	2.662	0.117

Key factors in the European corn borer population dynamics

The mortality of I-II instar larvae during the 1st generation development at the Krasnodar Territory

The average survival of I-II instar larvae varied from 6.2 to 29.4% during 1994-1998. The early instar larval survival was confirmed to correlate with the host plant resistance in maize (fig. 6). However, neither meteorological factor measured (mean, maximum, and minimum daily air temperature; maximum and minimum soil surface temperature; the least relative air humidity; precipitation) influenced significantly on the early instar larval survival. Perhaps, it was due to a short duration of larval stay outside the host plant. Nevertheless, it is not improbable that weather/climate can influence the larval survival by means of changing host plant suitability for insect feeding.

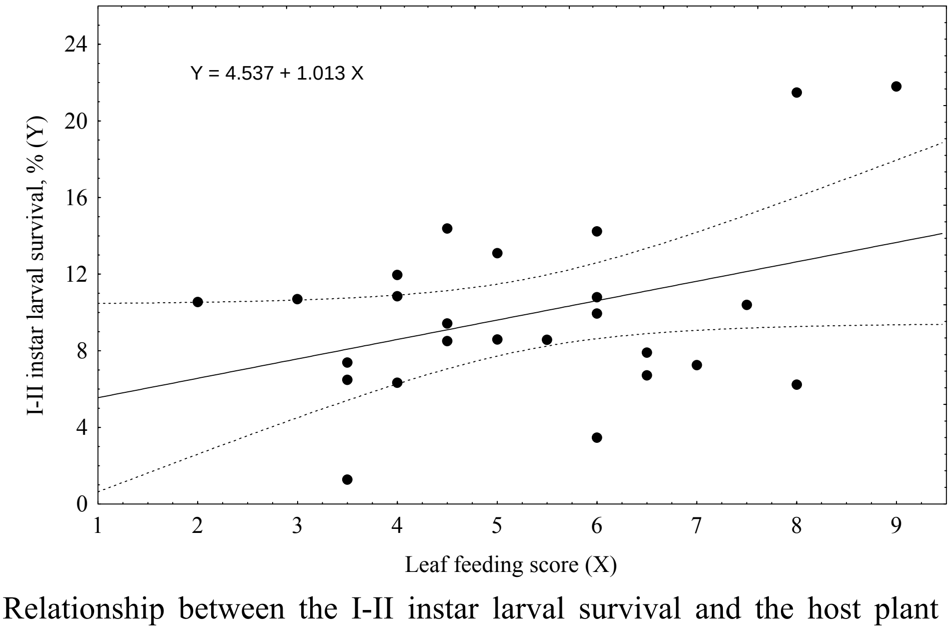

Figure 6. Relationship between the I-II instar larval survival and the host plant resistance in maize varieties measured by leaf feeding scores at KES (1994-1998)

On the other hand, the early instar larval survival demonstrated significant density-dependence proved at $p_a = 0.0001$ (fig. 7).

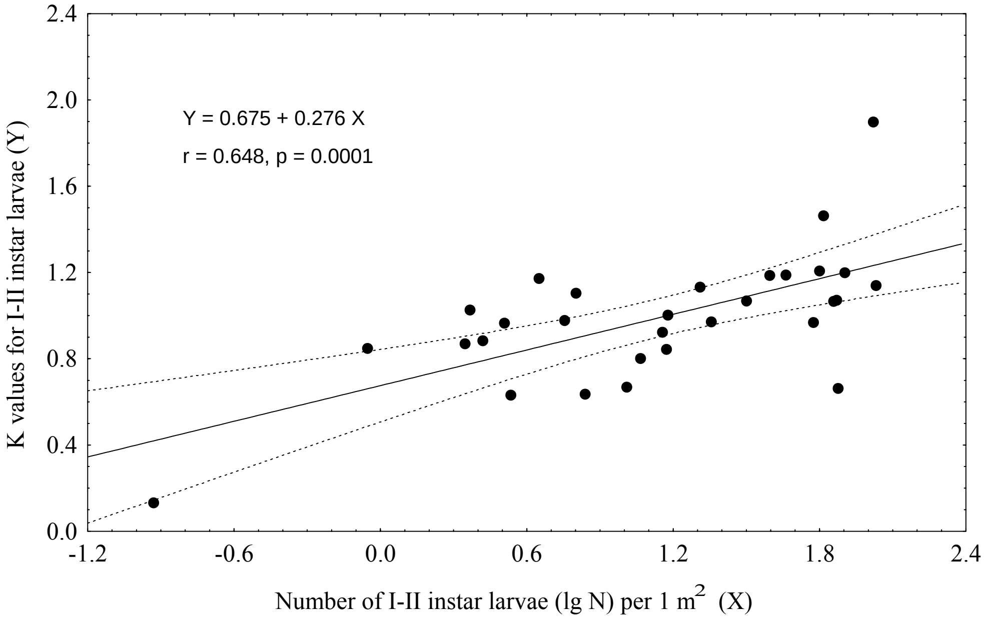

Figure 7. K values in relation with the I-II instar larval densities on maize fields inspected at KES (1994-1998)

In conclusion, the total insect mortality of both the 1st and 2nd generation appeared an evident tendency towards a dependence on initial density of eggs, providing the Krasnodar population with an obvious regulation event (fig. 8).

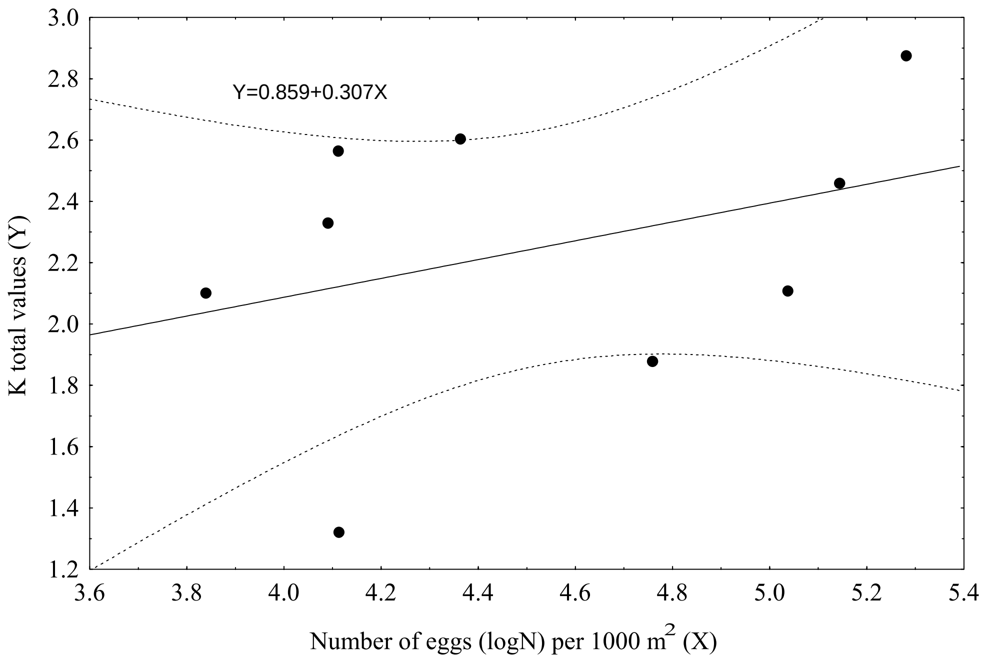

Figure 8. The relationship between total K for a generation and total egg numbers laid (logN) at KES (1994-1998)

The ECB larvae are supposed not to perform a cannibalistic potential. Most probably, the early instar larval density-dependence reflects behavioural reactions of insects to overcrowding; mortality due to predators and/or illness may be another factor promoting density-dependence.

The mortality of adults (normal females) in the Belgorod Province

Life tables involve two main estimates of adult density: 1) the initial number (=normal females) which accounts sex ratio and female fecundity potential before action of different ecological factors, and 2) the final number (=ovipositing females) which is defined by the actual quantity of oviposited eggs. In fact, the difference between expected and actual numbers of eggs in the next generation gives rise to measure drop from initial to final adult numbers during the present generation. Formally, the difference can be considered as adult mortality and/or emigration. However, very many events have happened in adult biology preceeding with egg laying. Consequently, a lot of ecological factors may cause population decline during activity of adults. For instance, after eclosion, but before egg laying, adults have to accomplish mating actions and repeated space movements (Showers et al., 1976; Frolov et al., 1996, etc.). So, it seems more correct to speak about a fall in adult capacity to realise its egg production rather than an adult (normal female) mortality. This fall in insect numbers can come from the effects of different abiotic and biotic factors having influenced both search and choice for mating places; meeting of sexes and copulation; spermatophorous transference; insect movements between aggregation sites and places of oviposition and conversely; searching for appropriate host plants for oviposition, and etc.

The data obtained during 1994-1998 showed that the adult capacity to realise its egg production has tended towards dependence on weather conditions during the ECB flight, i. e. mean air temperature in July ($r = -0.65$) and precipitation in June – July ($r = 0.60$). In spite of quite low r-values, weather effects do not excite any serious doubt (Barlow, 1971; De Rozari et al., 1977; Hudon, LeRoux, 1986, etc.).

On the other hand, the adult capacity to realise its egg production has manifested some tendency towards a density-dependence; the effect seems not statistically proved because of insufficient number of observations (fig. 9). Total egg densities displayed the same tendency; it can be regarded as a result of regulating action of the key factor (fig. 10).

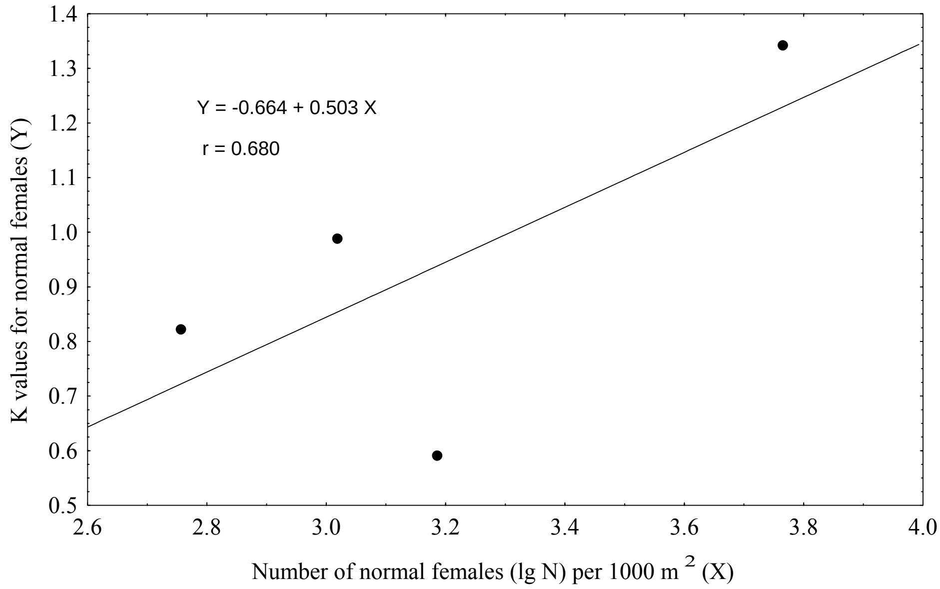

Figure 9. The relationship between a drop in actual egg numbers compared with expected numbers of oviposited eggs at the next generation (K) and the number of ovipositing females of the present generation in BSAA (1994-1997)

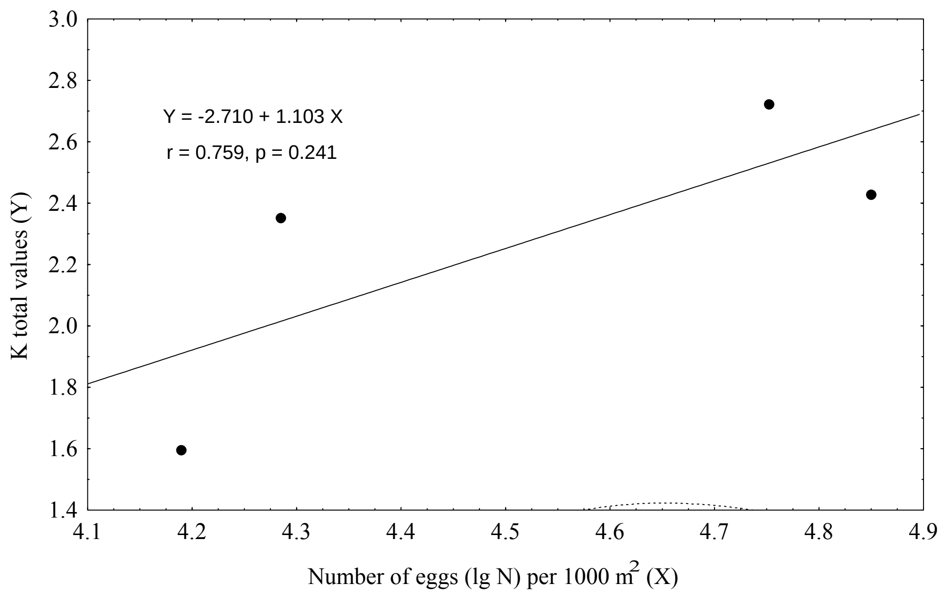

Figure 10. Total K values for a generation in relation with egg numbers laid on maize in BSAA (1994-1997)

An univoltine population dynamics of the ECB was studied in Quйbec, Canada during 8 years (1957-1965) (Hudon, LeRoux, 1986). The authors made the following conclusions. 1. Within the egg, larval and pupal stages, a population reduction remained relatively low and stable from year to year. 2. A mortality or emigration of gravid females from the study plots ranged from 68 to 98% (mean 95%) and was found the principal key factor affecting Quйbec population. 3. Weather conditions during egg laying influenced significantly moth mortality. Unfortunately, declared conclusions are not of universal value due to at least two obstacles. First, study plots were located far from commercial maize plantings resulted in a possible enhancement of adult flying away. Second, many common agricultural measures were unused, including those influencing insect numbers dramatically, e. g. tillage cultivation, mowing and threshing at harvest. However, it is of great surprising to find a real similarity in dynamics between the Quйbec and the Belgorod populations. Consequently, a question arises: either is a density-dependence the characteristic of an adult mortality/emigration in Quйbec? The answer is easy to obtain through the analysis of life tables being published entirely (Hudon, LeRoux, 1986). Figure 11 shows that the adult capacity to realise its egg production in Quйbec manifests a density-dependence very significantly. Accordingly, the egg number in Quйbec tends to be regulated as it does in the Belgorod Province (fig. 12).

Now we may even guess on the mechanism responsible for such a density-dependence in egg realisation by adults. It based most likely on behavioural reactions of adults leaving overpopulated places. Besides, it is not improbable that the growth in insect number can enhance a predator pressure, e. g. birds.

One way or the other identified key factors of the ECB population dynamics characterise with both the density-dependence and density-independence. This combination is ideally suited to the requirements of k-factors typical for herbivorous insects (Hassell et al., 1989). Nonetheless, the density-dependence in the ECB early instar larval mortality when feeding on maize was not detected until the present study, although it was observed when rearing in laboratory (Ramsey, Brown, 1984).

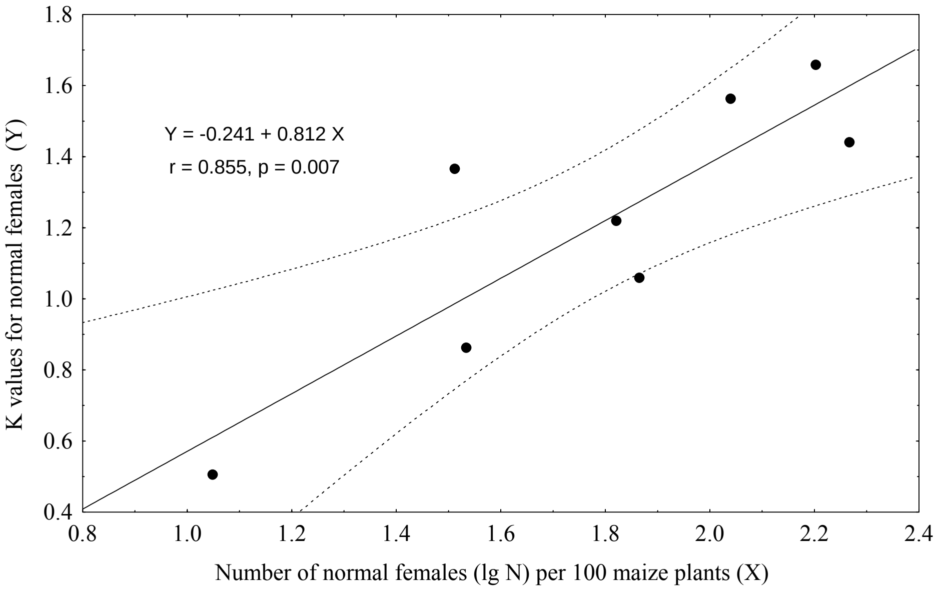

Figure 11. The relationship between a drop in actual egg numbers compared with expected numbers of oviposited eggs at the next generation (K) and the number of ovipositing females of the present generation in Quйbec (1957-1965) (the handling of data obtained by Hudon & LeRoux (1986))

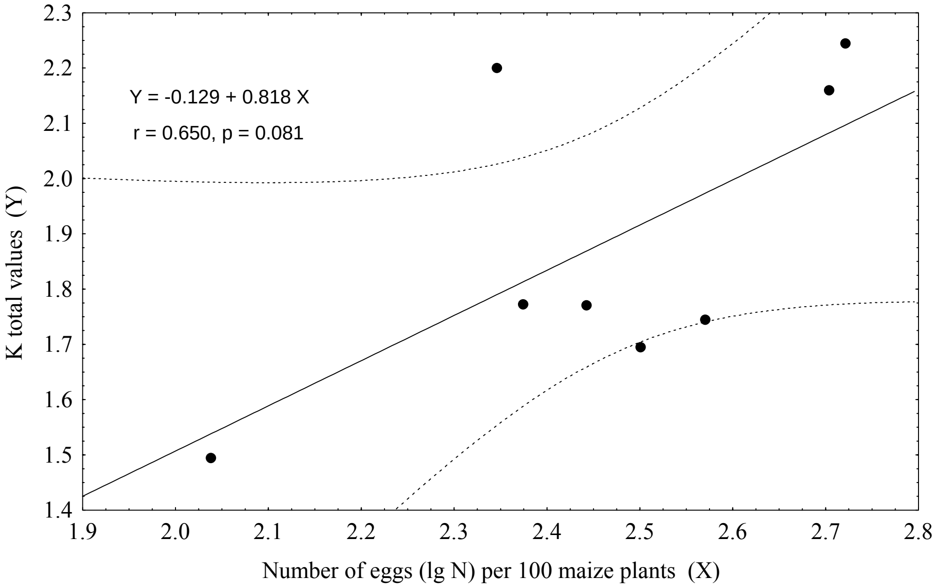

Figure 12. Total K values for a generation in relation with egg numbers laid on maize in Quйbec (1957-1965) (the handling of data obtained by Hudon & LeRoux (1986))

Plausible causes of the specificity in key factors for two populations tested

It was shown before (tables 1, 2) that the early instar larval mortality and the capacity of adults to realise its egg production made the most significant contribution to the insect death of two populations tested. However, an impact of these mortalities was rather different, and it is not improbable that the only mortality at unique age interval has come into critical importance for dynamics of the population. It means that only one key factor is in operation for the pest at a time.

In any event, the difference between borer populations inhabited the Krasnodar Territory and the Belgorod Province as regards key factors is easy to understand when imagine specificity in insect life cycles and their surroundings.

Feeding of I-II instar larvae is known to be a critical period in the ontogenesis of the ECB. The parts of a plant the insects feed on vary with the stage of growth in maize. Before tasselling, larvae have to feed on whorled leaves, and in such a case their death rate, even on susceptible plant genotypes, can reach 75% and more (e.g. Guthrie et al., 1960). Among the mechanisms of leaf feeding resistance, cyclic hydroxamates such as *2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one* (DIMBOA) can be mentioned as fairly well studied (e.g. Klun et al., 1967). At the Krasnodar Territory the great bulk of the 1st generation larvae would have to feed within the leaf whorl. In a consequence of it their mortality is very high almost each year (Frolov, Krapivenko, 1998). In the Belgorod Province a flight of overwintered moths goes on significantly later as compared with the Krasnodar Territory. As a result in average only approximately one-half of I-II instar larvae would be forced to feed on leaf tissues. Consequently, the rate of their death breaks down considerably.

On the other hand, the Belgorod Province and the Krasnodar Territory differ considerably in landscape. In particular, diverse agriculturally unused lands, e.g. ravines overgrown by forest, are rather typical for a forest-steppe in the Belgorod Province. In contrast, almost all the lands in the steppe region of the Krasnodar Territory are used for agricultural production. Besides, maize is the crop of very frequent occurrence at the Krasnodar Territory, as distinct from the Belgorod Province. So, it is quite reasonable to associate higher rate of adult mortality in the Belgorod with the greater efforts exerted by females to search for maize fields which are obviously less common and more hard to reach under more differentiated environment.

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