SZENT ISTVÁN UNIVERSITY

STUDY OF THE WESTERN CORN ROOTWORM'S (*DIABROTICA VIRGIFERA VIRGIFERA* LECONTE) DISPERSAL BEHAVIOR AND MODELLING ITS POPULATION DYNAMICS

LÉVAY NÓRA ANDREA

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PhD School: **Doctoral School of Plant Science**

Scientific branch: **Crop and Horicultural Sciences**

President: **Dr. Helyes Lajos, PhD**
Professor, Member of the Hungarian Academy of Science
Szent Istvan University
Faculty of Agricultural and Environmental Sciences
Institute of Horticultural Technology

Témavezetők: **Dr. Kiss József, PhD**
Professor
Szent Istvan University
Faculty of Agricultural and Environmental Sciences
Plant Protection Institute

Dr. Stefan Toepfer, PhD
Associate professor
Szent Istvan University
Faculty of Agricutural and Environmental Sciences
Plant Protection Institute
CABI Europe - Switzerland

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Dr. Helyes Lajos	Dr. Kiss József	Dr. Stefan Toepfer
Head of Phd School	Supervisor	Supervisor

1. Introduction

Central-America is the place of origin of the western corn roowtworm (Krysan, 1986). First European detection of its larval injury was detected near Belgrade airport in a continuous maize field, in 1992 (Bača, 1993). In Hungary, first adults were detected near Mórahalom, in 1995 (Princzinger, 1996). European spread of this pest is well documented (Kiss et al., 2005a,b). In most countries of Europe, the goal is to slow-down the spread and the population buildup of this pest. Considering the well-established populations, quarantine measure are no longer relevant. In the European Union, therefore in Hungary as well, western corn rootworm is no longer considered a quarantine pest (modification of the 7/2001 (I. 17.) regulation in Hungary).

The role of cultural practices, crop rotation in particular, were emphasised in the first reports of injury already (Gillette, 1912). Crop rotation is still a significant element in the management strategy (European Comission, 2003, 2006; Kiss et al., 2005c). Annual rotation of all maize fields is unnecessary both because of poor practicability (Kiss et al., 2005c) and low efficiency (Szalai et al., 2014). Szalai et al. (2014) proved in a population dynamic model that if the percentage of continuous maize field within all maize fields does not exceed 30%, population level will not rise above the economic threshold (0.7-2 adults/day/maize). The explanation for this phenomenon lays in the "dilution" of the population over larger area.

European populations of the western corn rootworm lay most of their eggs (>90%) in maize fields (Kiss et al., 2005c, Komáromi, 2008). Larvae hatching in the subsequent year can develop to adult stage, en masse, according to our present knowledge, only in the roots of maize (Branson és Ortman, 1970; Clark és Hibbard, 2004; Oyediran et al., 2004; Wilson és Hibbard, 2004; Breitenbach et al., 2005a,b), therefore considerable amount of adults can only emerge from continuous maize fields in Europe. Adults are active flyers (Spencer et al., 2009), part of the population that emerged in a continuous maize field will leave their natal field in search for new habitat patches. Mostly dispersing adults from neighbouring maize fields immigrate into first-year maize fields (Szalai et al., 2011b; Keszthelyi, 2005). Population level decreases in continuous-, whereas it increases in first-year maize fields due to the dispersal of adults among maize fields. By the time of egglaying, the initial population density dilutes, the distribution of adults becomes more even over the landscape of continuous- and first-year maize fields. In order to follow this process (i.e. population dilution), we should know the parameterized flight behaviour of this pest.

There is not much data in literature (Prystupa et al., 1988; Naranjo, 1990; Spencer et al., 1999) about whether or not adults are capable of actively orienting their flight towards maize fields and if yes, from what distance they can do that. How much their flight orientation is determined by wind conditions? What percent of a given population in a continuous maize field will leave their natal field? What is the rate of dispersing adults in a given population? What stress factors influence dispersal? If the rate of dispersing adults and the impact of environmental factors are known, will this modify the 30% upper limit of continuous maize within the maize rotation scheme (Szalai et al., 2014)?

Objectives:

1. Study of the flight orientation capabilities of western corn rootworm adults in a mark-release-recapture field study.
2. Study of adult dispersal among beetles emerged in continuous maize fields.
3. Constructing a population dynamic model based on the results of the dispersal field study and further development of IPM strategies against WCR.

1. Methods

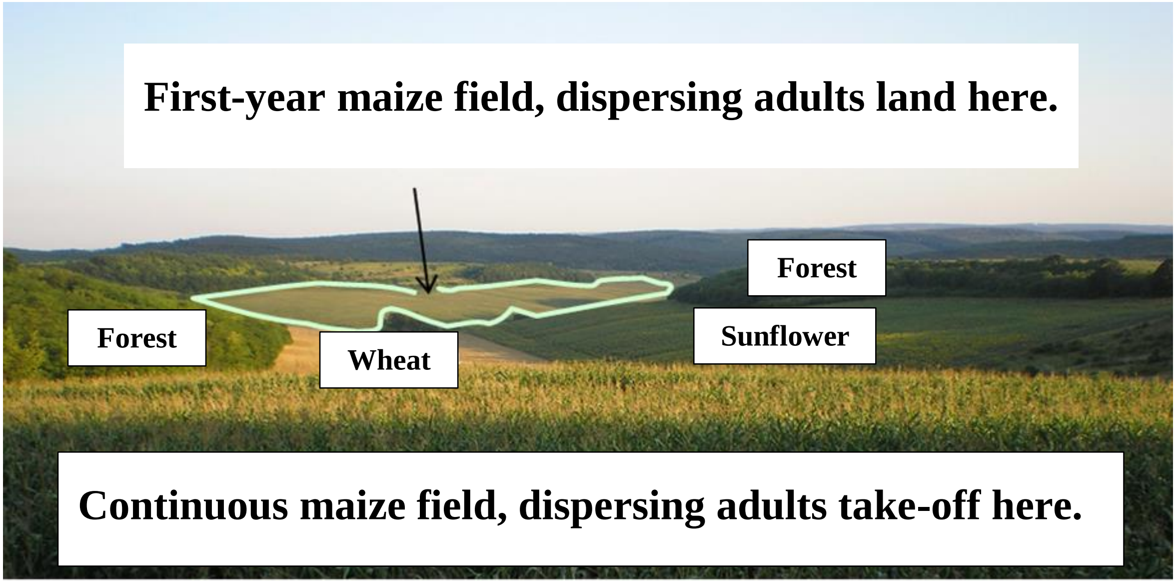
Mark-release-recapture study

Adults for the mark-release-recapture study were collected in continuous maize fields in Csongrád county, in 2003 and 2004. Adults were kept in climatized room in a 300x300x500mm rearing cage. There were cca. 3000 adults kept per cage. Adults were marked with fluorescent powder (Orange T1-0Y6612, Yellow T1-CH6620 Magruder Colour, Elizabeth, NJ, USA; Pink R17/M3115 Radiant Colour, Houthalen, Belgium) (Toepfer et al., 2005a). There were nine replicates, 5500-60 adults were released per replication. 5-7 days passed between collection and release. There were two experimental areas: *Experimental area „A”:* 80 ha grass steppe that was reaped once annualy (in June). The area was located in Csongrád county. There were two releases in 2003 and three relases in 2004. *Experimental area „B”:* 60 ha lucerne (*Medicago sativa*) field located ~25km south from experimental area "A". About one third of the field was kept in flowering fior seed production, whereas the rest of the field was reaped in every four weeks. There were two releases both in 2003 and 2004. In both experimental areas, two maize plots were planted 300-300m far from the central release point. Maize plots were 10x10m in size. In order to recapture marked adults, Pherocon AM® yellow sticky traps (Pherocon AM, Trece Inc., USA) were used (416 in year 2003 and 528 in year 2004). Traps were fixed on wood stick at 1.5 m height. Traps were placed in four circles (30 m, 105 m, 205 m, 305 m) around the central release point. Two days after release was the first trap check, which was folloed by two more checks (2-2 days after), hence there were three trap checks in total.

Statistical analysis of recaptured adults was done according to the procedures by Batschelet (1981), Zar (1998) and Services (2004). Concentration of flight vectors was calculated by Rayleight test. A flight was considered oriented if the concentration of the mean flight vector was significant. Comparison of the mean fligh vectors among releases and among trap check events was done by parametric, multi-factorial Watson-Williams F test (Fisher, 1993). Pre-condition of this test is that there must be at least five data points available. The relationship between the flight orientation of recapture, marked adults and wind conditions was analysed by the statistical procedure of Fisher and Lee (1983). Significance of the correlation was calculated by jack-knife procedure (Mardia és Jupp, 2000).

Dispersal study

Experimental desing of the dispersal study was based on the search for "quasi-isolated" pairs of maize fields. One pair consisted of a continuous- and a corresponding first-year maize field. Within a 3km radius circle around that part of the first-year maize field where traps were located, the one and only other maize field was the corresponding continuous maize field. Therefore, the majority of adults immigrating into the first-year maize field were supposed to originate from the corresponding continuous maze field. The percentage of immigrating adults arriving from maize fields other than the corresponding continuous maize field was considered negligible.



Twenty pairs of maize fields were studied in Csongrád and Tolna counties, in 2006 and 2007. Pherocon AM® non-baited yellow sticky traps (Pherocon AM, Trécé Inc., USA) were used for capturing adults. Four weeks capture data were statistically analysed. In case of seven field pairs, phenological data was also available. Phenological stage of a given maize field was derived from the following three numbers: (a) estimated percentage of pollinating plants, (b) estimated percantage of plants offering fresh silks, (c) estimated percentage of green leaf surface within the maize field. Arithmetic mean of the three estimated percentages represented the phenological stage of a given maize field. Captures were expressed as adult/trap/day, which was, in all cases, the arithmetic mean of the capture of three traps for each maize field and each trap change event. In most cases, the sizes of the fields varied within the field pair, so the raw capture data of the first-year maize fields were corrected, setting the sizes of continuous and first-year maize fields to 1:1 for comparability.

Correction of first-year maize fields' capture data was done by the following equation:
(raw capture data [adults/trap/day]) / correction factor, where:
correction factor=size of continuous maize field [ha]/size of first-year maize field [ha]
Dependent variable "dispersal rate" was derived from the corrected capture data as follows: total capture of continuous- and first-year maize field was considered 100% of the population based on the assumption that all adults capture within the field pair emerged in the same (continuous) natal maize field. Percentage of adults in the first-year maize field (i.e. dispersing adults) was expressed out of the total capture (continuous- and first.-year maize field). Sex rate was expressed as [male/female] whenever there were captures from both sexes in both continuous and first.year maize fields. Statistical analysis was done in R language (R Development Core Team, 2011).

Population dynamic model

Changes of population densities were simulated in both continuous- and first.year maize fields. In terms of its structure, the model simulates one generation in high number of replicates (Monte Carlo procedure). According to Pokorádi and Molnár (2010) Monte Carlo simulation is a probability sampling (estimating) process, where the statistical analysis of the high number of quasi-randomly generated values leads to conclusions. Model parameters were determined in a way that they stayed within the limits derived from literature data, however, within these limits, values were generated randomly. Results of the model were analysed by the methods of descriptive statistics (mean, percentiles). The concept of the model was simulating the process of "population dilution". The question was that by changing the ratio of continuous maize in the maize rotation scheme, what percent of the adult population can be "buffered" by the area-wide dispersal? Is it possible to manipulate the population level of this pest by designing the fragmentation of maize fields at the landscape level? The population dynamic model consisted of four structural elements: (a) population density of the parent generation, (b) population density of the offspring generation before dispersal, (c) dispersal, (d) population density of the offspring generation after dispersal. The population dynamic model was run at given ratios of continuous maize field. The ratio of continuous maize field started at 1% and increased to 99% by one percent steps.

2. Results

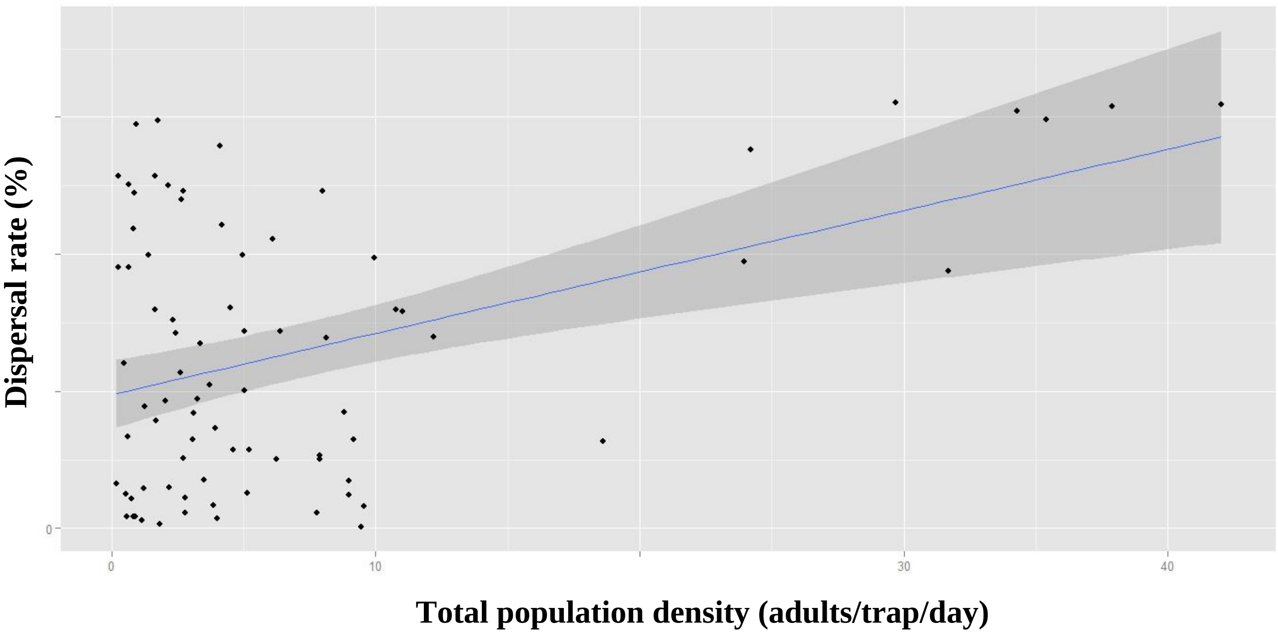
Mark-release-recapture study

Total of 289 adults were captured during the two years and nine replicates of the mark-release-recapture study, which represented a 0.9% recapture rate. 63% of released adults were males and 37% females (s.d.=16 %; n=9), whereas in case of recaptured adults 41 % were males and 59 % females (s.d.=39 %; n=9). Out of the 15 replicates (9 releases * 2 trap change events – 3 trap change events excluded from statistical analysis = 15 replicates) in five cases (38 %) there was one significant flight direction, in three cases (20 %) there were two significant flight directions and in seven cases (46 %) no significant flight orientation was observed. If trap change events' data was pooled, out of nine releases there were five cases of uni-directional, three cases of bi-directional flights and in only one case there was no clear flight orientation of adults. There was no significant difference between males and females neither in the oriented, nor in the non-oriented cases ($P > 0.5$, Watson-Williams F test).

In 10 cases out of the 15 (67 %) there was significant correlation between the beetles' flight orientation and wind direction. Nevertheless, the concentration of the mean flight vector (=the length of the mean flight vector) was not significantly correlated to the concentration of the mean wind direction vector (Pearson correlation, $p>0,05$). Similarly, there was no significant correlation between the concentration of the beetles' mean flight vector and wind speed (Pearson correlation, $p>0,05$). During the two years of the experiment, marked beetles did not fly more frequently towards the 10x10 m maize plots than towards any other habitat patch. This result stayed the same when data was analysed separated by year or by sex. At 1500m distance, flight orientation was significanty correlated to the location of maize fields ($t=2,4$; $df=138$; $p=0,015$). Separated by experimental locations, the attraction of maize fields at 1500 m distance was detectable thoughout the whole experiment at site "A" (grass steppe). On the contrary, at site "B" (lucerne) attraction towards maize fields was masked by the presence of flowering lucerne within a distance of 600 m. Marked, released adults significantly preferred staying within the flowering part of the lucerne field (300 m distance; $t=3,3$; $df=62$; $p=0,02$). In case of sunflower, no significant correlation was found. There was significant correlation between the flight orientation of male beetles and the location of small forest patches.

Dispersal study

In the entire twenty field pairs there were captured adults during the four weeks period of data collection, hence there occurred immigration into all of the studied first-year maize fields. Mean dispersal rate was 38.7 %±29.4 (20 filed pairs, 4 weeks capturing period, n=80). Observed dispersal rates varied greatly, with the lowest value of 0.4% and highest of 93.3%. Mean dispersal rate was significantly greater in 2007 (49.6 %±28.9) than in 2006 (31.3 %±27.6) (independent t test, $p<0.05$). Mean population density in twenty field pairs and during two years (population density of continuous- and first-year maize fields in total) was 7.0±9.4 adults/trap/day. In continuous maize fieds, population density varied between 0.05-15.06 adults/trap/day, whereas in first-year maize field it was between 0.05-11.4 adults/trap/day.



Linear regression model fitted on the pooled dataset, dark area represents confidence interval. Independent variable: total population density (X), dependent variable: dispersal rate (Y). Model equation: $Y=29.25+1.34X$. $R^2=0.1835$; $p<0.05$; df=78. $conf_{95}$: 0.70-1.98 (regression coefficient); 21.81-36.69 (constant).

As it can be seen in the plot of the linear regression model, datapoints tend to be separated in two distinct groups. At low population density (<8 adults/trap/day) no clear mathematical pattern can be assumed, whereas at high population density (>8 adults/trap/day) a strong positive linear correlation seems to be present. Therefore the pooled dataset was divided into two subgroups (low vs. high population density) and statistical analysis was carried on this way.

Pearson correlation (r) with significance test (p) and Spearmon rho values, dataset is divided into two subgroups (low vs. high population density), the dispersal study was carried out in Csongrád and Tolna counties between 2006-2007.

	Dispersal rate		
Low population density (<8 adults/trap/day)	rho	r	df
Total population density [adults/trap/day]	-0.04	-0.09 (p=0.51)	58
Distance between maize fields	0.25	+0.25 (p=0.05)	58
Julian Days	0.07	+0.11 (p=0.40)	58
Phenological stage of continuous maize	-0.33	-0.27 (p=0.27)	17
Phenological stage of first-year maize	-0.84	-0.02 (p=0.91)	17
Relative phenological attractiveness	0.58	+0.44 (p=0.06)	17
High population density (>8 adults/trap/day)		r	df
Total population density [adults/trap/day]	**0.80**	**+0.84 (p<0.05)**	18
Distance between maize fields	-0.37	-0.31 (p=0.18)	18
Julian Days	0.07	0.00 (p=0.99)	18
Phenological stage of continuous maize	0.15	+0.22 (p=0.56)	7
Phenological stage of first-year maize	0.07	+0.28 (p=0.48)	7
Relative phenological attractiveness	0.09	+0.08 (p=0.84)	7

Four models were selected in the frames of regression analysis, which are to be used in the population dynamic model later on:

(i) linear regression model for the case of high population density, independent variable: total population density (R^2=70 %)

(ii) multifactorial linear regression model for the case of high population density, independent variables are: total population density and distance between maize fields (R^2=73 %)

(iii) multifactorial linear regression model for the case of high population density, independent variables are: total population density and relative phenological attractiveness (R^2=71 %)

(iv) multifactorial linear regression model for the case of high population desity, indeoendent variales are: total population density, distance between maize fields and relative phenological attractiveness (R^2=78 %)

Sex ratios of continuous vs. first-year maize fields did not differ significantly from each other (continuous maize: 10.28 [male/female]; s.d.= 14.13; n=55; first-year maize: 7.34 [male/female]; s.d.=12.30; n=55). The difference was not significant either when data was separated by years.

Population dynamic model

Results of the population dynamic model can be summarized as follows:

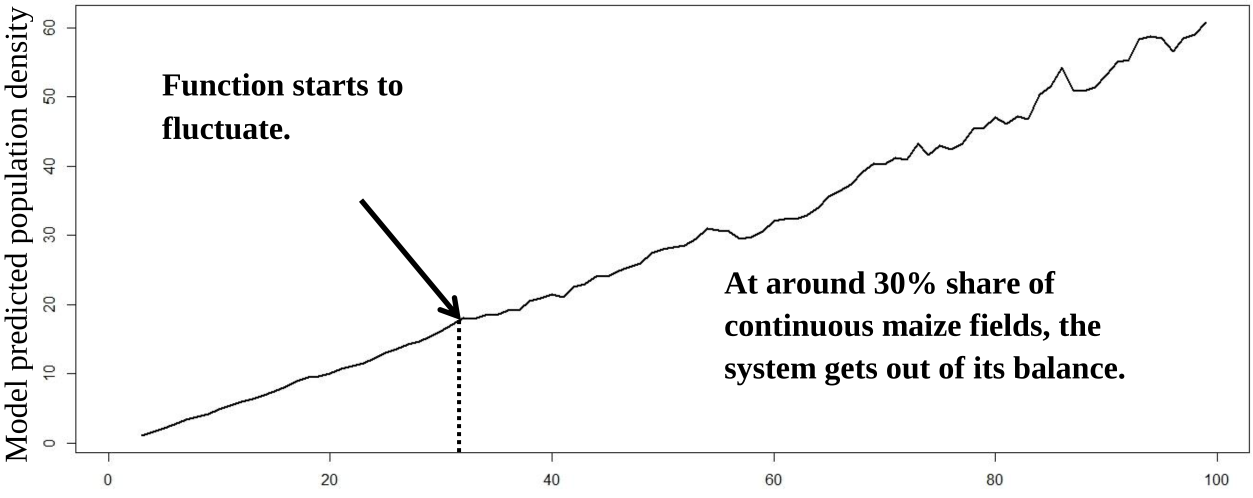
(i) At landscape level, the upper limit of continuous maize within the maize rotation scheme is determined by the population density of continuous maize. The population density of first-year maize has no impact on this issue.

(ii) The phenological stage of maize fields has no impact on the population density either in continuous, or in first-year maize, therefore it has no impact on the upper limit of continuous maize within the maize rotation scheme.

(iii) If dispersal rate for the case of high population density is determined by one single variable, i. e. total population density, the upper limit of continuous maize within the maize rotation scheme is (34%).

(iv) If dispersal rate for the case of high population density is determined by two variables, i.e. total population density and distance between maize fields, output variable responds on this sensitively by dropping the upper limit of continuous maize from 34% to 20%. If the original value of 34% is considered 100%, this drop represents a 41% decrease.

When running mean (n=3) is fitted on the maximum values of model output, a change can be observed in the behaviour of the function. At its initial stage, the function smoothly increases. In contrast, at around 30% share of continuous maize fields, the function starts to fluctuate; the system gets out of its balance.



Share of continuous maize within the maize rotation scheme.

3. Discussion

Mark-release-recapture study

When marked adults were released in non-maize habitats (grass steppe and lucerne field) in a marke-release-recapture study, some of the beetles moved randomly, and in some cases uni-directional and bi-directional flight patterns were observed. Naranjo (1994) reports on random movements among maize fields. However, we know little about the causes of such random movements (Toepfer et al., 2006). Spencer et al. (1999) claims that oriented flight of adults can be explained by two factors: partly by meteorological conditions, partly the reaction of beetles to chemical clues detected from longer distances. Despite the fact that in 10 cases out of the 15 the beetles' flight orientation significantly correlated to wind direction, oriented flight of western corn rootworm adults cannot be fully explained by wind conditions.

This study proved that under field conditions in non-maize habitats, movement of adult beetles can be considerably slowed down if alternative food sources are present and this phenomenon is independent from meteorological conditions. If attractive alternative food sources are present, adults do not orient their flight immediately towards maize fields despite the fact that they are capable of doing so. This can be valuable information for practical reasons, namely introduction events of this invasive pest usually occur in non-maize habitats (i.e. grass stipes around airports). Therefore planting alternative food sources as "trapping zones" around these areas can be a useful tool in the frames of quarantine measurements, wherever the quarantine situation is still valid.

Dispersal study

Dispersal rates varied greatly among locations and between years. Based on the observed dispersal rates it can be concluded that there exist two different behavioral patterns in the dispersal strategy of the western corn rootworm. The "baseline dispersal" is independent from all the studied potential environmental stress factors (phenological stages of maize, distance between maize fields, Julian Days) and population dynamic factor (density) and it varies around one third of the population. This behavioural pattern is expressed at low population densities and the assumed objective of such dispersal is the search for new food sources and oviposition sites.

In contrast, at high population densities the percentage of dispersing adults significantly correlates to total population density. For shorter periods, dispersal rate can increase even above

90% and considering the mean value over the main dispersal period of adults, dispersal concerns nearly half of the population. At high population densities dispersal rate can be well predicted by regression models. Population density (*non-environmental stress factor*) as a stand-alone factor can effectively predict dispersal rate, however, the accuracy of model prediction can be increased by involving additional variables (*environmental stress factors*) into the model

The evolution of different dispersal strategies has been in the forefront of behavioural ecology studies for a long time. According to our present knowledge both external (habitat carrying capacity, patch quality, local catastrophes) and internal (chaotic population dynamics, demographic stochasticity) factors act as driving forces in the selection for different dispersal strategies (Comins et al., 1980; Cohen és Levin, 1991; McPeek és Holt, 1992; Olivieri et al., 1995; Holt és McPeek, 1996; Cadet et al., 2003). Based on the results of this study, these findings are relevant in the case of the western corn rootworm as well, however, external (environmental) stress factors play a weaker role than the population dynamic (internal) stress factor in the area-wide spread of adults.

In this dispersal study the phenological stage of maize as a stress factor, could only contribute to a regression equation of strong predictive power at high population densities and when it was combined with other variables (population density and distance). The influence of the phenological stages of maize under field conditions and at the landscape level is much weaker than it was expected based on literature data.

The distance between maize fields influences the percent of successful immigrants in first-year maize at a given distance from continuous maize. Nevertheless, the relationship between distance and dispersal is not obvious. Despite the fact that in the present study, 1.38km distance was not a barrier for dispersing adults, it is assumed (based on GAM regression) that there exists a preferred range of distance (between 100 and 200 m) for dispersing adults. This assumption is strengthened by the fact that when the range of distance was arrowed to [40-250 m], 16% of the variance of dispersal rates could be explained by the distance between maize fields as a stand-alone factor.

Based on field observations in the USA, most of the dispersing adults are females, (Godfrey és Turpin, 1983; O'Neal et al., 1999; Levine et al., 2002; Schroeder et al., 2005; Spencer et al., 2005). The percentage of females in first-year maize fields were higher than in continuous maize fields in all cases in the present study as well, however, this difference never proved to be significant.

Population dynamic model

The model conslcusion is that if dispersal rates are predicted by total population density as stand-alone factor, te upper limit of continuous maize within the maize rotation scheme is aroud one third, which is 3-4% higher than the results by Szalai et al. (2014). Inclusion of mean distance among maize fields as an additional variable resulted in 14% drop in the upper limit of continuous maize: it decreased from 34% to 20%. Altough this value is still within the range of that suggested by Szalai et al. (2014), i. e. between 20-30%, this sharp decrease points at the influence of landscape fragmentation (distance among maize fields) on dispersal.

It was proven that differences among phenological stages of maize fields have no role in the distribution of adults at the landscape level. Based on my research findings, dispersal of adults is partly a fix element in the behaviour of this pest and partly it is a density dependent phenomenon. It is likely so that phonological differences among maize fields can only affect the preferences od dispersing adults. Those adults that are engaged in long.distance flight searching for new habitat patches, probably prefer phenologically more attractive maize fields. However, pehnological attractiveness alone will not engage individuals in long distance flight.

The initial phase of the running mean function fitted on the maximum values of continuous maize field's population density, increased smoothly. At around one third share of continuous maize, the function started to fluctuate and as te share of continuous maize increased, the amplitude of this fluctuation became greater. This phenomenon shows that landscape fragmentation as a buffer system can be saturated. Below saturation point, even the extreme values of input parameters can be buffered by the rotation system, however, this mechanism does not work above saturation. Obviously this does not mean that the share of continuous maize cannot be above the saturation point. Nevertheless, above the saturation point, the rotation scheme as a buffering system cannot compensate the extreme cases of input parameters. Despite, the share of continuous maize can be above 30% if economic threshold is fixed at a higher value (i.e. irrigated maize production).

5. Conclusion

Western corn rootworm adults can actively orient their flight towards maize fields. However, from non-maize habitats adults will not orient their flight towards maize fields immediately in case alternative food sources (flowering lucerne in this study) are available. Attraction of alternative food sources is significant, therefore it is suggested that around potential invasion hot zones (i.e. around airports) such habitat patches should be planted as part of the quarantine measurements.

Dispersal of western corn rootworm adults is partly a fix element in the behaviour of this pest that is independent from stress factors. In case of high population density, dispersal becomes density dependent. Phenological differences among maize fields as stand-alone factor do not explain dispersal. Phenological stage influences dispersal but only in combination with other variables. In the Carpathian Basin, under field conditions, phenological stages of maize fields have much less influence on dispersal than it was expected based on literature data. There was a significant correlation between dispersal rates and distance between maize fields. The mathematical relationship in the studied distance range (1,38 km) was not linear. There was a preferred range of distance for dispersing adults between 100 and 200 m, nevertheless distance up to 1.38 km was not a barrier for dispersal at population level. Due to the dispersal behaviour of this pest, manipulating the share of continuous maize in the maize rotation scheme can be a part of the area-wide management, therefore a tool for integrated pest management (by setting regulations for the share of continuous maize fields) against western corn rootworm.

It was proved in population dynamic model that phenological differences among maize fields have no impact on the upper limit of continuous maize fields in the rotation scheme. Fragmentation of the landscape (continuous- vs. first-year maize fields) has a buffering capacity, which is saturated at one third share of continuous maize fields. Saturation is independent from the economic threshold, therefore share of continuous maize can be above saturation point (i.e. irrigated maize production). However, above saturation, landscape fragmentation cannot buffer the population density of the pest, so the maize rotation scheme will be more exposed to the annual fluctuations of input parameters.

6. New scientific results

(i) Western corn rootworm adults are capable of actively orienting their flight towards maize under field conditions and this phenomenon is detectable up to 1500 m distance.

(ii) Western corn rootworm adults in non-maize habitats do not orient their flight towards maize fields immediately in case there are attractive alternative food sources (flowering lucerne) available.

(iii) There exis two different patterns in the dispersal behaviour of the western corn rootworm: at low population density the so-called baseline dispersal is expressed, wich is not related to the studied environmental and ecological stress factors. At high population density dispersal becomes strongly density dependent.

(iv) Phenological stages of maize fields do not explain dispersal as a stand-alone variable. Phenological differences play a role in determining dispersal only at high population density and in combination with other variables (population density and distance between maize fields).

(v) Distance dependence of dispersal is proved. The mathematical relationship between distance and dispersal is not linear. There exists a preferred range of distance for dispersing adults which is between 100 and 200 m, however, distance up to 1.38 km is not a barrier for dispersing adults.

(vi) It is proven by population dynamic model that at landscape level, te phonological stages of maize fields do not have impact on the upperlimit of continuous maize within the mize rotation scheme.

(vii) Fragmentation of continuous vs. first-year maize fields at the landscape level has a buffering capacity which becomes saturated at around one third share of continuous maize within the maize rotation scheme. The saturation is independent from what population density is considered an economic threshold. Above the saturation point, the function that estimates population density steps from its smoothly increasing phase into a fluctuating phase. Therefore, it becomes impossible to give robust prediction of population densities above the saturation point.

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3. S. Toepfer, **N. Levay**, J. Kiss (2006). Adult movements of newly introduced alien *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae) from non-host habitats. Bulletin of entomological research, 96(04), 327-335.
4. S. Toepfer, **N. Levay**, J. Kiss, (2005), Suitability of different fluorescent powders for mass-marking the Chrysomelid, *Diabrotica virgifera virgifera* LeConte. Journal of Applied Entomology, 129(8), 456-464.
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