

Prediction of Adult Western Corn Rootworm (*Diabrotica virgifera virgifera* LeConte) Emergence

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Abstract

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The sum of effective temperatures (SET) of adult western corn rootworm (WCR) occurrence was determined based on several criteria. The risk of WCR occurrence was mapped, and the areas of continuous reproduction of WCR in the Czech Republic were identified. The daily soil SET was observed until the initial adult WCR occurrence, and it ranged from 414 degree days (DD) when the lower threshold temperature (LTT) was 12.5°C at 0.02 m depth to 719 DD (LTT of 10°C at a depth of 0.05 m). The daily air SET ranged from 415 DD (LTT 12.5°C at a height of 2 m) to 726 DD (LTT of 10°C at a height of 0.05 m).

Keywords: corn insect pest; *Zea mays* L.; soil temperature; effective temperature sum

Western corn rootworm (*Diabrotica virgifera virgifera* LeConte) was introduced into Europe in the 1990s, and its area of occurrence has been extending every year. The future simulation of BAUFELD and ENZIAN (2005) showed the ongoing dramatic spread of the borders of western corn rootworm (WCR) in several European countries. DIFFENBAUGH *et al.* (2008) analysed WCR extension in the predicted climatic conditions of 21st century North America. The authors observed that elevated greenhouse gas concentrations and subsequent climate change could lead to the range expansion of WCR. Other models have also been reported for WCR, but detailed validation of modelled egg development is usually performed only under laboratory conditions.

The Czech Republic (CR) is divided into three zones: area of the continental expansion of WCR (the eastern part of the territory), buffer zone (the central part), and not-infected area (the western part of the territory). The increased percentage of continuous maize planting (maize for biogas, etc.) may have increased both the number of dispersing females and the survival potential of progeny from

the founding female WCR that dispersed ahead of the front (MEINKE 2009). In areas where WCR persists in continuously grown maize, yield losses between 5% and 10% are observed after 5 years (MACLEOD *et al.* 2007). Therefore, the effective management of adult WCR requires knowledge of its emergence so that insecticide applications against adults can be accurately timed (NOWATZKI *et al.* 2002). WCR development and phenology are temperature dependent and are thus influenced by spatially variable edaphic factors that affect soil temperatures, such as soil type, soil moisture, snow cover or crop residue (ELLSBURY *et al.* 1998a,b).

The precise definitions of WCR thermal constants require results that represent continuous maize monoculture soil temperature measurements and direct pathogen observations.

MATERIAL AND METHODS

Study area. An evaluation of the relationship between soil and air SET and the emergence of

adult WCR was performed at the experimental field station Žabčice (Europe, the Czech Republic, South Moravia).

The precision monitoring results were compared with available data from the State Phytosanitary Administration (SPA) in Polešovice and Čejč and the Czech Hydrometeorological Institute (CHMI) in Staré Město and Velké Pavlovice. The compared SPA and CHMI locations were chosen based on their distance (a maximum of 10 km) and the length of observation. The possibility of generalisation of precision microclimatic monitoring was tested. The test was based on a comparison of soil SET measured in maize and at CHMI station (with grass surface).

The experimental area, Žabčice (Zab.), is located in the floodplain of the Svatka River at an altitude of approximately 184 m a.s.l. in a maize production area. The annual temperature is 9.2°C, and the annual precipitation total is 483 mm. According to agroclimatic classification (KURPELOVÁ *et al.* 1975), the location belongs to the warm macro area, predominantly warm (annual air SET above 10°C 2840 DD) and dry sub-region (annual potential evapotranspiration minus annual precipitation total 15.5 mm) with mild winters (average of annual absolute minimum air temperatures –17.4°C, annual average number of days with snow cover occurrence 45.6). Soil types were classified according to NĚMEČEK *et al.* (2001). The soil in the experimental plot is heavy clayey-loam Gleyic Fluvisol with 49–58% of the content particles measuring < 0.01 mm. The field was planted with maize from 2003 onward. The spacing of the canopy was 0.75 m between rows and 0.16 m between plants in a row, which resulted in a population of 83 thousand plants per ha. The canopy was planted during the last week in April.

Initial data on adult WCR occurrence at the SPA locations (Polešovice) were compared with the soil SET assessed from the CHMI automatic climatological station data in Staré Město (Uherské Hradiště district). The altitude of the station is 235 m a.s.l., the annual temperature for the period from 1961 to 1990 was 8.8°C, and the annual rainfall was 534 mm. The soil type is light, loamy-sand and sandy Arenic Chernozem. Ten to 18% of the particle content measured < 0.01 mm. The distance between the SPA and CHMI stations is approximately 8 km.

The SPA Čejč location (Hodonín district) data were compared with the soil SET from the CHMI station in Velké Pavlovice. The altitude of Velké Pavlovice

station is 196 m a.s.l., the annual temperature for the period from 1961 to 1990 was 9.2°C and the annual rainfall was 491 mm. The soil type is medium sandy-loam Cambic Leptosol. 21% to 28% of the particle content measured < 0.01 mm. The distance between the SPA and CHMI stations is approximately 10 km.

Insect sampling. The monitoring of adult WCR occurrence in the Žabčice experimental area was performed during 2006 and from 2008 to 2011, in Čejč during 2003 and from 2005 to 2007 and from 2009 to 2010 and in Polešovice-Nedakonice from 2005 to 2010. The sticky cloak traps, Csalmoson® PALs (Plant Protection Institute, Budapest, Hungary), composed of a yellow sticky sheet and floral bait (which attracts mainly females but also males) were used for the monitoring of adult WCR activity. In addition to the sticky cloak traps, Csalmoson PAL® that consisted of clear sticky boards and synthetic sex pheromones (that attracted only males) were installed at the Žabčice location.

In the SPA locations, the pheromone traps, Csalmoson® PAL, were installed in standard commercial maize canopies (5–10 m from the field edge and 1.30 m above the ground) in early July. Adult WCR occurrence was checked once a week until mid-October. In the Žabčice location, the traps and plants were covered by an insulator (constructed from tulle material) and the adult WCR occurrence was checked every 3 days.

Air and soil temperature measurement. Žabčice: soil temperature was measured by automatic electric soil thermometers (PT100s; AMET, Velké Bílovice, Czech Republic) which were permanently placed in the soil under the maize canopy at depths of 0.05, 0.10, and 0.20 m. The data were measured and stored in a data logger in fifteen-minute intervals.

The air temperature at 0.05 m and 2 m above the ground was monitored by two Onset temperature sensors: the Hobo RH/Temp logger (for the 2006 to 2010 seasons) and the Hobo U23 Pro v2 Temp/RH Data Logger (in the 2011 season) (both (Onset Computer Corporation, Bourne, USA). Sensors with radiation covers were placed near the soil temperature sensors and insulator with traps. The temperature was automatically registered in fifteen-minute intervals. Hourly and daily values of air and soil temperatures were obtained as the arithmetic average of fifteen-minute data.

CHMI automatic stations: soil temperature was measured by electrical thermometers at depths of

0.05, 0.10, 0.20, 0.50, and 1 m under the standard grass surface. The measurement interval was twenty seconds with an average fifteen-minute output (a 10-min output in 2011). Air temperature was measured by a standard thermometer at 2 m above the grass surface.

Degree-day method computation. WCR thermal constants are based on the sum of effective soil temperatures (SET). According to the available results, the temperatures of 10°C and 12.5°C were tested as a lower threshold for development (the lower threshold temperature – LTT). WILDE (1971) determined the developmental threshold to be 11°C for eggs that were collected in Minnesota and 12.8°C for eggs that were collected in Kansas. STEVENSON *et al.* (2008) calculated the sum of WCR DD as 10°C. An upper threshold temperature (12.7°C) for WCR development was used (DIFFENBAUGH *et al.* 2008). JACKSON and ELLIOTT (1988) reported the following minimum threshold temperatures and temperature sums (based on laboratory experiments of male WCR developmental stages): 1st instar larvae = 10.5°C and 59.9 DD, 2nd instar larvae = 9.6°C and 56.6 DD, 3rd instar larvae = 8.3°C and 144.4 DD, and pupae = 9.7°C and 112.1 DD. Complete male development requires a minimum temperature threshold of 9.2°C and 403 DD, and female development requires a minimum temperature threshold of 8.2°C and 466 DD. Adult male WCR begin to emerge before females, and the peak (50%) cumulative male emergence also occurs earlier than the peak female cumulative emergence (DARNELL *et al.* 2000).

ÁVILA *et al.* (2002) evaluated adult WCR occurrence according to the soil SET measured at a depth of 0.10 m and air temperature measured at 2 m. Similarly, DERRON *et al.* (2005) evaluated soil SET at depths of 0.05 and 0.10 m, ELLSBURY *et al.* (2005) evaluated soil SET at a 0.10 m depth under a grass stand, and SCHAAFSMA *et al.* (1991) evaluated soil SET at 0.05 and 0.10 m in field conditions, etc.

Due to the ecological demands of WCR (development in the upper soil layer), soil temperatures at 0.05, 0.10, and 0.20 m were analysed. Hourly average soil temperature, daily average soil temperature and hourly average air temperature were used for the analysis. The starting date was January 1st. The biological reference date (the beginning of temperature summation) was the first occurrence of soil temperatures above the threshold (10.0°C and 12.5°C, respectively) in a particular year.

The calculation of SET was $ET = T_{AVG} - T_{LTT}$, where: ET – effective temperature, T_{AVG} – average temperature (hourly or daily), T_{LTT} – lower threshold temperature (10°C or 12.5°C), provided that $T_{AVG} \geq T_{LTT}$. Temperatures exceeding the threshold (the effective temperature) were summed from the date of the initial adult WCR occurrence according to the equation: $SET = \sum_{i=1}^n ET$, where: i – date of the initial occurrence of T_{LTT} (BIOFIX) and n – date of adult WCR emergence. The hourly effective temperature sums were expressed in degree hours (DH). The daily effective temperature sums were expressed as degree days (DD).

Mathematical and statistical analyses. SETs were calculated and graphically expressed by STATISTICA software (StatSoft, Inc., Version 7). Box plots graphically show the minimum, maximum, average and standard error of the analysed file. The coefficient of variation $V_x = s_x / \bar{x}$, where s_x – standard deviation and \bar{x} – arithmetic average, expressed the statistical variability of the file.

Synthetic map construction of the initial occurrence of adult WCR and definition of risk areas in CR. A synthetic map of the initial adult WCR occurrence in the average year was constructed based on the following:

- (1) The defined thermal constants of WCR adults;
- (2) Long-term data on soil temperatures for the climatological CHMI stations;
- (3) A determined regression relationship between soil temperature under grassland and under maize canopy.

Additionally, the areas of improbable WCR occurrence (low-risk areas) and areas of high-risk WCR occurrence (high-risk areas) were determined (Figure 1).

A map was created by ArcView GIS software, Version 9 according to the following conditions:

- Only altitudes up to 650 m a.s.l. were included in the map creation because no intensive planting of maize is expected at higher altitudes. Therefore, areas above 650 m were labelled as “Non-Risk Areas”.
- The evaluated season was from March 15th (the initial potential occurrence of soil temperature was typically above 10°C) to September 30th (the threshold date for significant flight activity of adult WCR).
- The average daily soil temperatures measured at a 0.05 m depth of 67 CHMI automated climatological stations were used for the period from 2001–2010. The soil temperatures at the

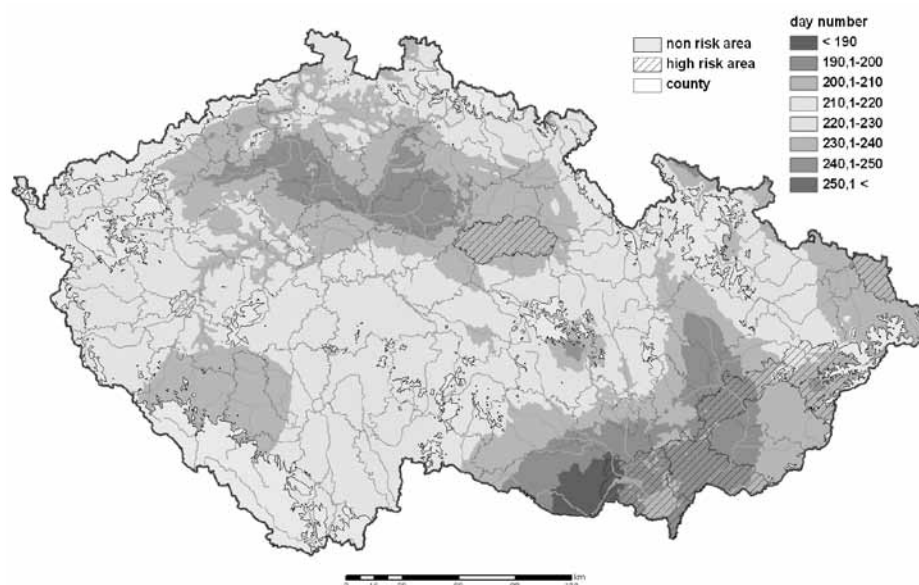


Figure 1. A synthetic map of the initial adult WCR occurrence and definition of risk areas in the CR

CHMI stations were measured under grassland. The values were corrected by the regression equation $y = -1.2774x + 0.0135x^2 - 0.5376$. The regression equation quantifies the relationship between the soil temperature at 0.05 m under grassland and the soil temperature at 0.05 m under maize canopy. The equation was obtained by comparing the two-year data series from Žabčice (under maize canopy) and the CHMI station Lednice (under grassland). For surface expression, the data from the CHMI stations were interpolated based on altitude.

- The date of the initial occurrence of adult WCR was determined by reaching the soil SET above 10°C at 0.05 m and 719 DD. Areas where this value was not reached until August 30th were marked as “Non-Risk Areas”.
- The areas with an average initial occurrence of soil SET above 10°C at 0.05 m and 719 DD were marked on the map (soil temperatures under maize canopy were obtained by converting the soil temperatures under grassland).

- Districts with a high concentration of maize on arable land (typically over 20%) were marked as “High Risk Areas” (according to the Czech Statistical Office data for 2007 and 2011; i.e. Plzeň-město d. 27%, Pardubice d. 20%, Břeclav d. 25%, Hodonín d. 26%, Kroměříž d. 20%, Vsetín d. 25% and Karviná d. 23%).

RESULTS AND DISCUSSION

Five-year average soil and air SET from all variants of the Žabčice station are shown in Figure 2. The average hourly soil and air SET from an exceeded threshold until the initial capture of an adult WCR are shown in Figure 2a. The average soil SET 5-year values range from 10 082 DH (LTT of 12.5°C at a depth of 0.20 m) to 17 630 DH (LTT of 5.0°C at a depth of 0.05 m). The average 5-year air SET values range from 11 824 DH (LTT of 12.5°C at a depth of 2 m) to DH 19 170 (LTT of 10.0°C at a depth of 0.05 m). The variability of the maize soil

Table 1. Statistical evaluation of soil SET variability under maize canopy (Žabčice location)

	Hourly data (DH)						Daily data (DD)					
	S10/5	S10/10	S10/20	S12.5/5	S12.5/10	S12.5/20	S10/5	S10/10	S10/20	S12.5/5	S12.5/10	S12.5/20
5 th year average	17 630	16 658	15 133	12 459	11 546	10 082	719	684	626	500	468	414
Standard deviation	934	880	1 218	942	960	1 263	32	32	45	34	37	49
Variation coefficient	5.3	5.3	8.0	7.6	8.3	12.5	4.5	4.7	7.1	6.8	7.9	11.9

S10/5 = the hourly soil SET sum above 10°C at 0.05 m depth; S10/10 above 10°C at 0.10 m depth, etc.

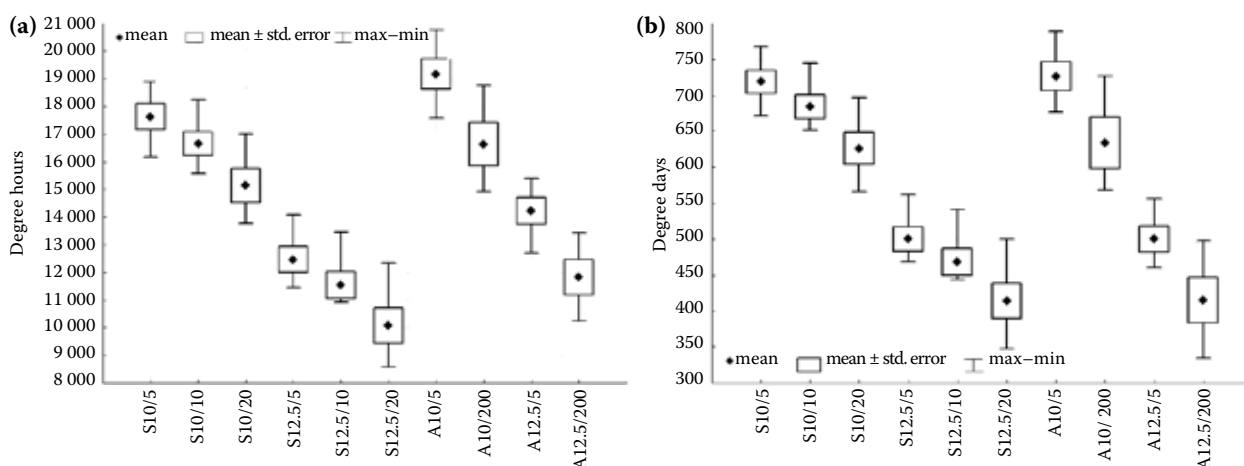


Figure 2. The hourly soil SET (a) and daily soil SET (b) until the initial occurrence of WCR (five-year average)

S10/5 = hourly soil SET sum above 10°C at 0.05 m depth; S10/10 above 10°C at 0.10 m depth, etc.

A10/5 = hourly air SET sum above 10°C at 0.05 m height; A10/200 above 10°C at 2 m height, etc.

SET (Table 1) and air SET (Table 2) hourly values measured is relatively small (the coefficient of variation from 5.3% to 12.5%). The minimum values of dispersion (the coefficient of variation 5.3%) were calculated for the soil SET of a 0.05 m soil depth and threshold temperature of 10.0°C. The same degree of variability (5.3%) was detected for the soil SET of a 0.10 m soil depth and threshold temperature of 10.0°C. In regard to the low values of dispersion, these parameters seem to be usable for predicting adult WCR occurrence.

Figure 2b shows the five-year averages of daily soil and air temperature sums from Žabčice. The average soil SET ranges from 414 DD (LTT 12.5°C, 0.20 m) to 719 DD (LTT 10.0°C, 0.05 m). In particular, the soil temperatures at shallow depths (0.05 and 0.10 m) are characterised by relatively low volatility (the difference between the minimum and maximum of the observed SET).

DERRON *et al.* (2005) evaluated soil SET in the maize canopy to predict adult WCR occurrence in Switzerland. The authors observed the initial adult occurrence in the maize monoculture when

the soil SET of $600 \pm 40^\circ\text{C}$ at 0.05 and 0.10 m was reached (DD above 10.5°C). The occurrence of adults was recorded in uninfected plots (with crop rotation) when the soil SET was approximately about 200 DD higher (approximately 15 days later).

ÁVILA *et al.* (2002) observed 449 SET DD based on the average daily soil temperature above 11.04°C at 0.10 m depth under maize canopy. STEVENSON *et al.* (2008) calculated the sum of degree-days for phenological events from the emergence onset to 99% adult WCR emergence. According to this model, the initial occurrence of WCR (1% occurrence) is expected after the air SET above 10°C and 600 DD. BAKER *et al.* (2003) and MACLEOD *et al.* (2007) used a CLIMEX model to identify the critical parameter to define the northward limit of WCR distribution in North America, i.e. an accumulated temperature threshold, and then applied this model to the United Kingdom at improved spatial and temporal resolutions under current and future climates. It was noted that considerable uncertainty remains regarding the choice of an 11°C

Table 2. Statistical evaluation of air SET variability in maize canopy (Žabčice location)

	Hourly data (DH)				Daily data (DD)			
	A10/5	A10/200	A12.5/5	A12.5/200	A10/5	A10/200	A12.5/5	A12.5/200
5 th year average	19 170	16 639	14 234	11 824	726	634	500	415
Standard deviation	1 104	1 556	959	1 290	40	72	35	63
Variation coefficient	5.8	9.4	6.7	10.9	5.5	11.3	7.1	15.2

A10/5 = the hourly air SET sum above 10°C at 0.05 m height; A10/200 above 10°C at 2 m height, etc.

minimum threshold and the annual accumulated temperature limit set at 670 degree days.

The air SET values in Žabčice ranged from 415 DD (LTT of 12.5°C at a 2 m height) to 726 DD (LTT of 10.0°C at a height of 0.05 m). The air SET results correspond with the results of MODIĆ *et al.* (2007). The authors assessed the air SET for an LTT of 11°C at a height of 2 m from 535 to 869 DD and another air SET for an LTT of 12.7°C at a height of 2 m from 385 to 714 DD for Slovenian conditions. ÁVILA *et al.* (2002) observed the air SET of 387 DD for an LTT of 11.04°C at a height of 2 m. In the USA, the emergence of WCR is observed from mid-July to mid-August (O'DAY *et al.* 1998) by 1800–2200 DD (the air temperature was cumulative from January 1st).

The daily values of the soil SET (Table 1) and air SET (Table 2) in Žabčice varied between 4.5% and 15.2%. A significantly higher dispersion of values was observed for air temperature. The smallest dispersion of values (coefficient of variation 4.5%) was shown by the soil SET at 0.05 m and LTT of 10.0°C. The daily soil SET above 10.0°C at 0.05 m (measured under maize canopy) is the most suitable criterion for predicting the WCR occurrence.

The microclimate of agricultural crops is often different from the microclimate at the standard climatological CHMI stations (STŘEDA *et al.* 2011; KRÉDL *et al.* 2012). The correlation between microclimate measurements at the climatological stations and the canopies strongly depends on the canopy structure, as well as on the height the measuring sensors are positioned at (CHELLE *et al.* 2009).

The differences between canopy microclimate data and standard climatological station data were evaluated by an output comparison. The soil SET (at 0.05, 0.10 and 0.20 m under permanent grassland at the Velké Pavlovice and Staré Město locations) for an LTT of 10.0°C and 12.5°C are shown

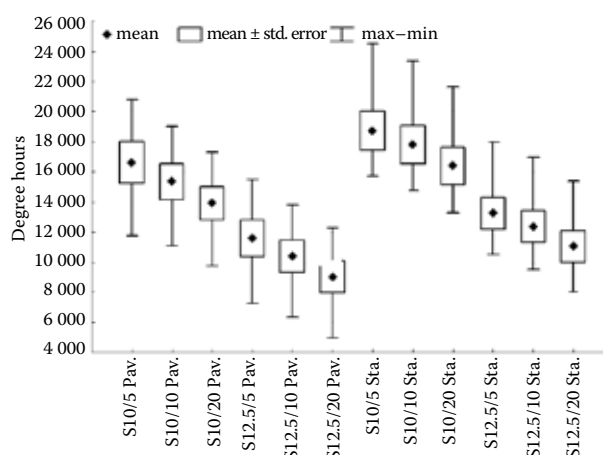


Figure 3. The hourly soil SET under grassland: Velké Pavlovice and Staré Město locations

S10/5 Pav. = hourly sum of effective soil temperatures above 10°C at 0.05 m in Velké Pavlovice; S10/10 above 10°C at 0.10 m in Velké Pavlovice, etc.

S10/5 Sta. = hourly sum of effective soil temperatures above 10°C at 0.05 m in Staré Město; S10/10 above 10°C at 0.10 m in Staré Město etc.

in Figure 3. The six-year hourly average soil SET ranged from 9023 HD (LTT of 12.5°C at a depth of 0.20 m) to HD 16618 (LTT of 10.0°C at a depth of 0.05 m) at the Velké Pavlovice CHMI station and from 11043 HD (LTT of 12.5°C at a depth of 0.20 m) to HD 18730 (LTT of 10.0°C at a depth of 0.05 m) at the Staré Město CHMI station.

The soil temperature was measured up to the initial occurrence of adult WCR at the nearest observation point of SPA. If a low range of annual values occurred, the method was applicable for extrapolation to larger areas. The model can be refined by the regression relationship between air and soil temperatures. ELLIOT *et al.* (1990) used a temperature-dependent, multiple-cohort model to predict adult WCR emergence. The authors successfully used hourly soil temperatures, which were

Table 3. Statistical evaluation of soil SET variability (hourly data – HD) at the Velké Pavlovice and Staré Město stations

	Velké Pavlovice						Staré Město					
	S10/5 Pav.	S10/10 Pav.	S10/20 Pav.	S12.5/5 Pav.	S12.5/10 Pav.	S12.5/20 Pav.	S10/5 Sta.	S10/10 Sta.	S10/20 Sta.	S12.5/5 Sta.	S12.5/10 Sta.	S12.5/20 Sta.
6 th year average	16618	15351	13903	11583	10377	9023	18730	17807	16395	13247	12367	11043
Standard deviation	3076	2668	2506	2740	2419	2309	2919	2857	2816	2352	2338	2322
Variation coefficient	18.5	17.4	18.0	23.7	23.3	25.6	15.6	16.0	17.2	17.8	18.9	21.0

S10/5 = the hourly soil SET sum above 10°C at 0.05 m depth; S10/10 above 10°C at 0.10 m depth, etc.

predicted from the daily minimum and maximum air temperatures using a soil-temperature model that accounted for edaphic factors. ELLSBURY *et al.* (2005) used the soil LTT of 10°C at 0.10 m under grassland to determine the growing degree days of adult WCR. The initial occurrence of adults in the area with light, loamy soil was observed when the DD was 1000 in a wet year and when the DD was 1125 in a dry year. The initial adult WCR were detected in dark areas with clay soil when the DD was 1300 and 1125.

Figure 3 shows a significantly higher variability of values in comparison with the meteorological data measured in the maize canopy. The data file dispersion was expressed by the coefficient of variation and varied from 15.6% (LTT of 10°C at a depth of 0.05 m in Staré Město) to 25.6% (LTT of 12.5°C at a depth of 0.20 m in Velké Pavlovice) (Table 3). The precise prediction of WCR activity based on soil temperature from the nearest climatological station is thus limited.

The annual difference may be caused by SPA observation point differences in soil conditions, slope, land orientation, etc. (the observation points within one cadastral territory were not identical each year). A minor distortion could also be caused by the weekly trap observations. The gradually growing WCR population could be accelerated by the long-term cultivation of maize in one field in consecutive years. In connection with the rising number of biogas stations in the CR, the increase of maize included in crop rotations, including multi-annual monocultures, is expected.

The survival rate and concentration of WCR individuals increase with the density of individuals. These effects may subsequently affect the initial occurrence of adults. Figure 4 shows the soil SET dynamics (LTT of 10°C at a depth of 0.05 m) from five years of monitoring at CHMI stations based on adult WCR observations at SPA observation points. The data fit to a logarithmic trend. In regard to the specific meteorological conditions in 2010 (precipitation was up to three times higher in May, June and July compared with the long-term average), this year is not included in the graph.

Figure 1 defines the areas suitable for the continuous survival of WCR in the CR (according to conditions specified in the Material and Methods section). The probable date of the initial occurrence of adult WCR was assessed based on reaching the soil SET threshold. Areas with a high-risk of WCR spread and potential harmfulness are also defined. These

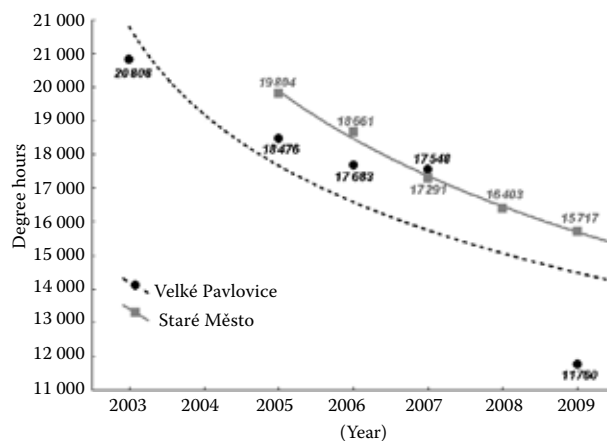


Figure 4. The trend of SET for adult WCR development with a logarithmic trend curve at the Velké Pavlovice and Staré Město stations

areas have favourable agroclimatic conditions and increased maize concentrations on arable land. The areas of improbable WCR occurrence and survival are marked (high-altitude or areas with SET lower than the minimum threshold).

In regard to geographical and climatic conditions, the areas of the highest risk are marked in Figure 1 by dark shades of grey colour in combination with hatching. The warm climate, low altitude and soil conditions allow for the complete adult WCR development since the initial decade of July (before the 190th day of the year). Every-year occurrence and intensive propagation of WCR (forced by increased concentrations of maize on arable land – the shaded area) can be expected in these areas. These areas are primarily the border districts Znojmo, Břeclav, Hodonín and the district of Kroměříž in the southeastern region of the CR. The central part of the country, the Pardubice district and the Polabská nížina lowland, are exposed to a particular risk.

Based on terrain orography and location, the districts Karviná, Vsetín and Plzeň-město are not included as high-risk areas. Suitable conditions for the complete adult WCR development (minimum soil SET) were also detected in the middle part of the Českomoravská vrchovina highlands, Jeseníky and Krkonoše Mountains. Low-risk areas are mainly located in the foothills and mountain areas at an altitude of 650 m a.s.l. and in the cold areas of CR. These climatic conditions allow for the development and survival of WCR in a significant part of the CR territory. The only exceptions are the upper part of the Českomoravská vrchovina highlands and all border mountains.

Egg mortality is mainly influenced by abiotic factors, especially by the soil temperature (ELLSBURY *et al.* 1998a,b). In addition to temperatures above the developmental threshold, post-diapause eggs require water uptake to complete their development (KRYSAN 1978). The eradication of WCR due to low winter temperatures, i.e. the mortality of eggs when the soil temperature is -7.5°C at a depth of 0.075–0.15 m (GUSTIN 1981), can be expected during the winter with a frost period without snow cover (e.g. the winter of 2011/2012). Similarly, the non-termination of adult WCR development can be expected locally during temperatures that are significantly below normal annual averages.

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