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Abstract

The western corn rootworm *Diabrotica virgifera virgifera* LeConte is a major insect pest of field maize, *Zea mays* L. Larvae can cause substantial injury by feeding on maize roots. Larval feeding may destroy individual roots or root nodes, and reduce plant growth, stability, and yield. Costs associated with managing corn rootworms in continuous maize are annually one of the largest expenditures for insect management in the United States Corn Belt. Even though *D. virgifera virgifera* has been studied intensively for over 50 years, there is renewed interest in the biology, ecology, and genetics of this species because of its ability to rapidly adapt to management tactics, and its aggressive invasive nature. This article provides a comprehensive review of *D. virgifera virgifera* population dynamics, specifically: diapause, larval and adult development, seasonality, spatial and temporal dynamics at local and landscape scales, invasiveness in North America and Europe, and non-trophic interactions with other arthropods. Gaps in current knowledge are identified and discussed especially within the context of challenges that scientists in North America and Europe are currently facing regarding pest dynamics and the need to develop appropriate management strategies for each geographic area.

Keywords

Development, *Diabrotica virgifera virgifera*, diapause, Europe, invasiveness, maize, North America, population dynamics, seasonality, western corn rootworm, *Zea mays*

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RECENT RESEARCH ON THE WESTERN CORN ROOTWORM

Western corn rootworm (*Diabrotica virgifera virgifera* LeConte) population dynamics

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- 1 The western corn rootworm *Diabrotica virgifera virgifera* LeConte is a major insect pest of field maize, *Zea mays* L. Larvae can cause substantial injury by feeding on maize roots. Larval feeding may destroy individual roots or root nodes, and reduce plant growth, stability, and yield. Costs associated with managing corn rootworms in continuous maize are annually one of the largest expenditures for insect management in the United States Corn Belt.
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Introduction

The western corn rootworm (WCR) *Diabrotica virgifera virgifera* LeConte is a galericine chrysomelid species native to North America (Krysan & Smith, 1987). Because of its close association with maize *Zea mays* L. as a larval and adult host (Branson & Krysan, 1981) and the modern agricultural practice of planting maize after maize (continuous maize) in large monocultures, the WCR has become one of the most economically important insect pests of maize in the United States (U.S.) (Levine & Oloumi-Sadeghi, 1991; Sappington *et al.*, 2006). Larval feeding on maize roots can lead to root

injury, decreased plant growth, and reduced yield (Godfrey *et al.*, 1993; Gray & Steffey, 1998; Urías-López & Meinke, 2001). Costs associated with managing corn rootworms in continuous maize are annually one of the largest expenditures for insect management in the U.S. Corn Belt (Metcalfe, 1986; Steffey *et al.*, 1994; Sappington *et al.*, 2006).

Even though the WCR has been studied for over 50 years in the U.S. (especially from a pest management perspective), there is renewed interest in the biology, ecology, and genetics of this species because of recent events. The relatively recent invasion of the WCR into maize growing areas in the north-eastern United States, eastern Canada and Europe, and its increased importance in Texas and Mexico [WCR and subspecies Mexican corn rootworm (MCR) *Diabrotica*

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virgifera zea Krysan and Smith] elevates the pest status from one of regional to international importance. The WCR has evolved resistance to some insecticides (Ball & Weekman, 1962; Meinke *et al.*, 1998), and, in part of its range, to a simple crop rotation from a host crop to a non-host crop (i.e. maize–soybean rotation) by an apparent reduction in fidelity to maize. The latter phenomenon leads to an economically significant level of oviposition outside of maize by the ‘WCR variant’ (Levine *et al.*, 2002). Therefore, management of this species to minimize risk of economic loss has become more difficult in the U.S. A clear understanding of emerging rootworm management technologies (i.e. plant incorporated protectants in transgenic plants) and their potential impacts on WCR biology and ecology is needed to develop acceptable insect resistance management strategies (EPA, 2002; Glaser & Matten, 2003). Finally, environmental regulatory constraints in the U.S. and Europe may dictate the need for more ecologically-based sustainable rootworm management strategies in the future.

Aspects of WCR biology and ecology have been reviewed by Chiang (1973), Krysan and Branson (1983), Krysan and Miller (1986), Krysan (1999), and Vidal *et al.* (2005). However, a comprehensive overview of WCR population dynamics has not been compiled since Chiang’s review (1973). Therefore, this article provides a current review of WCR diapause, larval and adult development, seasonality, spatial and temporal dynamics at local and landscape levels, invasiveness in North America and Europe, and non-trophic interactions with other arthropods.

Egg diapause

The WCR is univoltine, overwintering as an egg in the soil (Ball, 1957; Chiang, 1973). During the overwintering stage, the egg is exposed to harsh conditions for an extended period, resulting in high mortality (Gustin, 1981, 1986; Levine & Oloumi-Sadeghi, 1991; Godfrey *et al.*, 1995; Toepfer & Kuhlmann, 2006). Eggs surviving the winter determine the maximum level of damage to be inflicted in an infested field, and the dynamics of egg dormancy is a key to understanding the species ecology as a whole (Schaafsma *et al.*, 1991; Woodson & Gustin, 1993; Ellsbury *et al.*, 1998; Ellsbury & Lee, 2004). Winter dormancy consists of two phases, an initial obligate diapause followed by facultative quiescence governed by environmental conditions (Krysan, 1978). In temperate regions, eggs are oviposited in the soil during July to September. Embryogenesis presumably begins at oviposition or soon after, but development halts within about 11–13 days at 20°C as the egg enters diapause (Krysan, 1972). Krysan *et al.* (1977) reported 100% of eggs examined had embryos in the diapause form by 18 days post-oviposition at 25°C. Continuous chilling of the egg before reaching diapause is ‘detrimental’ (B.W. George, unpublished data, cited in Chiang, 1973), and a 2–3 week period at 25°C is routinely employed when rearing eggs through to hatch to allow prediapause development before chilling (Jackson, 1986). At the point of entering diapause, the embryo is immersed in the yolk as an undifferentiated germinal disc about 90 µm in length, and it remains at this stage until diapause is terminated (Krysan, 1972). Reported mean duration of diapause

(also referred to as ‘diapause intensity’) varies widely among studies and latitude, ranging from 78 to 163 days, and is quite variable among individuals within a population (Branson, 1976a; Krysan, 1982). Termination of diapause does not require chilling or other known environmental cues, but is an event apparently governed by time (Krysan *et al.*, 1977; Krysan, 1978). Under natural conditions in temperate regions, termination occurs during midwinter when soil temperatures are still below 11°C, the thermal threshold for development (Wilde, 1971; Schaafsma *et al.*, 1991; Levine *et al.*, 1992). Thus, postdiapause eggs remain dormant in a facultative state of chill-quiescence until the soil temperature warms above 11°C (Krysan, 1978; Gustin, 1981; Krysan *et al.*, 1984). Most WCR eggs in temperate regions follow this pattern, but Levine *et al.* (1992) reported <1% of eggs from several WCR populations exhibited prolonged diapause and egg hatch after two simulated winters.

At soil temperatures >11°C, postdiapause development commences until hatching, which begins by 14–20 days and peaks by 18–43 days post-chill at constant 20–25°C in the laboratory, again depending on the study and on the latitude of the subject population (Wilde, 1971; Branson, 1976a, b, 1987; Krysan *et al.*, 1984; Fisher, 1989; Schaafsma *et al.*, 1991; Levine *et al.*, 1992). Fluctuating laboratory rearing temperatures tracking outdoor soil temperatures in South Dakota increased post-chill time to hatch by 45–50 days over that (19–24 days) at a constant 25°C (Fisher, 1989). Musick and Fairchild (1971) found egg hatch in northwest Missouri was usually completed within 35 days. Both linear and non-linear models have been developed to predict postdiapause development time to egg hatch based on accumulation of heat units (Fisher, 1989; Elliott *et al.*, 1990; Schaafsma *et al.*, 1991, 1993; Levine *et al.*, 1992). The optimum temperature for postdiapause egg development is about 28°C (Schaafsma *et al.*, 1991). Numerous factors such as microclimate, tillage, and soil characteristics affect soil temperature at a given depth, and thus affect predictability of egg hatch (Pruess *et al.*, 1968; Bergman & Turpin, 1986; Elliott *et al.*, 1990; Schaafsma *et al.*, 1993; Godfrey *et al.*, 1995).

In addition to temperatures above the developmental threshold, postdiapause eggs require uptake of water to complete development (Krysan, 1978). In the absence of water, postdiapause development stalls at various stages, with embryos ranging mostly from 300 to 600 µm in length. The eggs remain in this facultative state of dry-quiescence until water contacts the egg and is absorbed (Krysan, 1978). Water is not absorbed during diapause itself, indicating a change in egg permeability after diapause is terminated (Krysan, 1978). The uptake of water during embryo development is reflected by a decrease in specific gravity of the egg (Palmer *et al.*, 1976, 1977).

Evidence supports a tropical or subtropical origin of WCR, with subsequent colonization of temperate North America (Branson & Krysan, 1981; Krysan, 1982; Segura-León, 2004). WCR/MCR egg diapause in Mexico occurs during the dry season, when maize is not available, followed by a dry-quiescence (Krysan *et al.*, 1977; Branson *et al.*, 1978). Onset of the rainy season (summer) at planting time allows continuation of postdiapause development and egg hatch in synchrony

with host development (Krysan *et al.*, 1977; Branson & Krysan, 1981; Cocke *et al.*, 1994). Thus, it is thought that egg diapause in WCR/MCR evolved as a strategy to survive dry conditions, and that diapause pre-adapted the WCR to survive the cold season in temperate regions (Krysan *et al.*, 1977; Krysan, 1982; Ellsbury *et al.*, 1998).

There is a geographic cline in diapause duration, which decreases from south to north (Wilde *et al.*, 1972; Krysan & Branson, 1977; Krysan *et al.*, 1977; Krysan, 1982; Schaafsma *et al.*, 1991; Levine *et al.*, 1992). Diapause duration is under genetic control, with artificial selection for early hatching (i.e. shorter diapause duration; Krysan, 1978) resulting in a 'non-diapause' colony of WCR (Branson, 1976a), still widely used in research because of its short generation time (Kim *et al.*, 2007). Diapause duration in MCR averaged 253 days compared with 73 days for WCR from South Dakota under the same conditions (Krysan & Branson, 1977). Reciprocal crosses between these two populations and with the non-diapause selected colony produced offspring with intermediate diapause durations, but with evidence of a maternal effect (Krysan & Branson, 1977). A long-duration diapause is thought to be necessary in the tropics to maintain dormancy until the true rainy season begins, rather than relying on dry- quiescence which might break prematurely with an unseasonal winter shower (Krysan *et al.*, 1977). In the north, diapause need only be long enough to ensure dormancy until winter, after which cold-quiescence is an efficient enforcer of dormancy until spring (Krysan *et al.*, 1977; Krysan, 1978, 1982; Ellsbury *et al.*, 1998).

Diapause termination is often said to be 'spontaneous', i.e. under the control of time alone (Krysan, 1978, 1986). But chilling has the effect of synchronizing postdiapause development, or concentrating the period of hatch (Branson *et al.*, 1975; Branson, 1976a; Krysan *et al.*, 1984; Jackson, 1986), and synchronization is affected differentially by chill durations up to 3–6 weeks (Branson, 1976b; Krysan, 1982), so diapause duration cannot be entirely spontaneous. Furthermore, if the time-keeper mechanism is physiological, then it would be expected to respond to temperature, based on the principle of physiological ageing as opposed to calendar ageing in poikilotherms (Elliott *et al.*, 1990; Spurgeon & Raulston, 1998). Krysan (1982) found little effect of temperature at 15, 18, or 25°C on diapause duration. However, a mechanism for maintaining circadian rhythms at different temperatures along latitudinal gradients has been described for *Drosophila* (Sawyer *et al.*, 2006).

The genetic nature of diapause is not well understood. The pattern of response to recurrent selection for shorter diapause duration (Branson, 1976a) suggests this trait is polygenic. Reciprocal crosses indicate a strong maternal effect on diapause duration (Krysan & Branson, 1977), but the nature of this effect is unknown. It could be sex linked, or it could be as a result of maternal factors in the cytoplasm of the egg. The presence of a cline implies a fitness advantage to shortened diapause duration with increasing latitude (Tauber & Tauber, 1976; Krysan, 1982; Endler, 1986; Levine *et al.*, 1992), but the nature of the advantage (or the disadvantage of retaining a long diapause) is unknown. Because the WCR range expansion through most of North America occurred

recently, local adaptation also occurred rapidly (Krysan, 1982). Thus the question arises whether the same kind of latitudinal adjustments in diapause duration are occurring in Europe as populations expand into new latitudes or altitudes. The speed of such adjustments may limit the rate of spread of WCR in Europe (see Hemerik *et al.*, 2004). It is possible that initial diapause duration in newly introduced populations (Miller *et al.*, 2005) may provide a clue to the latitude of origin.

Larval and adult dynamics

Larvae occupy plant roots and the soil around roots, with the pre-pupal stage forming a discrete earthen cell for pupation (Chiang, 1973; Krysan, 1999). Initial larval eclosion from eggs is variable over years but usually occurs during late May to early June in the U.S. Corn Belt and in Central and Eastern European countries. Eclosion duration has been reported over a mean of 29 days for males and 32 days for females (Musick & Fairchild, 1971; Branson, 1976a; Palmer *et al.*, 1977; Krysan *et al.*, 1984; Levine *et al.*, 1992). Larval development progresses through three instars (George & Hintz, 1966; Hammack *et al.*, 2003). Males complete larval/pupal development faster than females within a temperature range of 18–30°C (i.e. 0.9–2.8 days depending on temperature) but both sexes have a lower threshold of development near 9°C (Jackson & Elliott, 1988). Rate of development of immature stages is temperature dependent (Kuhlman *et al.*, 1970; Fisher, 1986; Jackson & Elliott, 1988). Average female neonate to adult emergence times ranged from 45.0 to 20.7 days at 18–30°C (Jackson & Elliott, 1988). Temperatures between 21 and 30°C result in the greatest mean head capsule width and survival to the adult stage, whereas temperatures greater than 30°C are detrimental to immature development (Jackson & Elliott, 1988). In maize fields, survival of natural WCR populations from egg to adult is variable among years but has been reported to range from 6.7 to 11% (Gray & Tollefson, 1988a, b; Pierce & Gray, 2007).

In the U.S. Corn Belt, WCR adult emergence may begin in late June to early July with peak emergence often occurring during July (Quiring & Timmins, 1990; Darnell *et al.*, 2000; Nowatzki *et al.*, 2002a). This general pattern is consistent in Central and Eastern European countries (i.e. Croatia, Serbia, Hungary) and U.S. geographical areas inside and outside of the areas where crop rotation-resistant (Pierce & Gray, 2006a) or organophosphate-resistant populations occur. In Croatia, initial adult emergence was recorded from 17 June to 2 July during 1998–2000 (Bazok, 2001). Peak (50%) emergence has occurred during the first to third weeks of July in Croatia and Hungary (Bazok, 2001; Bayar *et al.*, 2003). The duration of WCR emergence can be highly variable among fields and years. In Iowa U.S., duration of emergence from 78 continuous maize fields over a 6-year period averaged 33.4 days for males and 51.3 days for females (T. M. Nowatzki, unpublished data). Various models have been developed to predict WCR adult emergence patterns that have been based on calendar date, air or soil degree-day accumulations, and specific development thresholds (Ruppel *et al.*, 1978; Bergman &

Turpin, 1986; Hein *et al.*, 1988; Fisher *et al.*, 1990; Davis *et al.*, 1996; Nowatzki *et al.*, 2002a).

Adult males begin emerging before females, and peak (50%) cumulative male emergence also occurs earlier than peak female cumulative emergence (Darnell *et al.*, 2000; Nowatzki *et al.*, 2002a). This is a function of differences between sexes in both postdiapause embryonic development and post-hatch immature development (Branson, 1987). This phenomenon ensures that a significant number of males are sexually mature (Quiring & Timmins, 1990) and available to mate with females as they emerge (see Spencer *et al.*, 2009 for an indepth discussion of WCR mating behaviour and associated fitness). Sex ratio of total emerged adults can be highly variable among fields and years (e.g. Sutter *et al.*, 1991; Darnell *et al.*, 2000). A 1:1 male/female sex ratio has been observed especially when larval densities and associated root injury are low (Weiss *et al.*, 1985). However, seasonal total male/female sex ratios from field emergence cages are often skewed toward one sex or the other in continuous maize (Sutter *et al.*, 1991; Darnell *et al.*, 2000; Bayar *et al.*, 2003).

The WCR sex ratio of adults counted or collected using various monitoring tools can vary considerably throughout a season (e.g. emergence cages, Darnell *et al.*, 2000; cucurbitacin vial traps, Pierce & Gray, 2006a). In continuous maize, sex ratios shift from a male bias early in the season to a female bias late in the season (Short & Hill, 1972, sampling technique: 10-min beetle collections). First-year fields often have a higher proportion of females than continuous maize (Godfrey & Turpin, 1983, sampling techniques: yellow sticky traps, hand collections). Factors that determine sex ratio in the landscape appear to be complex and the impact of sex ratio (especially as it interacts with adult density/crop phenology factors) on overall population dynamics in various landscapes is poorly understood. Because sex ratios derived from sampling programmes are often highly biased by the type of trap employed (i.e. design, baited vs. unbaited), trap location, and time of year (Witkowski *et al.*, 1975; Weisling & Meinke, 1991; Kuhar & Youngman, 1995; Campbell & Meinke, 2006) it is important to clearly understand how adult sampling data relates to actual sex ratios present in the field. In general, WCR beetle collections at ear zone height from unbaited sticky traps or cucurbitacin vial traps are more skewed toward males than hand-aspirated collections (Godfrey & Turpin, 1983; Kuhar & Youngman, 1995).

Various factors can affect adult emergence timing, total adult emergence, and size of emerged adults. Delayed planting of maize delays initial adult emergence and reduces total emergence (Musick *et al.*, 1980; Bergman & Turpin, 1984; Meinke, 1995). The effects of late planting in relation to WCR egg hatch patterns presumably reduces availability of maize roots and larval colonization sites resulting in mortality of earliest eclosing larvae (Bergman & Turpin, 1984; Boetel *et al.*, 2003). The presence of grassy weeds (e.g. *Setaria* spp.) that can serve as alternate WCR larval hosts in maize fields can also delay adult emergence (Breitenbach *et al.*, 2005; Ellsbury *et al.*, 2005) and reduce mean beetle size (Ellsbury *et al.*, 2005) when compared with weed-free maize. This is consistent with published data that indicate

Setaria species are sub-optimal larval hosts (Branson & Ortman, 1967, 1970; Clark & Hibbard, 2004). Adult emergence may be delayed in conservation tillage systems, but total cumulative emergence is often comparable across tillage systems (Gray & Tollefson, 1988a). Cooler soil temperatures, especially during the egg-larval periods, caused by insulating soil surface debris may contribute to adult emergence delays observed in reduced tillage fields (Gray & Tollefson, 1988a). Reduced row spacing in maize (i.e. 38 cm vs. 76 cm row spacing) can lead to greater total adult emergence per m² (Nowatzki *et al.*, 2002b).

As density of larvae on maize roots and associated root injury increases (especially very high densities), total adult emergence and mean adult size decreases (Branson & Sutter, 1985; Weiss *et al.*, 1985; Elliott *et al.*, 1989). High larval densities also lead to prolonged mean development time from neonate to adult (Weiss *et al.*, 1985; Elliott *et al.*, 1989; Sutter *et al.*, 1991). Onstad *et al.* (2006) recently developed equations from published data that clarify and confirm density-dependent effects on survival from egg to adult.

Total adult emergence, and in some cases emergence patterns and sex ratios of emerged adults, can be altered in maize fields where soil insecticide applications have been used for rootworm control (Sutter *et al.*, 1991; Gray *et al.*, 1992a; Boetel *et al.*, 2003). While different effects on adult parameters have been reported for various insecticides, it is unclear whether effects on WCR population dynamics are directly caused by sublethal exposure to the insecticide, or indirectly as a result of environment/insecticide/rootworm density interactions. A recently commercialized plant incorporated protectant (Vaughn *et al.*, 2005), also appears to alter rootworm life history parameters. Under low-to-moderate larval densities, WCR larvae reared on transgenic maize plants expressing the *Cry3Bb1* protein developed slower, adult emergence was delayed, and the sex ratio of emerged beetles became skewed more toward females when compared with a non-transgenic isolate (Becker, 2006; L. J. Meinke, unpublished data). The mechanism is unclear, but it appears to be a complex interaction of behavioural and physiological responses of larvae to the *Cry3Bb1* protein (Becker, 2006; Clark *et al.*, 2006).

Onstad *et al.* (2001a) estimated that the WCR carrying capacity (the asymptotic densities of WCR) of a typical U.S. continuous maize field was 15 million eggs per ha in the fall and 0.7 million emerging adults the following season. Onstad *et al.* (2003a) simulated a higher carrying capacity of 2 million adults per ha. However, densities of natural infestations have been reported to be as high as 29–100 million eggs per ha (Gray & Tollefson, 1987; Pierce & Gray, 2006a, b) and from 0.5–10.9 million adults per ha (Onstad *et al.*, 2006) in the U.S. Questions remain about the sustainability of high population densities in continuous maize (Onstad *et al.*, 2006). This is especially important in the U.S. because continuous maize hectareage is increasing in response to biofuel initiatives and a changing agricultural economy. The WCR has clearly adapted to use of maize as a superior larval host (Branson & Krysan, 1981; Clark & Hibbard, 2004; Wilson & Hibbard, 2004) so the proportion of hectares planted as continuous maize greatly favours survival and the build-up of

population densities in a region over time (Hill & Mayo, 1980). In southern Hungary, a range of 0.14–0.39 million WCR eggs per ha has been reported (Bayar *et al.*, 2003). It is currently unknown what the WCR carrying capacity may be under European conditions (both in continuous or highly rotated cropping environments). It also is unknown whether the reported egg density from Hungary is typical of what could be expected in continuous maize in the future or if egg densities could approach those reported in the U.S. if more continuous maize is planted and the WCR further adapts to European conditions.

Within and among field distribution

Adult WCR population densities vary within and among fields over time (Darnell *et al.*, 2000; Park & Tollefson, 2005a). Adults can often be found in and around maize fields until early fall or first frost (Short & Hill, 1972; Krnjajić, 1995; Bazok, 2001; Komáromi *et al.*, 2001; Komáromi & Kiss, 2004) and peak densities are often correlated with peak emergence patterns, namely late July to early August (Darnell *et al.*, 1999; Bazok, 2001; Komáromi & Kiss, 2004). Because of all of the abiotic and biotic factors that may potentially interact to cause WCR mortality (Toepfer & Kuhlmann, 2005; Onstad *et al.*, 2006) or affect fitness, it is difficult to predict changes in density within and among years. The number of beetles emerging from within a continuous maize field is often a primary contributor to the total population density in a field but emigration and immigration rates can significantly affect the population density during a specific period (Meinke, 1995; Darnell *et al.*, 2000). Total seasonal adult densities are often greater in continuous maize than first-year maize (Godfrey & Turpin, 1983; Kiss *et al.*, 2005a), but peak densities may occur later in first-year maize (Godfrey & Turpin, 1983) or crops rotated with maize (e.g. WCR variant in Illinois, U.S., Pierce & Gray, 2007). The mobility and reproductive potential of adult females enables the WCR to quickly colonize new areas or recolonize where densities have been greatly reduced by crop rotation (Godfrey & Turpin, 1983), adult management (Pruess *et al.*, 1974) or weather (i.e. winter egg mortality, Godfrey *et al.*, 1995). Various types of deterministic (Elliott & Hein, 1991; Onstad *et al.*, 2001a, b; Hemerik *et al.*, 2004; Crowder & Onstad, 2005; Crowder *et al.*, 2005) and stochastic models (Storer, 2003; Caprio *et al.*, 2006) have been developed to address temporal and spatial questions pertaining to WCR population dynamics.

WCR adults are attracted preferentially to silking maize (Prystupa *et al.*, 1988), so maize phenology temporally affects WCR adult distribution at the landscape scale (Bergman & Turpin, 1984; Naranjo, 1991, 1994; Campbell & Meinke, 2006). However, the same effect can be seen at smaller scales, because the distribution of silking maize is not uniform on any given date within a field and adults concentrate in clusters of silking plants (Darnell *et al.*, 1999; Park & Tollefson, 2006a; Toepfer *et al.*, 2007). This effect appears to be stronger for females than males (Toepfer *et al.*, 2007), and depends on the presence of a phenological contrast detected

by the beetle (Naranjo, 1994; Darnell *et al.*, 2000). Rapid changes in population densities can occur among fields in response to phenological differences (Darnell *et al.*, 2000). Naranjo (1991) studied the movements of adults between early- and late-planted maize fields. Using a simulation analysis, he found that the net seasonal emigration out of early-planted maize towards late-planted maize was about 62%. Campbell and Meinke (2006) examined adult habitat use of *Diabrotica* species at prairie-maize interfaces, and concluded that (especially for WCR) the contrast in plant phenology was a key factor affecting habitat choice between maize and non-maize habitats. WCR adults preferred a primary habitat (maize) but moved towards secondary habitats if the relative attractiveness of the primary habitat decreased.

Beckler *et al.* (2004) studied adult WCR distribution and abundance in relation to landscape attributes in a 6.4 × 6.4-km agricultural area of high maize hectareage in South Dakota over 5 years. They reported a non-random distribution associated with landscape metrics both for locally emerged adults and for a probable mixture of local and immigrant adults collected on Pherocon AM yellow sticky traps. In each year of the study, WCR abundance was significantly correlated with elevation and soil texture. More adults than expected were captured in areas with loam and silty clay loam soils and at elevations of 500–509 m above sea level in a landscape ranging from 494 to 519 m. The nature of these associations is unknown, but may reflect the influence of moisture on oviposition and immature survival because soil texture and elevation differences are associated with drainage (Turpin *et al.*, 1972) and possible moisture gradients. Total abundance also depended on availability and proximity of continuous and first-year maize patches (Beckler *et al.* 2004). Analyses suggested that natal continuous maize fields reached their carrying capacity relatively fast, thus, WCR adults tended to disperse away from these fields in search of new habitats. Large first-year maize patches nearby the natal fields were more attractive than small distant patches.

The interaction of ecological and environmental factors leading to temporal and spatial changes in adult WCR distribution is still poorly understood. It is especially unclear how adult density-dependent factors in various environments potentially affect adult movement and associated oviposition in individual fields or the landscape. Storer (2003) developed a spatially-explicit, simulation model of WCR population dynamics and genetics that reflected the ecology of the WCR in much of the U.S. Corn Belt. He concluded that the model was highly sensitive to dispersal parameters and that spatial heterogeneity in the agroecosystem, such as non-agricultural land and barriers to dispersal, may significantly influence distribution. This was reinforced in a European mark-release-recapture experiment, where Toepfer *et al.* (2006) reported that WCR beetles could make significant use of alternative host plants during dispersal flights and be arrested for some time in attractive non-maize habitats. Perhaps as the relationship of agroecosystem heterogeneity to WCR distributional patterns is more completely understood, planned landscape structure could be used as part of future sustainable ecological strategies to manage WCR densities on an area-wide scale.

Just as adult WCR densities vary spatially across the landscape, distributions of the different life stages within a field are usually not homogenous (Bergman *et al.*, 1983; Tollefson & Calvin, 1994; Hibbard *et al.*, 1999; Park & Tollefson, 2006a; Toepfer *et al.*, 2007). Infestation can be quite variable within a field, with hotspots and coldspots occurring in certain areas for reasons that are difficult to discern (Kirk *et al.*, 1968; Toepfer *et al.*, 2007). The lack of consistency in distribution can complicate design and interpretation of experiments relying on natural infestations, such as screening for host plant resistance or insecticide efficacy trials (Sutter & Branson, 1986). It also makes adequate spatial sampling more time consuming and elaborate (Weiss *et al.*, 1983; Fisher & Bergman, 1986; Tollefson & Calvin, 1994), and can make interpretation of sampling data problematic, increasing the level of uncertainty when making management decisions.

There are a number of factors that can cause spatial variation in WCR infestations within a maize field (Park & Tollefson, 2005b). Although larvae can move short distances in the soil (Suttle *et al.*, 1967; Short & Luedtke, 1970; Strnad & Bergman, 1987; MacDonald & Ellis, 1990), the only substantial dispersal within a generation occurs via adult flight. Accordingly, spatial patterns of infestation are dependent in part on adult female distribution and choice of oviposition sites (Chiang, 1974; Kirk, 1979; Tollefson & Calvin, 1994; Ellsbury *et al.*, 1998). Adult distribution in a field is usually aggregated (Midgarden *et al.*, 1993; Park & Tollefson, 2006a), although this relationship is density dependent, tending to disappear at low population densities (Steffey & Tollefson, 1982; Park & Tollefson, 2005b). Midgarden *et al.* (1993) determined that sticky traps should be deployed at least 30 m apart to ensure spatial independence of samples. Darnell *et al.* (1999) found spatial dependence among whole-plant counts of adults at distances of 30–40 m, but only during peak pollination periods. Spatial dependence of adults apparently translates into spatial dependence of eggs and larvae at similar scales (Park & Tollefson, 2006b). Superimposed on ovipositional site selection, spatial variation in infestations can be generated by differential mortality of eggs or larvae in different areas of the field (MacDonald & Ellis, 1990; Ellsbury *et al.*, 1998; Ellsbury & Lee, 2004). Thus, identifying conditions both that affect where the eggs are laid and that influence mortality of the immature stages after oviposition is important to explaining and predicting the ultimate spatial distribution of root injury within a field.

Adult WCR distribution within a field tends to be positively correlated with the spatial distribution of larvae and adult emergence (Beckler *et al.*, 2004; Toepfer *et al.*, 2007). This relationship suggests that beetles either preferentially inhabit areas of fields where survival of the immature stages is greatest, or they simply remain near their emergence sites. The latter seems unlikely given that the beetles are quite mobile, with much evidence for significant short-range (Naranjo, 1991; Darnell *et al.*, 2000; Toepfer *et al.*, 2006) and long-range (Coats *et al.*, 1986; Grant & Seevers, 1989; Naranjo, 1990; Isard *et al.*, 2004) dispersal. The possibility that adults select the areas of the field that are also most conducive to larval survival is supported by the adult density

distribution being consistently positively correlated with adult distributions at different times within the summer, and from 1 year to the next (Toepfer *et al.*, 2007). Larval damage distributions are not always correlated with the previous year's adult distribution (Stamm *et al.*, 1985; Toepfer *et al.*, 2007) although Park and Tollefson (2005b) did find a spatial correlation between ear zone counts of adults at peak density and adult emergence the next year. The authors attributed the correlation in part to the interplay between oviposition behaviour and adult distribution as influenced by dense phenology. The presence of a correlation may be dependent on population density (Park & Tollefson, 2006a; Toepfer *et al.*, 2007).

Kirk *et al.* (1968) observed that females preferred the presence of clumps of foxtail grass (*Setaria* spp.) when choosing oviposition sites, but Johnson and Turpin (1985) found at most a minimal and unpredictable affect of foxtail populations on oviposition in the field. Toepfer *et al.* (2007) reported that adult female (but not male) densities were higher in areas with a high density of grasses, mainly Johnson grass *Sorghum halepense* (L.), in Hungary. Otherwise, adult density was not correlated with vegetation cover, weed diversity, weed density, or maize density (Toepfer *et al.*, 2007).

Females prefer to oviposit in moist soil (Kirk *et al.*, 1968; Gustin, 1979), and female density was positively correlated with soil moisture in a field study in Hungary (Toepfer *et al.*, 2007). Because male density was not correlated with moisture in the latter study, female association may have been related to ovipositional preference rather than adult survival per se. About 60–65% of WCR eggs are usually found in the upper 10 cm of soil (Ball, 1957; Hein *et al.*, 1988; Pierce & Gray, 2006b), although significant numbers of eggs can be found as deep as 30 cm (Gray *et al.*, 1992b). The percentage of eggs in the upper 10 cm of soil increases in irrigated fields (Weiss *et al.*, 1983). Females cannot burrow into the soil, but must gain access via soil cracks (Kirk, 1979), open earthworm tunnels (Kirk, 1981a), or piled clods (lumps of soil) created by farm implements (Kirk, 1981b). Once under the surface, females do not oviposit until reaching moist soil (Gustin, 1979; Kirk, 1979), and egg distribution is shifted to deeper levels when the soil is dry (Weiss *et al.*, 1983).

Female ovipositional preference for moist soil seems intuitively reasonable, in that very dry soils may decrease survival of young larvae (MacDonald & Ellis, 1990), and completion of postdiapause development of the egg requires contact by water (Krysan, 1978). On the other hand, there is considerable evidence that wet conditions caused by excessive rainfall, irrigation, or poor drainage are not favourable to survival of WCR eggs or larvae. Eggs are quite tolerant of prolonged immersion in water (Hoback *et al.*, 2002), but they are less tolerant of cold temperatures in moist soil owing to compromised supercooling capacity (Ellsbury & Lee, 2004). Larval density is inversely correlated with soil moisture (Elliott *et al.*, 1989; Toepfer *et al.*, 2007). WCR larvae cannot survive much longer than a day in saturated soil, because of the accumulation of lactic acid (Hoback *et al.*, 2002). Spike and Tollefson (1988) observed lower survival of artificially infested eggs to adulthood in a wet year, where there was saturated soil during the larval stage, than in a dry year.

Differences in soil texture may affect distribution of WCR within a field. Lower infestations seem to be associated with sandy soil (MacDonald & Ellis, 1990). Soil texture appears to influence egg survival indirectly through its effects on soil moisture and temperature (Godfrey *et al.*, 1995). However, larval survival can be affected directly in that abrasion of the cuticle by sand particles may lead to desiccation (Turpin & Peters, 1971). Turpin *et al.* (1972) found a positive correlation between percentage clay content in the soil and root injury. Soil physical factors (e.g. bulk density, pore size) can also affect larval movement and initial establishment (reviewed in Spencer *et al.*, 2009) which can directly or indirectly affect spatial distribution.

Mortality of overwintering eggs can be caused by extreme cold temperatures (Calkins & Kirk, 1969; Chiang, 1974; Gustin, 1981; Ellsburly & Lee, 2004). However, the temperatures experienced by an egg depend on several factors, which can vary spatially. The deeper eggs occur in the soil, the more they are buffered from extreme temperatures (Calkins & Kirk, 1969), and, as described above, depth of oviposition is partly a function of soil moisture experienced by the female. Depth of eggs can change when the soil is disturbed by tillage (Pruess *et al.*, 1968; Godfrey *et al.*, 1995). Soil texture and moisture affect the temperature profile with depth (Bergman & Turpin, 1986), and therefore can differentially affect egg survival at a given depth depending on location in a field. Spring egg densities and subsequent root injury are sometimes higher in no-till fields than conventional tillage fields (Gray & Tollefson, 1987; Nelson *et al.*, 1994). This is not due to ovipositional preference by females (Johnson & Turpin, 1985), but to increased survival of overwintering eggs caused by the insulating effects of crop residue (Godfrey *et al.*, 1995; Ellsburly *et al.*, 1998). Similarly, snow can insulate the soil from extreme cold temperatures (Ellsburly *et al.*, 1998), and topography can cause differences in snow cover through differences in exposure to wind.

A greater understanding of the causal relationships behind spatial variation at smaller scales could open the door to more site-specific management strategies by focusing scouting and control efforts in areas of the field where economic infestations are most likely to occur (Kirk, 1979; Heermann *et al.*, 2002; Beckler *et al.*, 2004; Park & Tollefson, 2005a, 2006b). To date, a universal methodology for successfully predicting spatial distribution of rootworm injury within fields remains elusive.

Western corn rootworm as an invasive species

Dynamics of spread in North America

Historical knowledge of WCR distribution began with its description by LeConte in 1868 from specimens he collected in what is now Wallace County in far western Kansas (Smith & Lawrence, 1967). Smith and Lawrence (1967) suggest that this species may have been collected by Say in 1820 in central or southeastern Colorado, but the specimens have been lost. For many years it was simply one more of hundreds of

obscure New World diabroticite species until it started damaging maize in north central Colorado in 1909 (Gillette, 1912). Before it became a serious pest of maize in the 1940s, population densities were low (Branson & Krysan, 1981) and reports of its presence were scattered and infrequent. In addition to Colorado and western Kansas, pre-1940 reports included New Mexico, Arizona, Sonora, Mexico (Horn, 1893; Bryson *et al.*, 1953), southwestern Nebraska (Bare, 1930, 1931, Tate & Bare, 1946), and apparently south-central and far western South Dakota (Kantack, 1965). Judging from these accounts, the WCR may have been resident in low densities in northwestern Nebraska, eastern Wyoming, and southeastern Montana as well.

By 1940, the WCR was routinely damaging maize in south-central Nebraska, and it became a problem in Norton County maize fields in northwestern Kansas in 1945 (Tate & Bare, 1946; Bryson *et al.*, 1953; Burkhardt & Bryson, 1955). This marked the beginning of a dramatic eastward range expansion, with WCR reaching New Jersey, Maryland, and Delaware along the Atlantic Coast by the mid-1980s (Krysan, 1986; Sutter, 1999). This species is now established from Montana (Smith & Lawrence, 1967; Krysan & Smith, 1987) and North Dakota (Glogoza & Boetel, 2005) in the northwest, to Quebec (Meloche *et al.*, 2005) and New England (Boucher, 2006) in the northeast, and to northern Georgia (Hudson & All, 1996) and Alabama (Flanders, 2006) in the southeast. The MCR was first reported as a pest of maize in Texas in 1977 (Sutter & Stewart, 1995), and is established in Oklahoma and many maize-growing regions of Texas, south through Mexico to Costa Rica (Krysan & Smith, 1987; Stewart, 1999).

Except in areas where rotation resistance has spread (Levine *et al.*, 2002), continuous maize production is necessary for WCR densities to build because of this species' life history characteristics of fidelity to maize for oviposition, univoltinism, the egg as the overwintering stage, and relatively poor survival of larvae on many non-maize hosts (Krysan *et al.*, 1977; Branson & Krysan, 1981; Levine & Oloumi-Sadeghi, 1991; Onstad *et al.*, 1999; Boriani *et al.*, 2006). It is possible that some WCR adults are produced on grasses other than maize (Branson & Ortman, 1970; Clark & Hibbard, 2004; Moeser & Vidal, 2004; Oyediran *et al.*, 2004, 2005; Breitenbach *et al.*, 2005; Chege *et al.*, 2005), but utilization of alternate hosts when maize is nearby probably is uncommon (Campbell & Meinke, 2006).

The initiation of the range expansion was facilitated by increased adoption of planting maize following maize after World War II, which in turn was made possible by the development of irrigation systems and the introduction of synthetic fertilizer and soil insecticides in western Nebraska and Kansas (Smith, 1966; Chiang & Flaskerd, 1969; Luckmann *et al.*, 1974; Ruppel, 1975; Hill & Mayo, 1980; Metcalf, 1986; Kuhar *et al.*, 1997; Sutter, 1999; Isard *et al.*, 2001, 2004). Grower preference for planting continuous maize created conditions suitable for rapid WCR population growth, and thus increased the number of individuals dispersing from an infested area.

Rate of range expansion is determined both by local inter-field movement and by long-range dispersal (Liebhold &

Tobin, 2008). Population growth and local movement create a continuous invasion front that advances into previously uninfested territory linearly over time (Skellam, 1951), an expansion that can be described as neighborhood diffusion (Shigesada *et al.*, 1995). Patterns of local movement and the factors that affect them include those discussed above under *Within and Among Field Distribution*, and in Spencer *et al.* (2009). However, a major factor influencing the rate of range expansion by WCR in North America was long-distance dispersal, and such movement will be the focus here. Long-distance movement of WCR is evidenced by founder populations that jumped ahead of the main front of invasion (Chiang & Flaskerd, 1969; Chiang, 1973; Ruppel, 1975), and ahead of the advancing front of rotation resistance (Onstad *et al.*, 1999). Thus, WCR exhibits stratified diffusion or dispersal (Shigesada *et al.*, 1995; Liebhold & Tobin, 2008), a phenomenon that increases the rate of range expansion as founder populations spread backward to coalesce with the main front while also spreading forward.

Metcalf (1983, 1986) noted that the initial expansion through Nebraska and Kansas was relatively slow. In Nebraska, the eastern expansion of the WCR moved from Furnas and Gosper counties (eastern limit 1931, Bare, 1931) to Hall County by 1945 (~8 km/year, Tate & Bare, 1946), to Seward and Saline Counties by 1948 (~35 km/year, Hixson *et al.*, 1949), and to the Iowa border in 1954 (~19 km/year, Ball, 1957). This was in contrast to the subsequent expansion across the Midwest, reaching west-central Wisconsin by 1964 (~190 km/year) and northwest Indiana by 1968 (~110 km/year). Metcalf (1983, 1986) pointed out that the accelerated period of range expansion coincided with development of resistance to cyclodiene insecticides, first detected in southern Nebraska in 1959 (Ball & Weekman, 1962). Cyclodiene resistance spread throughout the WCR range, so that populations along the expanding species boundary were nearly uniformly resistant by 1964 (Hamilton, 1965; Siegfried & Mullin, 1989). Metcalf (1983, 1986) proposed that the resistant insects were behaviourally different so that they dispersed further per year than susceptible beetles, but this suggestion is unsupported. For insects like WCR that exhibit stratified dispersal, the rate of expansion can accelerate as the length of the front increases (Shigesada *et al.*, 1995; Liebhold & Tobin, 2008), which seems a more plausible explanation of Metcalf's observation.

Rate of expansion across the U.S. actually varied widely depending on location, year, and direction. Based on the map of WCR range expansion drawn by Metcalf (1983), Onstad *et al.* (1999) calculated a variety of rates of spread depending on the direction and time period. The rate generally declined from 1963 to 1979. The eastward flow was calculated to be 138, 115, and 38 km/year, respectively, for the periods 1963–64, 1964–68, and 1968–74. From 1968–74, the eastward rate was 38 km/year and the northeastward rate was much greater at 77 km/year. From 1963–79, the eastward flow of WCR averaged 63 km/year, whereas the northeastward flow from 1963–73 averaged 92 km/year. Such differential rates of spread depending on direction were due mainly to prevailing direction of wind and storm fronts (Ruppel, 1975; Grant & Seevers, 1989; Onstad *et al.*, 1999, 2003b; Isard *et al.*, 1999, 2001,

2004). Ruppel (1975) observed the invasion of WCR into Michigan from 1971 to 1974, and the rates of spread calculated by Onstad *et al.* (1999) varied from 66 km/year to 125 km/year depending on the direction (northward, eastward, or northeastward) and counties chosen for estimation, with a typical rate of 96 km/year. In Ohio, Clement *et al.* (1979) observed the southeastward to eastward invasion of WCR during 1974 to 1978. Onstad *et al.* (1999) calculated a mean rate of spread of 44 km/year. The lower rate of spread in Ohio (Clement *et al.*, 1979) compared with that for Michigan (Ruppel, 1975) may have been due to the prevalence of northeastward flowing storms depositing WCR in northeastern counties in the lower part of Michigan. This phenomenon would not be apparent in Ohio because the invasion began in northwestern counties (Onstad *et al.*, 1999).

Other rates reported or estimated from the literature include: from western Nebraska and Kansas to Maryland and Delaware, averaged ~64–80 km/year over 25–30 years (Sutter, 1999); western Kansas to northeastern Illinois, averaged ~60 km/year over 15 years (Smith, 1966); southeastern to east-central South Dakota, ~80–120 km/year (Kantack, 1965); east-central South Dakota to southeastern North Dakota, ~20 km/year over 6 years (Kantack, 1965; McBride, 1972); within Minnesota ranged from ~20–200 km/year (Chiang & Flaskerd, 1969); within Virginia ranged from ~40–180 km/year (Youngman & Day, 1993); western Ontario to eastern Ontario from 1976–1990, averaged ~45 km/year (Foott & Timmins, 1977; Meloche & Hermans, 2004); eastern Ontario into western Quebec in 2000, ~45 km/year (Meloche *et al.*, 2001). Note that the range of rates within the state of Minnesota alone (20–200 km/year) (Chiang & Flaskerd, 1969) encompasses the range of rates before (20 km/year) and after (190 km/year) development of insecticide resistance as estimated by Metcalf (1983, 1986).

Another major factor affecting rate of WCR spread was the percentage of the landscape in continuous maize production ahead of the front (Chiang & Flaskerd, 1969; Youngman & Day, 1993). For example, invasion of western, central, and north-central Virginia during 1985–1988, where only 39% of the maize hectareage was rotated, was much more rapid than in eastern and southeastern parts of the state from 1989–1992 where 92% of maize hectareage was rotated (Youngman & Day, 1993). The higher percentage of hectares planted to continuous maize may have increased both the number of dispersing females and the survival potential of progeny from founding WCR females that dispersed ahead of the front.

In North America, the potential effects of topographical barriers on WCR dispersal are not well understood. It is possible that the Great Lakes posed a barrier to WCR range expansion. Atmospheric conditions encountered by beetles flying in association with a cold front at the interface of land and lake are probably responsible for frequent large depositions of WCR along the southern shore of Lake Michigan (Grant & Seevers, 1989; Isard *et al.*, 2001). However, it is not known if downdrafts associated with the cold front deposit all of the beetles into the lake, or if some make it across to the far shore. The Appalachian Mountains in the eastern U.S. may have slowed or diverted range expansion, but published data have not been examined in this light. This mountain range is

not very high, and it had no obvious effect of slowing the eastward spread to the coast. The WCR is present in some southwestern and west-central states of the U.S., but the Rocky Mountains, unfavourable prevailing winds, and scarcity of cultivated maize in this formidable range apparently have combined to protect California from this pest to date (Summers, 2006). However, the potential for inadvertent human transport (e.g. airplane) from the eastern U.S. across the Rockies must be considered a substantial threat to uninfested states. The increase in maize production in response to bio-fuel initiatives and rising maize prices could likewise improve the opportunity for establishment of a founding population.

Long-distance movement of adult WCR is one of the outstanding issues that needs research attention. Although considerable evidence for long-range movement has accumulated, the distances covered by individuals, the proportion of the population that engages in flights of various durations and distances, sex-specific dispersal behaviour, and possible effects of population density on these parameters are unknown, although laboratory flight mill studies provide clues (Coats *et al.*, 1986; Naranjo, 1990; Hemerik *et al.*, 2004; Stebbing *et al.*, 2005). There is evidence that young mated females may be particularly prone to engage in long-distance dispersal (Coats *et al.*, 1986; Isard *et al.*, 2004; Spencer *et al.*, 2009), and maximum rates of range expansion documented in North America are around 200 km/year as evidenced by infestations well ahead of the more continuous advancing front. However, it is likely that more than one gravid female is necessary to found a new population, so 200 km probably underestimates individual dispersal capacity. Population genetics studies to estimate gene flow hold promise for characterizing long-distance movement of WCR, but initial surveys suggest that genetic artifacts left over from the range expansion may make gene flow estimates somewhat difficult to obtain (Kim & Sappington, 2005).

Dynamics of spread of the rotation-resistant WCR variant in the U.S.

Spread of the rotation-resistant variant of the WCR in the U.S. is well documented (Levine *et al.*, 2002), with the origin pinpointed to a 3-km² area near Piper City in Ford County, Illinois beginning in 1986 (Levine & Oloumi-Sadeghi, 1996). According to the model of Onstad *et al.* (1999), the rotation-resistant variant of WCR spread 10–30 km/year from 1986 to 1997 depending on the directions of the prevailing storms and winds. The maximum modelled rate was 33 km/year, which is much lower than the observed rates of eastward spread of the species as a whole before 1979. Of course, the spread of the species during the early invasion of the eastern U.S. was not necessarily under the same restraints as the spread of a trait with potential fitness costs (less ovipositional fidelity to maize, larvae feeding on non-host crops die). Model results supported the hypothesis that the population of variant WCR infesting soybean originated in Ford County, Illinois. The predictions of the simple model for spread of rotation resistance fit the observed rate of spread well for three of four geographic directions up to 1997 (Onstad *et al.*, 1999).

Levine *et al.* (2002) used the model of Onstad *et al.* (1999) to predict the westward and northward expansion of rotation-resistant WCR into Iowa and Wisconsin, respectively. Qualitatively, model predictions were correct as the crop-rotation variant has spread into both Wisconsin (Cullen, 2007) and Iowa (Prasifka *et al.*, 2006) in recent years although the model underestimated the rate of spread to the west.

Eastward expansion of rotation resistance has recently stalled in Michigan, Indiana, and Ohio, and models suggest that this was as a result of increased landscape diversity (i.e. the proportion of non-maize and non-rotated soybean vegetation in a geographic region) ahead of the front (Onstad *et al.*, 2003b). However, this trait is not selectively neutral, and the mechanism for landscape diversity effects on rate of spread is unknown and probably more complicated than its effects on simple spread of wild-type populations into virgin territory (Onstad *et al.*, 2001b). Landscape diversity hypotheses could be further tested by use of grid sampling data collected on finer scales than was available for initial analyses (Onstad *et al.*, 2003b) which would increase resolution of the distribution of rotation-resistant WCR populations and vegetation patterns associated with farmland, park, and forests.

Factors other than landscape diversity may also help account for the spatial distribution of rotation-resistant WCR. Onstad *et al.* (2001b) suggested that a landscape with at least 20% continuously-grown maize could also slow the evolution of rotation resistance by promoting the fitness of wild-type WCR. Future modelling should attempt to account for maize phenology and the proportion of continuously-grown maize fields in each county, but this would require extensive data collection.

Introduction routes of invading populations and dynamics of spread in Europe

The history of the first detections of WCR in Europe gives a picture of the probable history of invasion of the Old World by this pest species. First detected in Serbia (in former Yugoslavia) near Belgrade airport in 1992 (Baca, 1993), it is believed that the WCR originated on intercontinental flights from the Midwestern U.S. A broad international cooperative network subsequently developed to monitor the spread of this invasive species in Europe from its initial focal point of infestation (Edwards *et al.*, 1999). The spread of the WCR throughout former Yugoslavia and neighbouring countries has resulted in a large and continuously growing infested area of more than 400 000 km² (Kiss *et al.*, 2005b; J. Kiss, personal communication). Up to 2007, this area included all or parts of Austria, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, Hungary, Montenegro, Romania, Serbia, Poland, Slovak Republic, Slovenia, and Ukraine (Edwards & Kiss, 2008). The rate of range expansion has differed greatly from year to year, averaging 40 km/year, but ranging from 1 to 5 to 80 km/year (Kiss *et al.*, 2005b; Edwards & Kiss, 2008).

Factors contributing to the rate and pattern of spread of this pest in Europe are not clearly understood (Hemerik *et al.*, 2004). Topographical features such as high elevation mountain ranges and large bodies of water may affect the

rate and direction of spread in Europe, but they do not appear to be insurmountable (Yakobtsuk *et al.*, 2006). High mountains may be penetrated by WCR adults via road and railway passes along narrow valleys. The recent expansion of the WCR distribution from Hungary into the Ukraine by way of the Verecke Pass in the Carpathian Mountains is a good example of this (Yakobtsuk *et al.*, 2006). Temperatures at higher elevations or at northern latitudes may also limit range expansion. The ability of the WCR to adapt to colder temperatures and make latitudinal adjustments in diapause duration may be key factors that affect rate of range expansion in some areas. A model developed by Hemerik *et al.* (2004) predicted that the WCR range would not expand from the border of its 2000 range in east-central Europe into the Netherlands until 2018 because of limitations related to sub-optimal temperatures.

The WCR population density in the source region may also impact rate of spread in Europe. A high percentage of fields in continuous maize production in a local area coupled with late detection of invasive WCR populations will contribute to an increasing WCR source population density. These factors appear to have contributed to increased spread of a local WCR infestation in the Lombardy region of northern Italy (Boriani & Gervasini, 2001). Increasing the percentage of maize fields that are rotated in areas ahead of the front in Europe should slow the spread of WCR considerably (Boriani *et al.*, 2006), but how deep into virgin territory such an alteration would have to penetrate to be effective is not known. WCR adults have been collected in colour and pheromone traps at elevations of 800–900 m, where small maize plots, or even home gardens with a few maize plants, offered suitable food and survival sites for WCR under less than favourable conditions (Pai *et al.*, 2005). Little data are available on survival of very low natural WCR densities (Onstad *et al.*, 2006). Additional study of low densities may be warranted as a mosaic of small infestations could play an important role in the landscape dynamics and spread of this species. In Central and Eastern European countries, it will be important to characterize how different cropping practices and rootworm management technologies that may be employed in the future (such as rootworm-protected transgenic plants, crop rotation patterns) will impact WCR population dynamics (e.g. WCR gender, age, density, and dispersal differences among crops in the landscape).

Since 1998, isolated WCR outbreaks, disconnected from the large spreading area of Central and South-Eastern Europe, were also discovered in a number of European countries: North Eastern Italy in 1998, 2002 and 2003, North Western Italy and Switzerland in 2000, near Paris, France in 2002, 2004 and 2005, Eastern France, Switzerland, Belgium, the United Kingdom and the Netherlands in 2003, and Germany in 2007 (Reynaud, 2002; Kiss *et al.*, 2005b; Kuhlmann, 2007; Edwards & Kiss, 2008). Before 2005, given the timing and locations of these first detections, it was assumed that the isolated outbreak populations were 'secondary' introductions coming from the expanding Eastern Europe population. An analysis of the introduction routes conducted by Miller *et al.* (2005) showed that this assumption is probably invalid.

Miller *et al.* (2005) conducted an analysis of the genetic variability of American and European populations of WCR to infer the introduction pathways of the maize pest. This analysis was confined to five Western European outbreaks: Roissy (north-east of Paris, detected in 2002), Alsace (eastern France, detected in 2003), Val d'Oise (north-west of Paris, detected in 2004), Piedmont (north-western Italy, detected in 2000), and Friuli (north-eastern Italy, detected in 2003). It was assumed that the extensive population in Central and south-eastern Europe (CSE Europe) was: (i) a direct introduction from North America, and (ii) a single introduction (samples from CSE Europe studied to this point were genetically homogenous). It also was assumed that the homogenous population that extends from the Corn Belt to the East Coast of North America (Kim & Sappington, 2005) represented the original American source population. This population genetics study lead to the conclusion that there had been at least three direct introductions into Europe from North America: CSE Europe, Piedmont, and Roissy. The study also showed that there have been intra-European introductions from CSE Europe into Friuli and with less certainty from Roissy into Alsace.

Although the original source population is North American, an important unanswered question is whether the assumption that the Corn Belt represents the original source population within North America is valid. The determination of the source populations of the European outbreaks is crucial because it determines the adaptive characters that may be present or will be present in European populations. The distribution of insecticide resistance and adaptation to crop rotation is known to be heterogeneous in the U.S. Thus, depending on the origin of the European invading populations, the detrimental effects of the invasions may greatly vary geographically. Moreover, if introductions from North America to Europe are a chronic event, the spread of WCR insecticide resistance and rotation resistance throughout North America may be a real danger for European agriculture once they reach populations at the embarkation point. The question of the origin of the European outbreaks may be addressed by performing population genetics analyses using assignment likelihood (Rannala & Mountain, 1997). These statistics, which are based on allelic frequency analysis, are roughly proportional to the probabilities that the individuals in an introduced population originate from each of a set of possible source populations.

A second important question, given the finding of multiple transatlantic introductions, is whether there has been more than one introduction into each outbreak. This point, yet to be investigated, is important because it affects overall genetic diversity of the invasive population, and thus the probability of adaptive character evolution (Sakai *et al.*, 2001; Lee, 2002; Suarez & Tsutsui, 2008) such as resistance to management practices in Europe. In principle, a population subject to repeated introductions might eventually obtain a level of genetic diversity equal to that of North America. Such a population would make it difficult to distinguish multiple transatlantic introductions from intra-European ones (see Miller *et al.*, 2009). The demographic parameters of the introduction process are also of interest. In particular, knowledge

of the minimum number of founders needed for a successful introduction and the typical time delay between introduction and detection would be helpful to European plant protection agencies.

Whatever the uncertainties about introduction routes of WCR, the recent burst of introductions from North America into Europe is not encouraging: in the case of multiple introductions, the genetic variability and the probability that adaptive alleles (e.g. insecticide-resistant alleles) are present in Europe may be larger than expected from a single invasion event (Suarez & Tsutsui, 2008). Multiple introductions compared with a single introduction also increase the probability of eventual introduction of the rotation-resistant WCR variant and possibly the northern corn rootworm (NCR) *Diabrotica barberi* Smith and Lawrence, into Europe. This highlights the need for continued detection of new introductions and surveys of resistance characters in WCR populations throughout Europe.

Non-trophic (direct or indirect) interactions with other arthropods

To date, very little data are available on non-trophic (direct or indirect) interactions of the WCR with other arthropods in maize fields. Pest and non-pest arthropods that potentially could interact with the WCR in the U.S. and Europe can be divided into two main groups: those primarily found at the soil surface or in the soil, and those found on or in maize plant tissues above the soil line.

An extensive field survey was carried out in Hungary in 2004 (Veres, 2005). A total of 53 maize fields were sampled by shaking the silk of the maize ears, and all arthropods falling from this microhabitat were recorded (57 morphotaxa, 7288 individuals, 308 WCR adults). The number of WCR adults was negatively correlated with most arthropod groups, although most correlation coefficients were non-significant. Significant negative correlations with WCR were observed with predatory and phytophagous mites and predatory thrips (*Aeolothrips* spp.). A significant positive correlation was only found with cereal leaf beetles (*Oulema* spp.). A possible explanation of the negative correlations is that feeding (i.e. silk clipping) by WCR adults may destroy the silk as a microhabitat. This disturbance seems to be unfavourable to certain small-sized arthropod taxa.

While WCR adults may have an impact on microhabitats on the maize plants, larval damage can change the structure and characteristics of the whole habitat (the maize field) by increasing the number of lodged or underdeveloped plants. White and Andow (2006) found that habitat modification via WCR larval damage can dramatically reduce parasitism of the European corn borer *Ostrinia nubilalis* (Hubner) in the same small plot. This indirect impact may have occurred because *Macrocentrus grandii* (Goidanich), a specialist parasitoid of *O. nubilalis*, prefers tall and dense maize stands.

The WCR and NCR, commonly occur together in maize production areas of the U.S. Corn Belt (Chiang, 1973). Little is known about interspecific interactions of adults or larvae, but the WCR has been reported to largely displace the NCR

when continuous maize is the predominant cropping pattern in a region (Hill & Mayo, 1980). Several greenhouse studies have been conducted to study interactions of WCR and NCR larvae on maize roots. Piedrahita *et al.* (1985) reported that the presence of WCR larvae caused spatial displacement of NCR larvae within the root system and decreased survivorship of NCR as determined by recovery of old larvae and pupae. The presence of NCR had no significant effect on WCR survivorship. Woodson (1994) confirmed that in general, the WCR is a superior competitor to the NCR, but this was somewhat dependent on the total density of the two species and their relative frequency. The NCR was significantly affected by both intraspecific and interspecific competition. In general, NCR survival declined as WCR density increased. When WCR density was held constant, increasing NCR density decreased NCR survival at high density. WCR survival was more dependant on intraspecific than interspecific competition, although, when both NCR and WCR densities were high WCR survival was reduced. The mechanisms driving the interspecific larval interactions between species remain unclear.

Rasmann *et al.* (2005) reported that some varieties of maize are able to signal to nematodes using volatile molecules. They demonstrated that maize roots attacked by WCR produce terpene molecules. In particular one such terpene, (E)- β -carophyllene, is produced by European varieties of maize, as well as by the maize ancestral plant, teosinte. Plants that produced this molecule showed a five-fold higher infection rate with the nematode and a corresponding fall in subsequent beetle density. Similarly, spiking the soil with the (E)- β -carophyllene near maize plants that did not produce the terpene reduced subsequent WCR adult emergence by 50%. Wireworms and other soil pests start feeding on maize roots and collars as maize seedlings emerge, usually more than 1 month before WCR egg-hatch begins (Furlan, 1998, 2004). It is unclear whether insect or nematode feeding will induce (E)- β -carophyllene production in maize plants, which could attract parasitic nematodes before WCR colonization of maize roots, leading to some level of rootworm density reduction. The relative attractiveness of wireworm damaged roots to WCR, and the potential impact of interspecific interactions of root feeding insects and WCR larvae on population dynamics and crop injury warrant further study.

Conclusion

As this review makes clear, much has been learned about the population dynamics of the WCR in North America over the last half-century of intensive study. This knowledge has facilitated the development of various tactics and strategies that have been used to manage the WCR in agroecosystems. However, this insect is a moving target when it comes to understanding key aspects of its ecology and developing effective methods of population suppression, because it has demonstrated an extraordinary ability to adapt rapidly to new environments and to management tactics. The overall situation is further complicated by its recent success as an invasive species in Europe, where environments and cropping

systems are often not directly comparable to those in North America, the historical source of most WCR research. More generally, even if we gain a more complete understanding of WCR biology and ecology, the nature of population dynamics is indeed 'dynamic'. A host of environmental and intrinsic variables interact in complex ways to affect the development, survival, and behaviour of the various stages of this insect. These interacting factors vary spatially at any given point in time, and temporally at a given location, producing different population outcomes depending on the scale at which the dynamics are measured. Consequently, as this review reveals, much relevant research remains to be done.

Because the WCR is a key pest on a major commodity, and a significant investment of resources is directed to the study of this species, the future opportunity exists to contribute greatly to our basic knowledge of diapause, population dynamics at various densities and scales, population genetics, adult dynamics/oviposition relationships, short and long-range dispersal, invasion biology, and community level interactions with other arthropods. Models of the WCR and its effective environment will continue to be useful to guide research and to help address the many complex biotic and abiotic interactions that affect population dynamics in the field. Finally, answers to applied questions relating WCR population dynamics to damage potential in maize, control tactics/technologies, and resistance management will continue to be needed to develop sustainable management strategies in North America and Europe.

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