Dispersal kernels of the invasive alien western corn rootworm and the effectiveness of buffer zones in eradication programmes in Europe

Carrasco, L R; Harwood, T D; Toepfer, S; MacLeod, A; Levay, N; Kiss, J; Baker, R H A; Mumford, J D; Knight, J D

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L. R. Carrasco, T. D. Harwood, S. Toepfer, A. MacLeod, N. Levay, J. Kiss, R.H.A. Baker, J.D. Mumford, J.D Knight

(2) **Abstract**

Europe, is attempting to contain or, in some regions, to eradicate the invading and maize destroying western corn rootworm. Eradication and containment measures include crop rotation and insecticide treatments within different types of buffer zones surrounding new introduction points. However, quantitative estimates of the relationship between the probability of adult dispersal and distance from an introduction point have not been used to determine the width of buffer zones. We address this by fitting dispersal models of the negative exponential and negative power law families in logarithmic and non-logarithmic form to recapture data from nine mark-release-recapture experiments of marked western corn rootworm adults from habitats as typically found in the vicinity of airports in southern Hungary in 2003 and 2004. After each release of 4,000 to 6,300 marked western corn rootworm, recaptures were recorded three times using non - baited yellow sticky traps at 30 to 305 m from the release point and sex pheromone-baited transparent sticky traps placed at 500 to 3500 m. Both the negative exponential and negative power law models in non-log form presented the best overall fit to the numbers of recaptured adults (1% recapture rate). The negative exponential model in log form presented the best fit to the data in the tail. The models suggested that half of the dispersing western corn rootworm adults travelling along a given bearing will have travelled between 117 to 425 m and 1% of the adults between 775 to 8250 m after one day. An individual-based model of dispersal and mortality over a generation of western corn rootworm adults indicated that $9.7 - 45.3$ % of the adults would escape a *focus zone* (where maize is only grown once in three consecutive years) of 1 km radius and $0.6 - 21$ % a *safety zone* (where maize is only grown once in two consecutive years) of 5 km radius and consequently current EC measures are inadequate for the eradication of WCR in Europe. Whilst buffer zones large enough to allow eradication would be economically unpalatable, an increase of the minimum width of the *focus zone* from 1 km to 5 km and the *safety zone* from 5 km to 50 km would improve the management of local dispersal.

(4) **Introduction**

The western corn rootworm (WCR), *Diabrotica virgifera* ssp. *virgifera* LeConte (Coleoptera: Chrysomelidae) is an important pest of maize *(Zea mays* L.) in the USA that is now posing a threat to maize production in Europe. The European Union has been facing WCR invasion since at least 1992 (Kiss *et al*. 2005), and attempting to eradicate and contain it (Anonymous 2003, 2006a & 2006b). Large-scale historical spread of WCR has been studied in the USA (Grant & Seevers, 1989; Onstad, 1999) and Europe (Baufeld & Enzian, 2005) and mark release recapture experiments have been used (Lance & Elliott, 1990; Naranjo, 1990; Oloumi-Sadeghi & Levine, 1990; Spencer, 1999) to study short-range WCR dispersal. However, the likelihood of an adult flying a certain distance from an accidental introduction point, and thus to breach zones of eradication and containment programmes, has not been assessed.

WCR is a univoltine insect that overwinters in the egg stage. WCR larvae attack the roots of maize leading to a decrease of nutrient intake, reduced growth of the plant and a higher risk of lodging (Gavloski *et al*., 1992). WCR adults feed on young leaves, silks, pollen and young kernels of maize as well as on other flowering plants, but larvae can only develop on maize and few alternative hosts (Moeser &Vidal, 2004). Moreover, a small fraction of the eggs can extend diapause and hatch one year later (Levine *et al*., 1992). Successful development therefore depends on sufficient maize and to a lesser degree on alternative host plants being available within the range of larval movement. Thus, crop rotation has traditionally been recommended as an effective control measure (Gillette, 1912). However, WCR is also capable of developing adaptation to crop rotation by changing its egg-laying behaviours, as observed in the USA for soybean-maize rotation (Onstad, 1999).

In contrast to the short distance movement of the larvae of WCR in the soil, adults are extremely mobile. Windmill experiments, for example, have shown that WCR adults are capable of making sustained flights of up to 24 km (Coats *et al*., 1986). Long distance dispersal events of WCR have been associated to human-assisted dispersal and airplanes are believed to be the mechanism responsible of transatlantic introductions of WCR in Europe (Guillemaud et al., 2005, Miller et al., 2005). WCR was first detected in Europe in the vicinity of Surcin airport near Belgrade, Yugoslavia (now Serbia) in a small maize plot (0.5 ha) in July of 1992 (Baca 1994). After first introduction, WCR rapidly spread throughout central and south-Eastern Europe at rates up 60-80 km per year (Baufeld & Enzian, 2005). Subsequently, there have been at least four independent transatlantic introductions of WCR in Europe (Miller *et al*., 2005). In 2008, the continuously expanding central and south-Eastern European population of WCR extended from Austria to the Ukraine and from Southern Poland to northern Bulgaria. Furthermore, a number of disconnected outbreaks have been detected in various countries almost every year since 1998, e.g. in Italy, France, Switzerland, Belgium, the United Kingdom, the Netherlands and southern Germany (Edwards and Kiss, 2008, MacLeod *et al*., 2003).

The European Commission (EC) has implemented measures aimed at preventing the spread of WCR in Europe. In 2003, the eradication and surveying measures were required by EC Decision 2003/766/EC (Anonymous, 2003). They were supplemented in 2006 by EC Decision 2006/564/EC (Anonymous, 2006b). The EC Recommendation 2006/565/EC (Anonymous, 2006a), made it possible to switch from an eradication policy to a containment policy.

Emergency measures to prevent the spread of WCR include EU Member States conducting official surveys for the presence of WCR in their territories in areas where

maize is grown (Anonymous, 2003). Then, when the presence of WCR is newly detected in a field, management measures are applied within radial zones around each infested field (Eyre *et al.*, 2007). They include rotation of maize within demarcated buffer zones in order to reduce the availability of susceptible hosts for WCR larvae and adults (Anonymous, 2003 & 2006a). Throughout this paper, the term "buffer zone" is used according to its standard definition, i.e. to refer generally to those demarcated zones surrounding new introduction points within which eradication or containment programme measures are applied. However, where italicised, *buffer zone* is used to refer to the specific nationally variable buffer zone defined in the EC eradication program (Anonymous, 2003), as described in Table 1.

In order to develop effective and efficient eradication and containment programmes that use buffer zones, it is necessary to describe the dispersal kernel for WCR adults. This study aimed to establish quantitative estimates for the relationship between the probability and the distance of WCR dispersal from new introduction points. Generic dispersal kernels were fitted to mark-release-recapture experimental results. Subsequently, an individual-based model of the lifespan dispersal of WCR adults based on the estimated dispersal kernels was developed, and used to assess the efficacy of buffer zones of different radii.

(TABLE 1)
(5) Estimation of dispersal kernels for the western corn rootworm.

Material and methods

Mark-release-recapture experiment
Nine mark-release–recapture experiments were carried out in two sites in a flat agricultural region in Csongrad County in southern Hungary in 2003 and 2004 (Table 2; Toepfer *et al.*, 2006). The site south of Szentes was an 80 ha grass steppe that was drying out in June and was cut once a year in late June. The site west of Maroslele was a 60 ha lucerne field (*Medicago sativa*), approximately 25 km south of the Szentes site. This site consisted of one section that served as forage crop and was cut at four-week intervals, and one section that remained uncut for seed production. Both sites were surrounded by agricultural areas mainly including fields of sunflower, maize and winter wheat (for details see Toepfer *et al.* 2006).
For the releases, adult WCR were mass–collected from highly infested maize fields in southern Hungary using a plastic funnel with a gauze bag attached. Maize plants infested with WCR were shaken, so that adults fell through the funnel into the gauze bag. Adults were maintained in cages (300x300x500mm) at 24 to 26 ºC during the daytime and 18 to 22 ºC at night. Soft maize kernels and water were provided (Branson *et al.*, 1975). Sex ratios were determined by dissecting sub-samples of 20 adults prior to release.
Adults were marked with different fluorescent powders for each release (Orange T1-0Y6612 or Yellow T1-CH6620 from Magruder Colour, Elizabeth, New Jersey, USA; Pink R17/ M3115 from Radiant Colour, Houthalen, Belgium) (Toepfer *et al.*, 2005). Three to five hours before release, three tea spoons, i.e. about 5 g, of fluorescent powder were thrown into a rearing cage containing approximately 3000 adults. Then the adults marked themselves through caged activity. The cages were also shaken to improve the distribution of fluorescent powder. This was done half an hour before release and the WCR adults were calm at the moment of release.

In total, nine releases of 4000–6300 adults each were carried out (Table 2). The estimated average age of the adults was 19 days (SD 12.36 days, d.f. = 8). The sex ratio of the released adults was 63% males to 37% females (SD 16%, d.f. = 8).

Adults were released in the centre of the experimental area between 0700 and 0800 am. To recapture adults, 415 to 536 non-baited yellow sticky traps (Pherocon AM, Trece Inc., USA; of an attraction radius of ca 1 m (M. Toth 2008 pers. comm.)) were used per release as well as 6 to 33 sex-pheromone-baited transparent sticky traps (female pheromone synthetic 8-methyl-2-decyl propanoate, Bedoukin Inc., Danbury, USA, on a CSALOMON® PAL trap, Plant Protection Institute, HAS, Budapest, Hungary (Tóth *et al.* 2003) of an estimated attraction radius of 30 to 32 m (L. Schaub, 2008, pers. comm.) (Table 2). Traps were fixed on 1.50 m long wooden sticks and placed in concentric circles around the release points (Table 3). Due to the potentially complex interpretation of results from pheromone-baited traps close to the release point (Byers, 1999), non-baited yellow sticky traps were used within 300 m of the release point and pheromone traps with higher recapture efficacy were used from 500m to 3500 m. The mean distances for each circle of traps were as follows: for non-baited traps: 30, 105, 205 and 305 m; for pheromone-baited traps: 500, 1000, 1500, 2000, 2500, 3000 and 3500 m. Adults were recollected from the traps in the morning on three occasions each two days apart. Recaptured adults were taken to the laboratory and the marking was checked under UV light. Sex was determined by dissection. The numbers of WCR adults released in each release, the number and type of traps and the number of recaptured WCR adults are presented in Table 2.

(TABLE 2)

Dispersal kernels

Two families of generic dispersal curve are commonly used in the analysis of dispersal data (Okubo & Levin, 1989, p 329), the negative exponential, with a rapidly declining probability after a certain distance, and the negative power law, which has a fatter tail allowing for occurrence of long distance dispersal events. Simple examples (Shaw, 1995) with a median dispersal distance from each family were fitted to the data; an exponential distribution,

$$p(r \mid \theta) = \frac{K}{\lambda \left(e^{r/\lambda} \right)} \qquad [1]$$

and a half Cauchy distribution,

$$p(r \mid \theta) = \frac{2K}{\pi \lambda \left(1 + \left(\frac{r}{\lambda} \right)^2 \right)} \qquad [2]$$

where $p(r|\theta)$ is the probability of a dispersal event to radial distance r along a bearing θ, and λ is the median dispersal distance (i.e. the distance that half of the WCR adults travelling along a given bearing θ are expected to reach). K is a vertical scale parameter that adjusts the height of the curve (Meats and Smallridge, 2007). The one tailed half Cauchy distribution (Shaw, 1995) is a leptokurtic curve which approximates the negative square power law distribution, but has the advantage of being a closed probability distribution with an explicit median distance. Through the paper the half Cauchy distribution (equation 2) will be referred to as a negative power law model. Both models were integrated to be able to calculate quantiles of adults being found within a certain distance after one day of dispersal and fitted in logarithmic (log) form to the log of the data

in order to weight the small deviances of the model from the recapture data in the tail (Taylor, 1978).

The R environment (R Development Core Team, 2005) was used to fit the models to the data. Initially, in order to estimate the model parameters, a non-linear least squares model with partitioned data according to the factor "type of trap" was employed using the library Linear and Non-Linear Mixed Effects Models (Pinheiro & Bates, 2000). Then, after removal of the effect of the type of trap, non-linear least squares with a Gauss-Newton optimization algorithm (Bates & Watts, 1988) and least squares linear regressions were employed.

Analysis of recapture data

Recapture results from all the mark-release-recapture experiments were pooled together for each distance from the release point. This was considered reasonable as traps captured only a small proportion of the adults released and consequently did not affect the number recaptured at further distances (Zolubas & Byers, 1995).

The total number of recaptures from each circumference of traps is proportional to $\Sigma p(r)$ (Taylor, 1978). The actual proportion of $\Sigma p(r)$ intercepted at a given radius is determined by the sum of the attraction diameter of all the traps relative to the circumference of a circle of radius r. Rather than assuming a specific attraction radius for the two trap types at this stage in the analysis, the effect of increasing circumference, was removed by taking a nominal trap radius of 1m for both trap types. A potential total number of recaptures in all directions was therefore calculated by multiplying the total number of recaptures at the radius by $2\pi r$/the number of traps at r. This was then divided by the number of WCR adults released/100 (Meats & Smallridge, 2007) and by the time of exposure of each WCR adult to the traps to give a percentage of recaptures over the total released at each radial distance per day of exposure to the traps. The resulting data set is demonstrated in Table 3, with the interception by the sub set of non-baited yellow sticky traps being considerably lower than that of the pheromone-baited transparent sticky traps as expected due to the wider attraction radius of the pheromone traps.

(TABLE 3)

In order to characterise the whole dispersal kernel, it was necessary to draw on both sets of trap recapture data: pheromone-baited and non-baited trap recapture results. As a first step, the compatibility of the two data sets was examined by fitting them to equations 1 and 2 mentioned above. The vertical scale parameter K is here a combination of the scaling of recapture data to the probability distribution, the attraction radius of the traps and the fact that pheromone-baited traps only attract males.

The vertical scale parameter K was significantly different from zero ($p < 0.05$) for all cases (Table 4). The median distance was also significant in the case of pheromone-baited transparent sticky traps for the negative exponential model but was only marginally significant ($p < 0.1$) for the negative power law model.

(TABLE 4)

(FIGURES 1 (a-b))

Estimates of λ for each trap type are comparable for both curve families, suggesting the possibility of pooling both pheromone baited and non-baited data sets together after re-

scaling (Figure 1), although the models fitted to the non-baited trap data set have a higher standard error than the models fitted to the pheromone-baited data set. However, whilst of the same order of magnitude, there is a discrepancy between the median distances estimated by the different trap types. Estimates of K from non-baited and pheromone-baited sticky traps differed by more than two standard errors, showing the significant effect of type of trap on the intercept of the models.

This effect was investigated by using the concept of Effective Attraction Radius or EAR (Byers, 1989), which represents the size of a non-baited trap that would yield the same number of WCR adults caught by the pheromone-baited trap.

$$EAR = (ATC \cdot LCSAPT \cdot PTC^{-1} \cdot \pi^{-1})^{\frac{1}{2}} \qquad [3]$$

Where ATC is the total number of recaptured WCR adults in a pheromone-baited (Active) trap, LCSAPT is the longitudinal cross-sectional area of a cylindrical non-baited yellow sticky trap and PTC is the total number of recaptured WCR adults in a non-baited (Passive) trap.

It was assumed that EAR remained constant with distance, such that the fitted values of K were proportional to the attraction radius of each trap type. Substituting $K_{pheromone}$ for ATC and $K_{non-baited}$) for PTC in equation 3, allowed EAR to be estimated.

$$EAR = (K_{pheromone} \cdot LCSAPT \cdot K_{non-baited}^{-1} \cdot \pi^{-1})^{\frac{1}{2}} \qquad [4]$$

$K_{pheromone}$ was weighted because pheromone-baited traps only attract males. The weighting factor was the average proportion (0.41) of males of the WCR adults released. Whilst the physical dimensions of the non-baited yellow sticky trap (0.23 m by 0.36 m rolled into a cylinder) give a LCSAPT of $0.0264m^2$, (giving estimates of EAR of 2.88 m and 3.47 m from the negative power law and exponential curves respectively), M. Toth (pers.comm..2008) estimates the attraction range of the passive trap at 1m due to its yellow colour. Taking LCSAPT as π (area of circle of radius 1 m) gives estimates of EAR of 31.65 m and 38.04 m for the negative power law and negative exponential models respectively. This is consistent with the estimated range of the pheromone traps of 30 to 32 m (Schaub *et al* pers. comm.).

The recapture data of the non-baited yellow sticky trap and the pheromone-baited traps were therefore pooled by scaling them to the same axis using the calculated K values on the assumption that differences in K were due solely to differences in attraction radius. Given that each family of curves yielded different K values and at this stage it was not possible to distinguish which family of curves were the most appropriate to fit the dispersal kernels, the pooling process by scaling to the same axis was conducted separately for the K values from both curve families. Hence two alternative pooled data sets were obtained: *A* which are the results of scaling the data using the vertical scale estimates of the negative exponential model and *B* by scaling the data using the vertical scales of the negative power law model (Table 4).

In order to fit the pooled data sets to the models in log-log form, the outer four categories (2000, 2500, 3000, 3500 m) were grouped into two categories (2250, 3250 m) to remove zero values. The pooled data sets with no zeros will be referred to as grouped data sets. To check the effect of the grouping process on the data, the models were fitted to the grouped data sets before log transformation. Estimates of the median distance within 0.01m of the ungrouped estimates were obtained, with a comparable goodness of fit

(increase in the Akaike information criterion (AIC) value from 27.5 to 29.5). It was hence assumed that the grouping did not lead to a loss of information from the data.

Effect of source field area

Shaw *et al*. (2006) demonstrated that the median dispersal distance from an extended source is a function of the source radius for a negative square power law model with a median dispersal distance of 2 m for the point source dispersal kernel. The importance of the size of the source field in the case of our point source functions with a larger median relative to field size was investigated. The WCR adult population was assumed to be homogenously distributed within the field, and dispersal from a range of source field areas was estimated by integrating the point to point functions over a regular grid of points at 200 m intervals within the field.

Results

Recaptures

On average, 0.97% (SD 0.71%, d.f. = 8) of the 4000–6300 released adults in each of the nine releases were recaptured. In total, 529 marked adults were recaptured and used for analyses (Table 2). Numbers recaptured showed a consistent decline with distance from the release point for each set of traps. The sex ratio of the recaptured adults was 41% males to 59% females (SD 39%, d.f. = 8). Adults were recaptured at all distances except for traps located at 2000 and 3000 m. A few adults were trapped in the outer boundaries of the experiment (traps at 3500 m). For a thorough analysis of the effect of surrounding habitat and wind on directional movements of the released WCR adults see Toepfer *et al*. (2006).

Dispersal kernels

Both the negative exponential and negative power law models in non-log form presented the best overall fit to the data and the negative exponential model in log form presented the best fit to the data in the tail. These models suggested that half of the dispersing western corn rootworm adults travelling along a given bearing will travel a distance ranging from 117 to 425 m and 1% of the adults will cover distances of over 775 to 8250 m within one day of dispersal from the release point.

Both model families in non-log form gave significant fits in all cases with a range of the median distance from 117 to 188 m. To give an idea of the maximum natural dispersal, the 99th percentile of the fitted non-log models was calculated: it ranged from 775 to 865 m in the case of the negative exponential model and from 7500 to 8250 m in the case of the negative power law model (Table 5).

Log models were fitted to the log transformed data (*grouped data sets*). For the negative exponential function, medians of 403 and 425 m were estimated, providing a better fit to the tail of the data, but reducing the quality of the fit close to the release point. The results of the four combinations for log and non-log models are shown in Table 5:

(TABLE 5 HERE)

Quality of fit was reduced in the grouped data log-log models with respect to the non-log models fitted to the scaled data. Log-log models yielded an increase in the median scale and hence on the 99th percentile of the dispersal kernels.

Figure 2(a) shows the fit of the negative exponential and negative power law models to the pooled data sets *A* and *B*. The same fit is compared to the grouped data sets on a graph with axis on a log-log scale in Figure 2(b). Figure 2(b) demonstrates how the negative power law model of median scales of 117 and 129 m fits better to the data at the tail than the negative exponential model of median scale of 168 and 188 m. Conversely, Figure 2(d) shows that, when fitted in log-log form, the negative exponential model of median scale of 403 and 425 m fits better to the tail than the negative power law model.

(FIGURE 2 (a-d))

Effect of source field area

The results of the integration showed that whilst there was a small positive effect of the size of the newly infested source field on the dispersal kernel predictions within 500 m of the field boundary, this effect was negligible beyond 500m due to the comparable magnitudes of the point source median and the source radius. For the purposes of

examining buffer zones beyond 1 km, the point source dispersal kernel was therefore used, taking the source as the field centre, without modelling source size.

(6) Analysis of the effectiveness of buffer zones using an individual-based model.

Methods

The effectiveness of the minimum widths for the buffer zones for WCR, as recommended by the EC (Anonymous 2003, 2006a, 2006b, Table 1), was assessed using a spatial individual-based model (de Roos *et al.*, 1991; Grimm, 1999) of the dispersal for one generation of WCR adults. The model was governed by a set of rules and was discrete in time (daily time step) and considered dispersing adults individually. The processes considered were dispersal and mortality. The location and survival of each individual was calculated daily, and the total distance from the source to the final destination calculated. The fitted dispersal kernels were used as dispersal predictors for the new position of the WCR adult after each time step. The distance dispersed daily by each individual was obtained by Latin Hypercube sampling of the fitted dispersal kernels. The number of iterations per simulation was 10000. Direction was assigned at random assuming no correlation with previous movements.

Daily mortality was incorporated as a stochastic function with the probability of mortality varying between food sources (Table 6b). Maize fields were assumed to have an arbitrary 0.5 probability of being in flower. In order to calculate the probability of a dispersing adult feeding on each source, it was initially assumed that dispersing individuals would have the same probability (0.5) of feeding between alternative food sources and maize if all fields are continuously producing maize, and no EC eradication measures were in place. Reduction in maize availability for the WCR adults diet, due to EC measures (Anonymous, 2003), was assumed to be substituted by a proportional increase in the probability of feeding on alternative food sources (Table 6c), with the probability of feeding on maize given by 0.5 * the number of years in the rotation. Furthermore, the model assumed that a constant proportion (0.2) of WCR adults that find and feed on a maize field will remain in that field indefinitely (Table 6 a).

Three scenarios were considered (see Table 1 for policy definitions). Since control measures are applied in the season following detection, and overwintering of larvae, adults are assumed to emerge into a landscape with control measures in place.

Scenario a): Dispersal in a landscape with the conditions of the *focus zone* (Anonymous, 2003).

Scenario b): Dispersal in a landscape where the minimum requirements from EC measures (Anonymous, 2003) for *focus* and *safety zone* are present and a 20 km width *buffer zone* is implemented.

Scenario c): Dispersal from the infested 10km band of the EC containment programme (Anonymous, 2006a) into adjacent un-infested zones. It was assumed that WCR adults would initiate dispersal from the edge of the infested band of the containment programme (Anonymous, 2006a).

Each of the above scenarios was investigated using the four estimated median dispersal distances for each curve family.

(TABLE 6)

Results

The assessment of the effectiveness of the buffer zones for WCR recommended by the EC (Anonymous 2003, 2006a, 2006b, Table 1) using the individual-based model is showed for the considered scenarios (Table 7). Due to the analysis of 6 potential dispersal kernels, results are presented as a range representing the maximum and minimum observed dispersal distances.

Scenario a): Spread on a landscape under *focus zone* conditions: 50% of the WCR adults will remain within a circle between 350 m and 2611 m, and 99% of the adults would remain within a circle of radius between 1800 and 47000 m.

Scenario b): Spread on a landscape with the minimum recommendations for buffer zones from the EC (Anonymous, 2003) and a 20 km *buffer zone*: 50% of the WCR adults would remain within a circle between 350 m and 2510 m, and 99% of the adults would remain within 1725 to 42000 m. 10.5 % to 47.6 % of the adults would breach the 1 km focus zone and 0 % to 8.4 % would breach the 5 km *safety zone*.

Scenario c): Spread from a containment area: 0 % to 2 % of the WCR adults would fly beyond the monitoring area of the non-infested zone. 50% of the WCR adults dispersing towards the non-infested area would be found between 375 m and 3215 m from the edge of the infested area and 99% of the WCR adults between 1850 m and 58000 m of the edge of the infested area.

(TABLE 7)

(7) Discussion

Mark-release-recapture experiment

The dispersal kernels of newly invading WCR adults were characterized through fitting negative exponential and negative power law models to recapture data, per day of exposure to the traps, of dispersing WCR adults. Two adults reached the furthest located traps, which might indicate that the experiment was outdistanced by the released adults (Follett *et al*., 1996) (to be expected due to the high mobility of WCR adults). Numbers recaptured declined slowly with time of exposure to the traps as was observed in other studies (Zolubas & Byers, 1995). This might be due to adults leaving the experimental site. After corrections for release period and radial dispersal, numbers recaptured decreased smoothly with distance from the release point, which suggested that the size of the experiment was adequate for the time of exposure considered.

In order to obtain a representative shape of the dispersal kernels from points close to the release point and from the tail, recapture data sets from pheromone-baited and from the non-baited sticky traps were combined. Recapture data needed standardisation before both data sets could be pooled together. This is a common problem in mark-release-recapture experiments dealing with short distance and long distance data sets (e.g. Meats and Smallridge, 2007). A standardisation process was developed in order to express both data sets at the same scale. It was based on the introduction of a vertical scale parameter into the models and the Effective Attraction Radius (EAR) concept (Byers, 1999). The differences in the estimates of the vertical parameters seemed to be due to the different characteristics of the trap type because the EAR obtained for pheromone-baited traps matched the estimates from other independent studies (L. Schaub, 2008 pers. comm.). One caveat was that the experiments of Byers (1999) showed a variation in EAR with distance from the release point. However, most of this variation was close to the release point, and results at greater distances were more consistent. The assumption of constant EAR in our experiment seemed reasonable given that the sampling with pheromone-baited traps started at 500 m from the release point. The utilisation of pheromone traps at 500m avoids problems of results interpretation due to overlapping of attractiveness ranges between traps. As a consequence of not having pheromone traps close to the release point, the proportion of adults recaptured might seem to be lower than other studies where pheromone traps are located closer to the release point (e.g. Turchin & Thoeny, 1993). We consider that our recapture rates were normal given the spatial characteristics of the experiment.

Dispersal kernels

The obtained dispersal kernels showed that, after one day of release, the median dispersal distance of the newly introduced adult WCR travelling along a given bearing ranged from117 to 188 m. The magnitude of the estimated median dispersal distances after one day or release was in accordance with other mark-release-recapture experiments for the study of insect dispersal. For example: *Ceratitis capitata* (Diptera: Tephritidae) (114 m) (Plant and Cunningham, 1991)*, Lucilia sericata* (Diptera: Calliphoridae) (103 to 150 m) (Smith and Wall, 1998) and *Diatraea grandiosella* (Lepidoptera: Crambidae) (93 to 97 m) (Qureshi *et al*., 2006).

Both models presented a remarkably similar quality of fit to the data and the medians estimated (168 to 188 m for the negative exponential model; 117 to 129 m for the negative power law model). The main differences laid in the predictions of long distance dispersal events (99th percentile 775 to 865 m for the negative exponential model; 7500 to

8250 m for the negative power law model). This was attributed to the fatter tail of the negative power law model with respect to the negative exponential model (Kot *et al.*, 1996). Because correct fitting of the tail of the dispersal kernels to data is crucial for the prediction of long distance dispersal events and thus the spread of invasives (Neubert & Caswell, 2000), the models were also fitted in log form to log transformed recapture data (Taylor, 1978). The negative power law model in its log form suggested that the median dispersal of the WCR dispersing in a given bearing was comparable to its non-log form (136 to 168 m). However, the negative exponential model in its log form suggested higher median distances (403 to 425 m) and higher 99th percentiles (from 1850 to 1955 m) than its non log-form. Both log-transformed models were compared and the negative exponential model presented a better fit than the negative power law model (see Akaike information criterion of 15 versus 31, Table 5), although both fits in log form were poorer than the fits of the models in non-log form. For this reason, the negative power law model in log form was not considered for further analysis. Due to the uncertainty about the overall best model and for the sake of comprehensiveness, both models in non-log form and the negative exponential model in log form were considered for further analysis.

Analysis of the effectiveness of the buffer zones

An individual-based model of the lifespan dispersal of WCR adults (de Roos *et al.*, 1991) that employed the fitted dispersal kernels as daily dispersal predictors was developed. The model assumed that directionality of the movements between consecutive time steps was uncorrelated. This assumption seemed reasonable regarding the analysis of directional movements of the mark-release-recapture experiment, where in nearly half of the introductions no directional movement took place with respect to surrounding habitat and wind (Toepfer *et al.*, 2006). However, in some cases the movement of WCR adults showed a slight correlation with wind and towards the direction of the maize fields (Toepfer *et al.*, 2006). For these cases, the model might underestimate the actual dispersal capabilities of WCR by not considering directional dispersal in cases where wind is directionally consistent for several days. Age is known to influence the dispersal patterns of insects (Johnson, 1969), and particularly the 15% of young mated WCR females that may perform long distance dispersal (Coats et al., 1986). Since these females may escape the experiment (if flying too high) without being detected by the traps, we consider that the individual-based model is a representation of the population that performs local dispersal. Equally, atmospheric conditions (Vanwoerkom *et al.*, 1983; Isard *et al.*, 2004) and landscape characteristics (Onstad *et al.*, 2003) are known to affect dispersal of WCR. It was considered that the conditions in which the experiments took place were representative of the climatic and landscape situations that WCR adults are expected to find during spread in Europe. Another implicit assumption of the model was that the fitted dispersal kernels were not affected by the mortality of the released adults and that an additional mortality function was necessary. This assumption was considered logical given the short period of time the dispersal kernel was examined and because the number of adults recaptured was small in comparison with the number of adults released. Furthermore, the marked WCR adults were released in a non-host habitat with the aim of reproducing the conditions that newly introduced adults find in buffer zones. This might lead to different results with respect to dispersal in regions of intensive maize production. Mortality due to lack of maize food sources will be higher in our experiments. However, WCR adults have more incentives to disperse in our experiments to search for host habitats.

The individual-based model was employed to simulate the spread of WCR adults under different scenarios. Scenario a), spread in a landscape under *focus zone* conditions,

aimed to provide an estimate of the adequate width of the *focus zone*. The width of the *focus zone* is relevant for eradication purposes because it is the only buffer zone where rotation practices guarantee eradication of extended diapaused eggs (Levine *et al*, 1992). Hence, eradication campaigns are likely to fail if considerable number of adults reaches the *safety* and *buffer zones* after breaching the *focus zone*. The results of the model showed that the width of the *focus zone* required to contain 99% of the adults would range between 4.5 km and 47 km (Table 7, negative exponential in log form and negative power law models respectively), which is in both cases greater than the 1 km minimum recommended width by the EC (Anonymous, 2003).

Under scenario b) spread under the minimum requirements for the buffer zones as recommended by the EC (Anonymous, 2003) was simulated. In this case 9.7 % to 45.3 % of the adults was expected to breach the *focus zone* and from 0.6 % to 21 % the *safety zone* (Table 7). For comparison with historical spread observations, the distance of the 1% furthest reaching individuals were calculated. These distances ranged from 1800 to 47000 m (negative exponential model and negative power law model respectively). These results appear to be smaller than the historical observed spread of WCR for the case of the negative exponential model in log form and, for the case of the negative power law model, of a relatively similar magnitude with the range of observed historical rates of spread of WCR adapted to soybean-corn rotation in the US, that ranged from 38 to 138 km/year (Onstad, 1999), and spread in Europe, where under EC measures, the rates of spread ranged from 60 to 80 km/year (Baufeld and Enzian, 2005). The reason why our predictions are smaller than historical rates of spread might be due to the fact that the model did not capture the effect of storms and human assisted dispersal. In Europe, long distance dispersal events have been associated to aeroplanes (Guillemaud *et al*., 2005, Miller *et al*., 2005) and major networks of distribution of goods and services. For instance, many of the initial trap detections in the south of Germany (un-infested region) occurred in locations situated near major traffic centres such as freeways, alpine tunnels for transeuropean roads and railways that connected to infested regions of southern Switzerland and northern Italy (Wudtke *et al*., 2005).

Assessment of containment measures in scenario c) suggested that less than 2 % (Table 7) of the dispersing adults will leave the *containment zone* without being detected by the pheromone traps in the uninfested area of 30 km wide adjacent to the infested area (Anonymous, 2006a). Thus, *containment zones* appeared to be an appropriate measure for the detection of the advancing front of the invasion.

Alternative modelling approaches

This study is limited in that it does not take into account the effects of long distance dispersal events (probably human-, wind- and storm-aided) which may be a key determinant of the total invasion speed (Neubert and Caswell, 2000). Nevertheless this study is of value for the assessment of local scale policy. Dispersal by multiple mechanisms (both local and long distance) is common to many pest and disease systems (e.g. Sarre, 1978), and requires the independent assessment of each component. Quantification and simulation of long distance dispersal events therefore presents itself as the next step in the progression towards an evidence based management framework. Storms and wind currents may carry flying adults up to 20 km in a rain cell (Onstad, 1999). A way to estimate these dispersal events would be to use Onstad's (1999) methodology by which frequency and length of raincells can be estimated. Next, the proportion of time during which these raincells match with the optimal flying conditions of

the WCR could be calculated to estimate the number of adults which could be potentially carried away by the storm. Also, a proportion of fertilised females can perform long sustained flights of up to 24 km (Coats et al. 1986); furthermore, human assisted dispersal by land transport systems could well account for long distance dispersal events (Wittenberg 2005). These factors could be considered using the following modelling approaches: spatio-temporal stochastic models to fit historical spread spatial data (e.g. Cook et al., 2007) and integration of the derived dispersal kernels into mechanistic models of spread that consider long distance dispersal events (e.g. Shigesada et al., 1995; Kot *et al.* 1996). These approaches would complement the present study by providing information on spread at the continental scale.

Management recommendations

In this study, we were able to describe the range of dispersal kernels for WCR adults performing local dispersal. We found out that current EC policy will not be able to prevent local spread of WCR. Long distance dispersal events were not accounted for by the model, but further point to the inadequacy of the current EC control measures.. In the light of the results, the question regarding alternative management is not how much larger buffer zones should be to eradicate WCR invasion, but which buffer zone width would be effective in slowing down the invasion and whether such efforts are cost-effective.

We make our management recommendations, assuming that slowing down the WCR invasion was considered cost-effective, based on the 47 km threshold for a buffer zone where eradicating measures are in place (Table 7, 99th percentile, scenario a). A focus zone (Table 1) of 47km (EC recommends currently a minimum focus zone of 1km) would have considerable economic impacts to farmers with constraints to rotation (MacLeod et *al.*, 2005). The individual-based model for the lifespan dispersal of WCR adults shows that the presence of higher maize densities in the safety zone (Table 1) as opposed to the focus zone (compare higher spread values in scenario a) relative to b) in Table 7, 99th percentile row) may act as a sink for numerous WCR adults that would otherwise continue spreading. Therefore, a combination of a focus zone with a safety zone, as recommended by the current EC measures (Anonymous, 2003), might be both effective and economically efficient. The following quantitative modifications from the original EC measures (Anonymous, 2003) would be necessary: a focus zone of at least 5km width (this would ensure that only 9.6% of the adults escape the focus zone, see Table 7, 7th row) combined with an increase in the safety zone from the currently recommended 5 km to at least 50 km (Table 7, 99th percentile of the negative power law model under scenario b). These measures are expected to be effective in reducing local dispersal. Further research should aim at estimating the economic benefits of reducing invasion spread velocity by detecting and controlling new foci versus controlling the main invasion advance front.

WCR continues to spread whilst the European Commission is attempting to contain, if not to eradicate it. The results of the present study question the approach of attempting to eradicate WCR because of its high mobility.

(8) **Acknowledgements**

(10) **Supplementary material**

(11) **Tables**

Table 1. Definitions of quarantine demarcated zones surrounding new introduction points of the invasive western corn rootworm (WCR) or along its distribution areas in Europe for different eradication or containment measures according to official decisions or recommendations by the European Community (EC) (Anonymous 2003 and 2006a).

Type of zone	Radius of zone	Measures *inter alia* within zone	EC directive
Focus zone	At least 1 km around a newly infested field in an un-infested region [+]	(i) Crop rotation where maize is grown only once in three consecutive years (ii) treatment on maize fields against WCR adults	EC Decision 2003/766/EC (Anonymous, 2003)
Safety zone	At least 5 km around the *focus zone* of a newly infested field in an un-infested region [+]	(i) Crop rotation where maize is grown only once in two consecutive years; or (ii) treatment on maize fields against WCR adults	EC Decision 2003/766/EC (Anonymous, 2003)
Buffer zone [++]	Radius determined by the Member State	(i) Member States may lay down that maize is grown only once in two years.	EC Decision 2003/766/EC (Anonymous, 2003)
Containment zone	At least 10 km within the infested zone and at least 30 km in the non-infested zone	(i) Maize grown only once in two years in the infested zone. (ii) Presence of WCR adults monitored in the uninfested zone along the infested zone.	EC Recommendation 2006/565/EC (Anonymous, 2006a)

[+] By 2008, all regions outside the distribution area of well-established WCR populations, i.e. outside the northwestern Italian and southern Swiss WCR population as well as outside the Central and south-eastern European population (Serbia, Croatia, Bosnia Herzegovina, Slovenia, Hungary, Ukraine, Romania, Bulgaria, eastern Austria, southern Germany, Slovakia, Czech Republic, and southern Poland, EPPO, 2008).
[++] *Buffer zone* is here used in accordance with the EC definition in Anonymous (2003).

Table 2. Mark-release-recapture experiments with western corn rootworm adults (WCR) in Csongrad County in southern Hungary in 2003 and 2004. Number of marked WCR adults released; numbers of non-baited yellow sticky traps and sex pheromone-baited transparent sticky traps used and the number of WCR adults recaptured per release, site and year. Lower recapture rates for pheromone baited traps at Maroslele are largely due to a smaller number of traps close to the source.

Site	Szentes						Maroslele			
Year	2003			2004			2003		2004	
Release	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	1st	2nd
WCR released	4000	6300	5250	6000	5300	5950	6300	5430	5950	6000
Non-baited traps placed	415	415	415	536	536	536	415	415	536	536
Pheromone-baited traps placed	29	30	29	33	33	31	7	7	6	28
Recaptured WCR in. non-baited traps	49	14	5	31	25	72	12	16	40	31
Recaptured WCR in pheromone baited traps	26	35	5	64	86	10	2	1	2	3

Table 3. Distance of recaptured WCR adults from release sites. Total number of recaptures was corrected for trap density per radial distance assuming an attraction radius of 1m for the non-baited yellow sticky trap and the pheromone-baited transparent sticky trap. The corrected number of recaptured is higher than 100 in the case of the pheromone traps because the effective attraction radius of the pheromone traps has not been accounted for at this stage. As a result, few traps at long distance appear to trap a high number of adults so the correction process leads to an inflated number of potential recaptures.

Trap type	Distance of placed traps from release point (m)	Total number of recaptured WCR adults	Corrected number of recaptured WCR adults
Non-baited	30	183	12.6
Non-baited	105	47	5.8
Non-baited	205	37	4.9
Non-baited	305	29	3.0
Pheromone-baited	500	174	1229.2
Pheromone-baited	1000	49	252.7
Pheromone-baited	1500	30	294.7
Pheromone-baited	2000	0	0.0
Pheromone-baited	2500	3	46.7
Pheromone-baited	3000	0	0.0
Pheromone-baited	3500	2	3.1

Table 4. Negative exponential and negative power law models fitted to the recapture data of WCR adults that were separated into two data sets according to the type of trap employed: non-baited yellow sticky traps and pheromone-baited transparent sticky traps. λ: median scale, K: vertical scale., s.e.: standard error, df: degrees of freedom. AIC: Akaike information criterion. Significance levels: *** at $p < 0.001$, ** at $p < 0.01$, * at $p < 0.05$, n.s. a $p > 0.1$; p = Probability($>$|t statistic|).

| | Type of dispersal kernel: | | | |
| | Negative exponential model | | Negative power law model | |
	Non-baited trap data	Pheromone-baited trap data	Non-baited trap data	Pheromone-baited trap data
λ (s.e., p)	165.13 (2442, n.s.)	411 (69, **)	127.71 (1375, n.s.)	443 (157, n.s.)
K (s.e., p)	2350.82 (2.42E4, *)	1.68E6 (1.46E5,***)	2544.70 (2.05E4, *)	1.26E6 (1.40E5,***)
Residual s.e.; df	84.09; 7		69.61; 7	
AIC	-141.88		-138.47	

Table 5. Negative exponential and negative power law models in log and non-log form fitted to the pooled recapture data of western corn rootworm adults. Recapture data with non-baited yellow sticky traps and pheromone-baited transparent sticky traps were pooled together after scaling the data down using the vertical scale parameters of the negative exponential model (data set *A*) and the negative power law model (data set *B*) fitted in Table 4. λ: median scale, s.e.: standard error, df: degrees of freedom, AIC: Akaike information criterion. Significance levels: *** at p < 0.001, ** at p < 0.01, * at p < 0.05, n.s. a p >0.1; p = Probability(>|t statistic|).

	Recapture data and type of dispersal kernel:			
	Data set *A*	Data set *B*	Data set *A*	Data set *B*
	Negative exponential model		negative power law model	
λ (s.e., p)	167.78 (12.77,***)	187.53 (16.12,***)	116.91 (9.86,***)	129.18 (11.67,***)
Residual s.e.; df	0.00033; 10	0.00036; 10	0.00039; 10	0.00039; 10
AIC	-141.89	-141.89	-138.75	-138.47
99th percentile (m)	775	865	7500	8250
	Log of data set *A*	Log of data set *B*	Log of data set *A*	Log of data set *B*
	Log negative exponential model		Log negative power law model	
λ (s.e., p)	402.94 (0.00014,***)	424.50 (0.00014,***)	136.16 (2.116E4, n.s.)	167.78 (3.056E4, n.s.)
AIC	14.99	14.74	30.85	30.79
Residual s.e.; df	0.45; 7	0.45; 7	1.09; 7	1.09; 7
99th percentile (m)	1850	1955	8600	10675

Table 6. Parameters of the individual-based model for WCR dispersal. (For dispersal parameters see Table 5).

Parameter	Value	Source
a) Probability of remaining in a maize field after finding it	0.2	Assumed.
b) Daily mortality of adults feeding on:		
Alternative food sources	0.1	Assumed
Pre- and post-flowering maize	0.072	Elliott *et al*. (1990)
Flowering maize	0.0064	Elliott *et al*. (1990)
Maize treated with pesticides	0.4	Estimated using (Greaves *et al*., 1994) and (Zhu *et al*., 2005) assuming Chlorpyrifos 8g/100l treatment after 60 days of application.
c) Probabilities of feeding from:		
Maize treated with pesticide and alternative food sources in the *focus zone*.	0.17; 0.83	Estimated from Anonymous (2003)
Treated maize, untreated maize and alternative food sources in the *safety zone*.	0.25; 0.12; 0.63	Estimated from Anonymous (2003)
Untreated maize and alternative food sources in the *buffer zone*.	0.25; 0.75	Estimated from Anonymous (2003)

Table 7. Percentage of dispersing western corn rootworm, median (m) and 99th percentile (m) of adults flying beyond buffer zones of different radii from new introduction points obtained by simulation of a individual-based dispersal-mortality model of WCR adults. The individual-based model depends on different values of the median scale parameter (λ, see Table 5) and the probability of remaining indefinitely in a field and daily mortality due to the food sources available. The European Commission recommends *focus zone* widths of at least 1km[+] and *safety zone* widths of at least 5 km[++] in eradication programmes (Anonymous, 2003) as well as containment zones of 30 km[+++] along the borders of areas with already established WCR populations (Anonymous, 2006a) (See Table 1 for further detail on the measures applied in each buffer zone). Scenario a): Spread on a landscape with *focus zone* conditions. Scenario b): Spread on a landscape with the minimum requirements for *focus* and *safety zone* and a 20km *buffer zone*. Scenario c): Spread from an infested area of 10km width to a non infested area.

		Dispersal kernels fitted to mark-release-recapture data:							
Buffer zone radius (km)	Scenario	Negative exponential model				negative power law model			
		λ=168	λ=188	λ=403	λ=425	λ=117	λ=129	λ=136	λ=168
1km[+]	a	9.7	13.7	43.3	45.3	33.0	35.6	36.8	41.9
	b	10.5	13.3	45.1	47.6	33.8	36.8	36.8	41.9
	c	11.1	14.6	46.0	47.1	38.8	40.9	42.2	47.8
2km	a	0.6	1.1	15.5	17.3	19.1	21.0	22.0	25.9
	b	0.4	0.6	12.3	13.8	18.8	20.1	20.8	24.3
	c	0.7	1.3	17.0	18.5	23.6	25.5	26.4	30.4
5 km[++]	a	0	0	0.5	0.5	9.4	8.8	9.6	11.8
	b	0	0	0.1	0.2	8.1	8.4	8.5	10.5
	c	0	0	0.6	0.8	10.5	11.6	12.0	14.3
10 km	a	0	0	0	0	4.5	4.8	4.9	6.3
	b	0	0	0	0	4.2	4.4	4.5	5.8
	c	0	0	0	0	5.4	6.2	6.2	7.7
20 km	a	0	0	0	0	2.2	2.3	2.6	3.0
	b	0	0	0	0	2.2	2.3	2.5	2.9
	c	0	0	0	0	2.7	2.9	3.2	3.8
30 km[+++]	a	0	0	0	0	1.5	1.5	1.7	2.0
	b	0	0	0	0	1.5	1.4	1.7	1.8
	c	0	0	0	0	1.8	2.0	2.2	2.7
40 km	a	0	0	0	0	1.1	1.2	1.3	1.5
	b	0	0	0	0	1.2	1.0	1.3	1.4
	c	0	0	0	0	1.4	1.4	1.6	2.1
50 km	a	0	0	0	0	0.9	0.9	1.1	1.2
	b	0	0	0	0	1	0.8	1.0	1.1
	c	0	0	0	0	1.1	1.2	1.3	1.7
Median	a	350	400	850	900	2511	2611	2820	3267
	b	350	400	900	950	2503	2510	2673	3075
	c	375	425	900	950	2938	3215	3377	4077
99th percentile	a	1800	2025	4450	4500	44000	47000	50000	55000
	b	1725	1825	3750	4000	50000	42000	51000	56000
	c	1850	2150	4550	4850	53000	58000	65000	93000

[+] At least 1 km of radius is suggested for focus zone around introduction points by the European Commission (Anonymous, 2003).

[++] At least 5 km of radius is suggested for safety zone around introduction points by the European Commission (Anonymous, 2003).

[+++] At least 30 km containment zone is suggested along the borders of areas with already established WCR populations by the European Commission (Anonymous 2006a).

(12) **Figure legends**

Figure 1. Fits of the negative power law and negative exponential models to mark-release-recapture data of western corn rootworm adults. (a) Fitted to the recapture data from the non-baited yellow sticky traps. (b) Fitted to the recapture data from the pheromone-baited transparent sticky traps. Data have been corrected (Table 3). Dispersal distance = distance of recaptured WCR adults from the release point. Recaptured = corrected number of recaptured adults.

Figure. 2. Fits of the negative exponential models and negative power law models to pooled mark-release-recapture data of western corn rootworm adults. Recapture data of non-baited yellow sticky traps and pheromone-baited transparent sticky traps were pooled together by scaling them down using the vertical scale parameters of the negative exponential model (to obtain data set A) and the negative power law model (to obtain data set B) (Table 4). (a) Models fitted to pooled data. (b) Models fitted to pooled data where zeros have been removed by reclassification of distances in the tail (*grouped data*) and expressed in log-log axis. (c) Log of the models fitted to log of pooled and *grouped data*. (d) Same fit as (c) but expressed in log-log axis. Dispersal distance = distance of recaptured WCR adults from release point. Probability = Probability of a dispersing WCR adult reaching a certain distance.
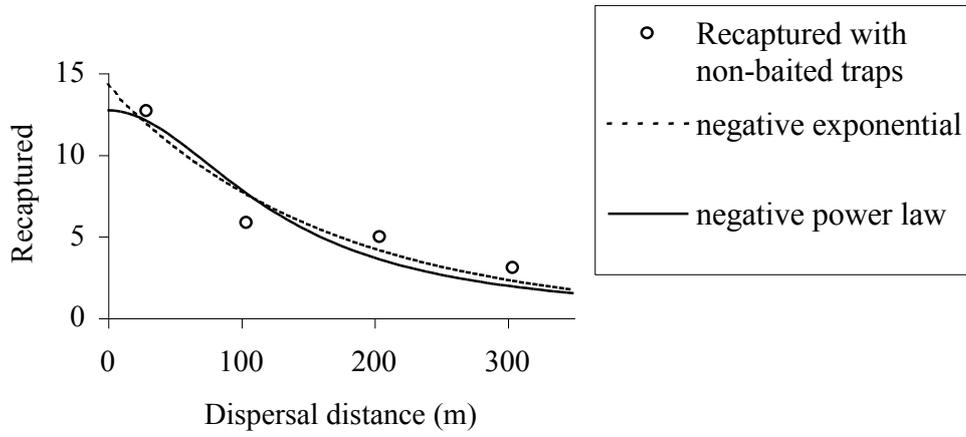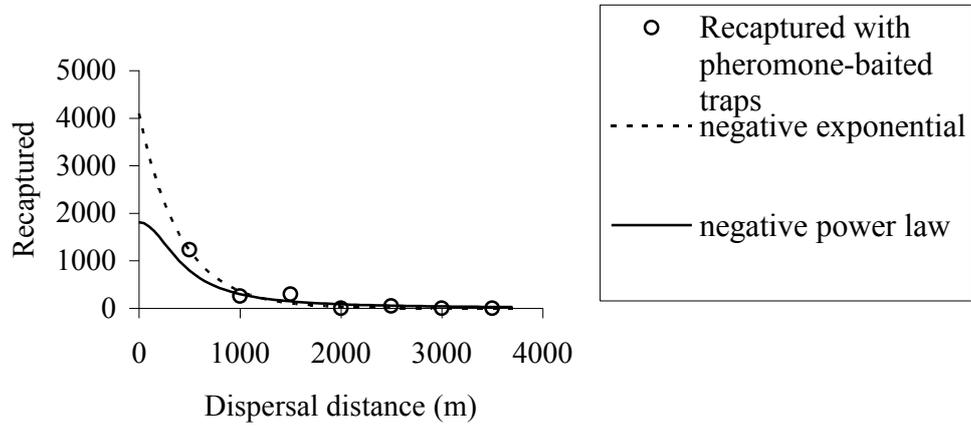
(13) **Figures**

Figure 1 (a)
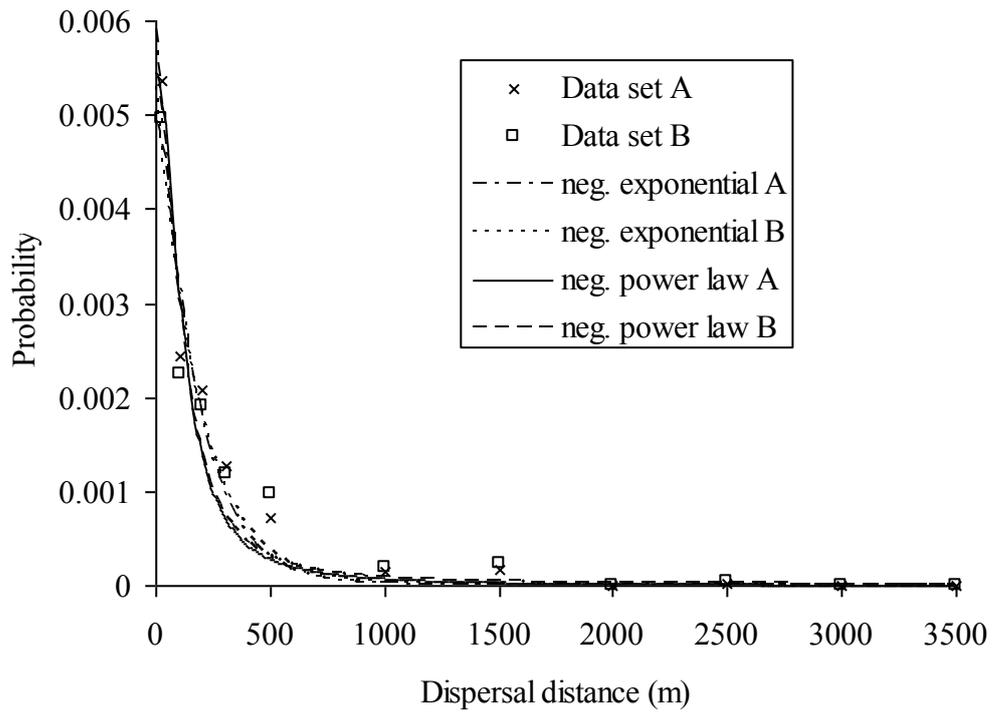

Figure 1 (b)

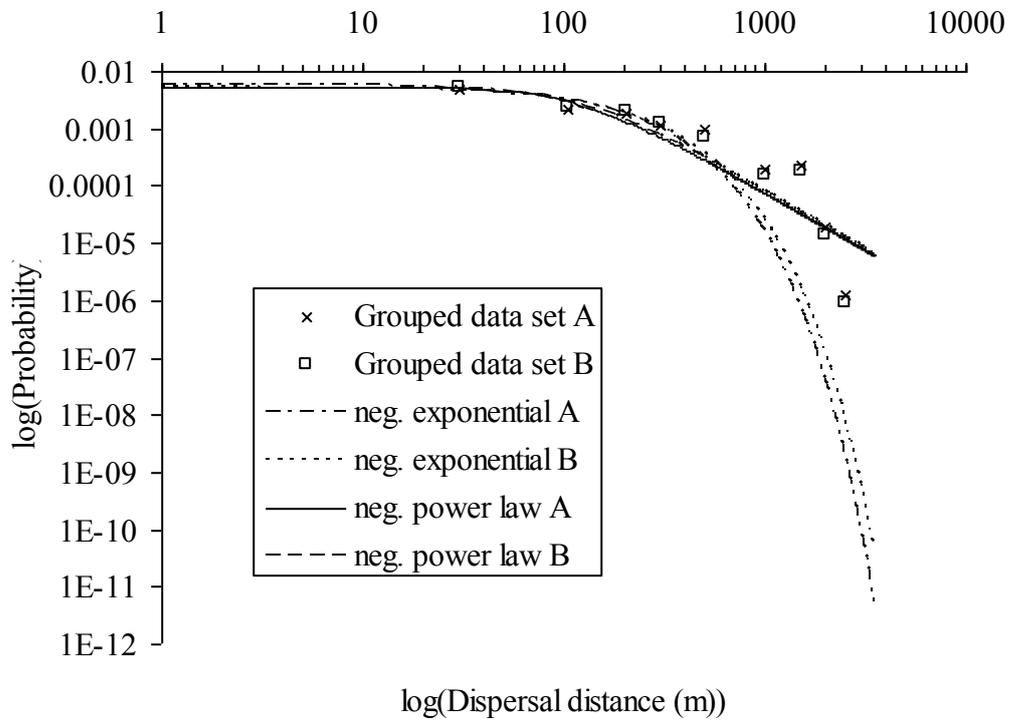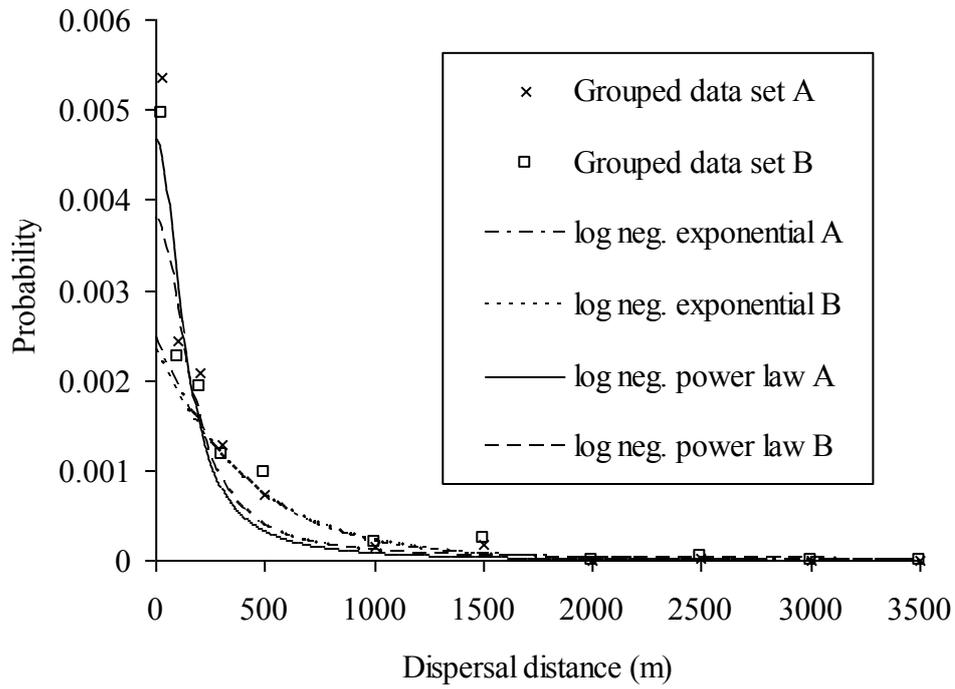*Figure 2 (a)*

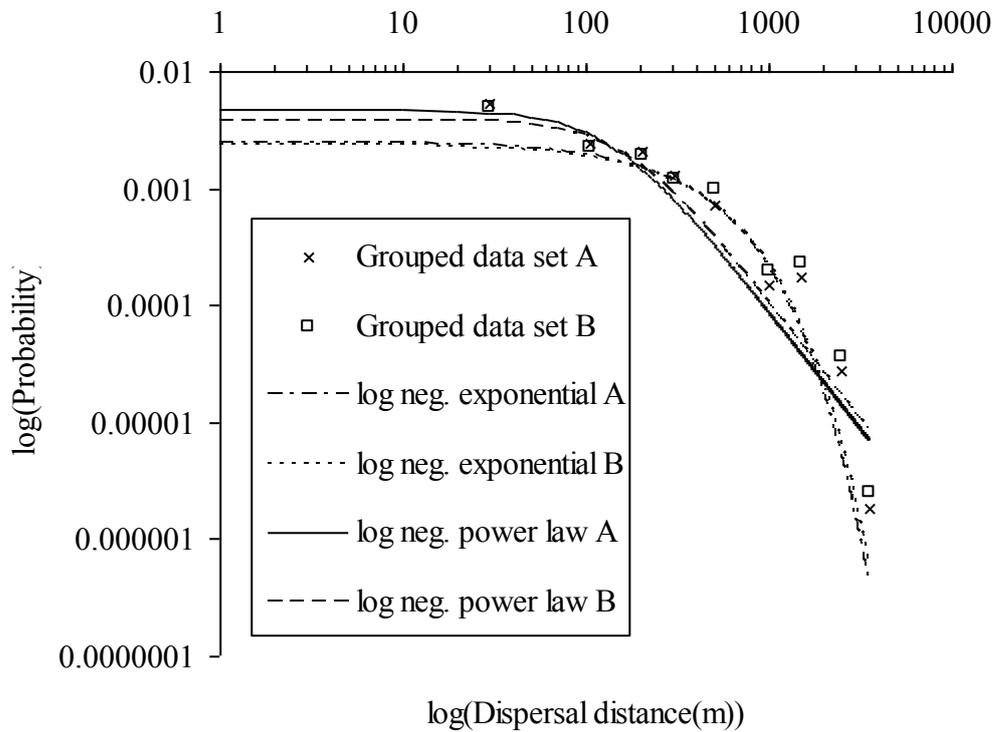*Figure 2 (b)*

Figure 2 (c)

Figure 2 (d)

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