Ann. Zool. Fennici 45: 1–14 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 28 February 2008

Spatial simulation model to predict the Colorado potato beetle invasion under different management strategies

Kata-Riina Valosaari*, Sami Aikio & Veijo Kaitala

*Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland (*corresponding author's e-mail: kata.valosaari@helsinki.fi)*

Received 17 Aug. 2007, revised version received 16 Jan. 2008, accepted 16 Jan. 2008

Valosaari, K.-R., Aikio, S. & Kaitala, V. 2008: Spatial simulation model to predict the Colorado potato beetle invasion under different management strategies. — *Ann. Zool. Fennici* 45: 1–14.

The Colorado potato beetle (CPB), a serious pest of potato, is currently spreading north in Europe. We investigated the risk of CPB establishment in Finland and control methods for the case when beetle life history characters change due to global warming or as an adaptation to colder climate. Analysis with a spatially explicit simulation model supported the current management policy in Finland (efficient eradication and one year field quarantine) but changes in CPB viability, such as decreased winter mortality or increased number of offspring would render them inefficient. Longer quarantine times would be needed to effectively prevent the CPB establishment and spread. As an option we investigated Bt-potato cultivation integrated to other control methods and found that it was already efficient when used as a sole strategy but its benefits may be reduced by the adaptability of the Colorado potato beetle.

Introduction

Biological invasions are among the most serious threats to biodiversity along with climatic change and habitat loss (Pimentel *et al.* 2001, CBD 2007). Alien species have caused enormous economic losses in agriculture and forestry as serious pest species (Pimentel *et al.* 2005). One of such highly invasive species is the Colorado potato beetle (CPB) *Leptinotarsa decemlineata* (Say) which is a pest species of many cultivated solanaceous plants, including potato (*Solanum tuberosum*), tomato (*Solanum lycopersicum*) and aubergine (*Solanum melongena*) (Crowson 1981, Hare 1990). The CPB originated from Mexico but has spread all over the continents of America and Eurasia (Cappaert *et al.* 1991, EPPO/CABI 1997). The current distribution is just east of Finland and spreading to the west (*see* Grapputo *et al.* 2005).

The ability of the CPB to spread so aggressively is due to efficient dispersal (Voss & Ferro 1990a, 1990b, Boiteau 2001), high reproductive capacity (Hare 1980, EPPO/CABI 1997), and high adaptability to varying environmental conditions including pesticides (Tauber & Tauber 2002). For instance the Russian populations have been shown to survive better and develop faster than their European counterparts (Boman *et al.* 2008). Also, predicted climate change, along with the beetle adaptability, can make northern regions more suitable for beetle population expansion (Jeffree & Jeffree 1996, McBean *et al.* 2005).

A wide range of different insecticides has been used in order to control the spread of the CPB and the damage it causes in potato cultivations. Unfortunately, the CPB has been quick to develop resistance (Whalon *et al*. 2004). Crop rotation, trap crops, physical and biological control, plant resistance induced by gene technology have been investigated as alternatives (Hare 1990, Hoy *et al*. 2000, Nault 2001, Cooper *et al*. 2004, 2006, Sexson & Wyman 2005). Genetically modified pest or disease resistant crop plants could be beneficial in farming practices because this would reduce the use of the synthetic, wide spectrum pesticides and insecticides (Huang *et al*. 2005, James 2006). This should also reduce negative environmental and health effects of pest control (Ferré & van Rie 2002, Shelton *et al*. 2002, Huang *et al*. 2005). Pest resistance is achieved in potato via the transfer of *Bacillus thuringiensis* (Bt) subsp. *tenebrions Cry3* (used against Coleoptera) toxin gene to crop plants (Shelton *et al*. 2002). However, the adoption of Bt-crops still has many concerns including marketing issues (Shelton *et al*. 2002), potentially harmful non-target effects (Losey *et al*. 1999, Romeis *et al*. 2004, 2006), though rarely observed (Andow & Zwahlen 2006), and the resistance development of target species against Bt (Cerda & Wright 2002, Andow & Zwahlen 2006).

CPB is not a serious pest in Finnish potato fields yet (EPPO/CABI 1997) but it may become such due to climatic change (Sutherst *et al*. 1995, Jeffree & Jeffree 1996, Heikkilä & Peltola 2007) and possible adaptation to colder climate (reviewed in Hare 1990, EPPO/CABI 1997). The large source populations in the Baltic States and Russia, where control is inefficient (Evira 2008), makes the invasion threat greater than in e.g., the UK where the beetle is effectively controlled in the Channel Islands, the main invasion route of CPB to Great Britain (Thomas & Wood 1980). Two main factors naturally restricting the CPB invasion and spread in Finland are the ability to develop from eggs to adults during the short growing season and the high winter mortality. The length of the beetle development from egg to adult stage is strongly regulated by the temperature (EPPO/CABI 1997). In Finland the warm period favourable to beetle development (15–30 °C) may be too short for larvae to mature. However, a recent study have shown that the average development time of the beetles' from 1st instar larvae to adult stage at 17 °C, which corresponds to mean temperature in June and July in Finland, is 46.4 days (Boman *et al*. 2008). This result suggests that there is enough time for the development of a new beetle generation that is capable to overwinter if the immigration takes place early enough during the season. First successfully overwinted beetles were already observed at potato fields in eastern Finland in summers 2004 and 2006 (Evira 2008).

The control methods currently used against the CPB in Finland are based on the European Union system of protected zones and the beetle is a quarantine pest set by law (EU 2002). In practice, after the beetle infection has been detected and verified by the plant-quarantine authorities as real, an attempt to eradicate the pest is undertaken, and the field is quarantined usually for one year. Small amount of potato is left as a trap crop on the quarantine field for the next year to catch and prevent the spread of the potentially over wintered individuals. So far these control methods have been sufficient to prevent CPB establishment (Evira 2008).

The aim of this study is to examine the impact of three optional control strategies and biological characteristics of the CPB on the population size of the beetle and the percentage of the potato fields infected in Finland. We construct a spatially realistic simulation model of the beetle dynamics and landscape structure of Finnish potato fields. As management strategies, we investigate the effect of rapid eradication of the beetles after detection, the length of field quarantine and, as a plantation strategy, either conventional potato or Bt-potato cultivation, following the quarantine phase. Despite the effective control strategy currently used in Finland, we show that changes in the beetle life history characteristics induced by climate change may have large impact on the choice of a control strategy.

Material and methods

Model

We constructed a spatially explicit model to study the invasion of the CPB in Finland. We modelled space as a two-dimensional lattice of

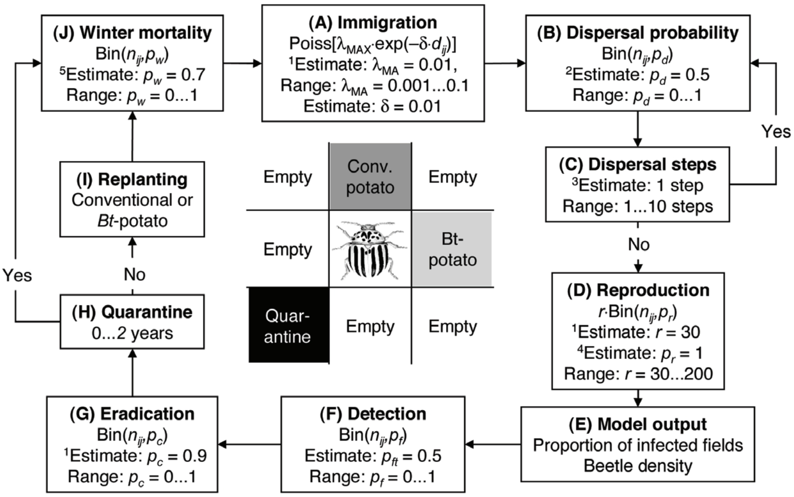

Fig. 1. The schematic representation of the Colorado potato beetle model. The grid at the centre is an example of the modelled landscape, being structured by conventional and Bt-potato fields, quarantine fields and empty (no potato) sites. The flow diagram shows how different stages in the beetle life-cycle and management actions take place during one modelled year. Each stage in the model is represented as a box, where the life-history or management process is given, along with the estimated parameter value and range of values used in sensitivity. Each process is described in more detail in the text. The parameter estimates are based on the following publications: ¹Evira 2008, ²Sandeson *et al.* 2002, ³Weisz *et al.* 1996, ⁵EPPO/CABI 1997, ⁴Harding *et al.* 2002.

square cells. Each cell presented one of the four habitat-types: conventional potato, Bt-potato, field in quarantine, and non-habitat area that could have a CPB population as a discrete number of individuals. We modelled the beetle life-cycle so that individuals were independent actors in events that took place during each simulated year (Fig. 1).

At the beginning of a modelled year (Fig. 1A), the beetles immigrated from a source that was located at the southeastern corner of the landscape (Fig. 2). The number of beetles immigrating in a cell was an integer value that was taken from the Poisson distribution with the expectation

$$\lambda = \lambda_{\mathrm{MAX}}\exp(-\delta d_{ij}). \qquad (1)$$

The rate of beetle immigration thus declined exponentially from the maximum value λ_{MAX} with the rate δ as the distance d_{ij} from the source (SE corner in Fig. 2) increased.

The immigrants mixed with the overwintered individuals within a cell, forming the spring density of the beetle. At each stage of the modelled year n_{ij} stands for the number of beetles in the cell ij that survived from the previous stage. The beetles may then disperse randomly to one of the four neighbouring cells (von Neumann neighbourhood) with a probability p_{d} (Fig. 1B). We varied the number of steps the beetles could take during the dispersal stage from one cell to the next (Fig. 1C). Each dispersal step was randomly directed and the beetles have no memory of their earlier steps. It is thus possible that a beetle returns back to a cell where it had already been, implying that most beetles will stay close to the original cell and few will disperse the maximum distance. After this local dispersal, the individuals that did not found viable habitat after dispersal died. The beetles that ended up on fields with Bt-potato survived with 5% probability but were unable to reproduce (Nault 2001). The beetles at conventional potato fields reproduced with an individual specific probability p_{r} and produced an integer r number of offspring (Fig. 1D). Reproduction was successful only at the cells that contained conventional potato, because the abundance of wild host species (e.g., *Solanum nigrum* and *S. dulcamara*) is low in Finland (Hämet-Ahti *et al.* 1998), and unlikely to maintain a persistent population of the CPB.

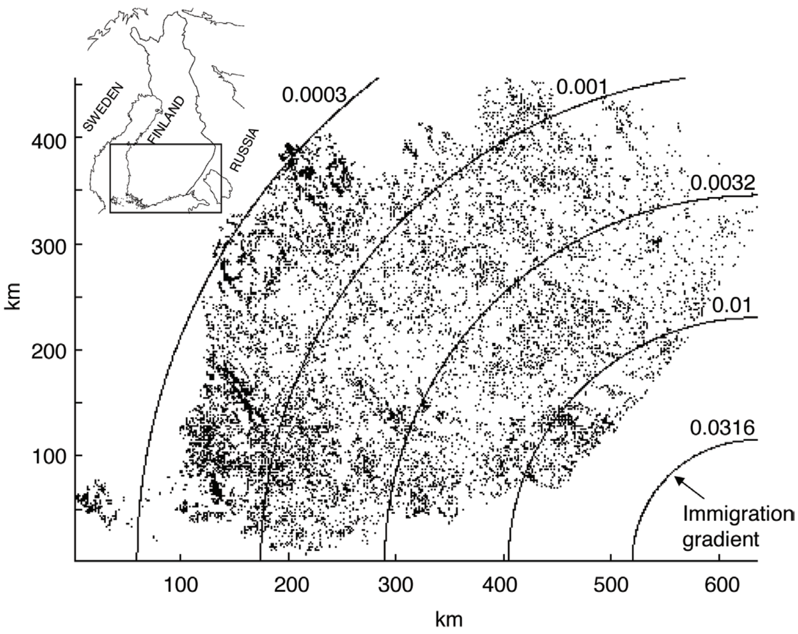

Fig. 2. Map of the occurrence of commercial potato fields in a 1 × 1 km grid southern and central Finland. The map shows the situation in 2005 and is based on approximately 25 000 potato fields. The rate of the beetle invasion forms a declining gradient from south-east to north-west. The number of each isocline is the $\log_{10}(\lambda)$ expected rate of beetle arrival as an annual Poisson process.

We measured reproduction as the number of offspring that survived to the adult stage and was capable of overwintering. The proportion of fields infected by the beetles and the number of beetles at the whole landscape was taken as the model output at this stage (Fig. 1E).

The reproductive phase was followed by an inspection of the fields, where each beetle individual had a probability p_{f} to be detected (Fig. 1F). The probability of detecting at least one beetle in a cell was thus

$$1-(1-p_{\mathrm{f}})n, \tag{2}$$

where n is the number of beetles in that cell. If at least one beetle was detected in a cell, the field was destroyed and beetles died at the individual probability p_{c} which we called the eradication efficiency (Fig. 1G). Eradication was followed by one of the strategies controlling the invasion: First, a decision was made if an infected cell is put to quarantine for a pre-defined number of years (Fig. 1H). If the field was in quarantine, the beetles that stayed there during next growing season were not able to reproduce and died. If an infected field was not quarantined or the quarantine period ended, the field was replanted with conventional or Bt-potato (Fig. 1I).

The beetles that survived eradication and management in conventional potato or Bt-potato cells die during winter with the individual probability p_{w} (Fig. 1J). This parameter also considered for those individuals that escaped control but could not complete the lifecycle during the growing season. To keep the model simple we did not model the possible dispersal of the beetles to separate overwintering sites (Weber *et al.* 1994), but assumed the beetles to diapause on those patches that they were placed after local dispersal.

We manifested the events that were expressed as individual-level probabilities at the patch-level as binomially distributed random numbers of individuals that dispersed, survived or reproduced. Thus, the number of individuals that withstand a probabilistic event (x), e.g. survived, was

$$x = \mathrm{Bin}(n_x, p_x), \tag{3}$$

where n_x was the number of beetles in the cell and p_x was the individual-specific probability of an event. In order to increase the speed of simulations, we approximated the number of successful stochastic events with normal distribution when $n_x \geq 100$, using the parameters

$$\mu \approx n_x p_x, \quad (4)$$
$$\sigma \approx \mu(1 - \mu)/n_x. \quad (5)$$

The resulting random numbers of individuals were rounded down to the nearest integer value (or zero, if negative). In case of dispersal, which was equally likely to all four directions of the von Neumann neighbourhood, we randomized the total number of beetles that would disperse from a cell, and distributed this total number of dispersers randomly between the four dispersal directions.

Parameterisation and analysis

The landscape data were based on the reference coordinates (known to the accuracy of one metre) of ca. 25 000 potato fields in commercial cultivation in southern Finland at year 2005 (unpublished data provided by the Information Centre of the Ministry of Agriculture and Forestry in Finland). We transformed the data for the 1 × 1 km lattice model by considering a grid cell to be a potato field if the reference coordinate was inside the grid cell (Fig. 2). The mean size of a potato field was ca. 0.67 ha ranging from 0.01 to 23.8 ha. The resolution of the model being coarser than the size of the largest fields means that the possible extension of a field over several grid cells could be ignored. We treated all landscape elements that were not potato fields (conventional or Bt) as non-viable habitat. We do not have data on the distribution of small scale domestic potato fields, which are therefore omitted from the analysis. The wild host plants of the CPB are very low in abundance in Finland and are therefore ignored in the analysis (Hämet-Ahti *et al.* 1998).

The modelled habitat patches/cells had no carrying capacity for the beetle density since the beetle may tolerate very high densities as long as the food plant is available (Sandeson *et al.* 2004). We assumed that each one-square-kilometre cell would receive beetles as a Poisson process with the expectation of 0.01 (i.e., one percent probability of getting one beetle) and the immigration rate would decline with distance from the modelled source at the exponential rate of 0.01 (i.e., 1% per kilometre). With these parameters, the expected number of CPB immigrating to Finland every year is 153.46 (± 11.80 SD). The value is about the same as the mean value of the reported observations by Evira (2008), however, their observation may contain also the offspring produced by the invaded (or overwintered) individuals in the same year and not only the immigrants. Where data are available from Finland or similar climatic conditions the beetle-specific probabilities of the model were parameterised according to published sources (Fig. 1).

We initiated the model system with all potato fields growing the conventional variety and the CPB being absent. The model was simulated for 30 years with 10 to 100 replications to control the demographic stochasticity of the individual-based parameters and the immigration rate. The response variables of the analyses were the percentage of potato fields that were infected by the CPB or under quarantine and the size of the beetle population. We express the results as the mean and standard deviation calculated over the replicated simulations.

First we analysed the effect of different control methods on the percentage of potato fields infected and the size of the beetle population. We fixed the CPB life history parameters to values estimated for the current climate in Finland and ran the simulations in 100 replicates (Fig. 1). Next we analyzed the three control methods used in combination (i.e., integrated management strategy). Here we fixed parameter values of beetle life history characteristics and made ten replicates of the simulations.

We investigated the effect of beetle life-history parameters and management actions by means of a sensitivity analysis, where we gave each parameter a range of different values (Fig. 1). We carried out the analysis for the beetle life history parameters out under the current control management policy of the CPB in Finland where the detection (50%) and the beetle eradication (90%) rates are high (Evira 2008). One-year quarantine is the common practice used after the infection but we applied quarantine lengths from zero to two years to find if the changing CPB life history characteristics affects on field quarantine efficiency. We ran the simulations for two plantation scenarios; (i) conventional potato only and (ii) Bt-potato only. In Bt-potato planta-

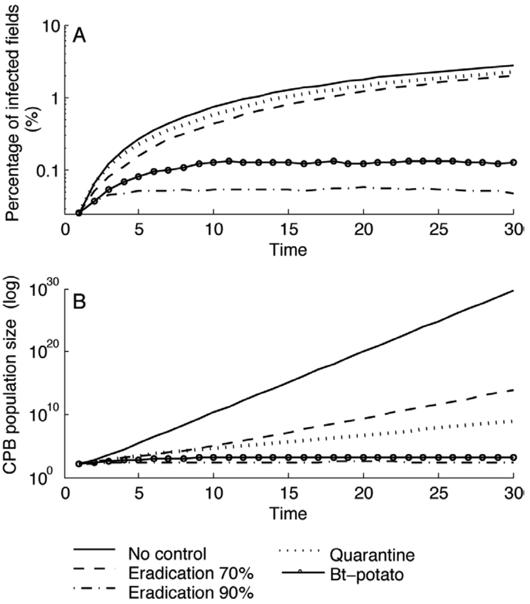

Fig. 3. Comparison of the effectiveness of different control methods on (**A**) the percentage of infected fields by Colorado potato beetle and (**B**) beetle population size in current climate.

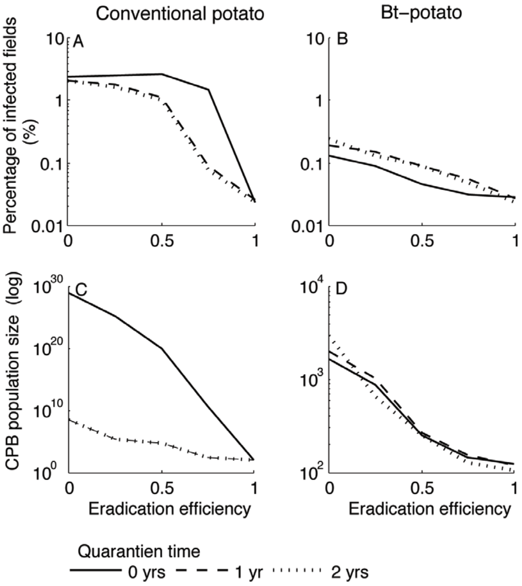

Fig. 4. The effect of the integrated control method on the percentage of infected potato fields and Colorado potato beetle population size. Beetle eradication efficiency and length of quarantine with (**A**, **C**) conventional and (**B**, **D**) Bt-potato plantations strategies investigated as control methods. Notice the difference in scales in panels **C** and **D**.

tion strategy, conventional cultivar was changed to Bt cultivar after beetle infection was detected in the potato field and the change was irreversible. Once a field was planted with Bt-potato, this variety was cultivated also in future, because a non-GM variety could not be marketed as GM-free due to likelihood of volunteer GM-cultivars being present in the soil.

Results

CPB control in the current climate

When no control methods were used, approximately 2.8% of the potato fields got CPB infection within thirty years (Fig. 3A). CPB population size increased exponentially in the absence of control or density dependence (Fig. 3B). A 70% effectiveness of beetle eradication from infected fields led to approximately 2% of potato fields being infected by CPB (Fig. 3A). Beetle population size increased exponentially (Fig. 3B). When the eradication efficiency of detected infections was 90%, the CPB spread in the landscape and population growth were efficiently prevented (Fig. 3A and B). However, a small percentage of potato fields were still infected by CPB due to annual immigration to Finland from abroad.

One year field quarantine alone was not sufficient to prevent the beetle spread: almost 2.5% of potato fields were infected by CPB in thirty years (Fig. 3A) and the beetle population size increased exponentially (Fig. 3B). The change of cultivation from conventional to Bt-potato a detected CPB infection was alone sufficient method for preventing CPB spread and population growth (Fig. 3).

The percentage of infected fields and CPB population size declined with increasing eradication efficiency when used alone or with quarantine (Fig. 4A and C). One and two years of field quarantine decreased the percentage of infected fields over the whole range of eradication efficiencies (from 0% to 100%) but the effect was strongest when eradication efficiency was approximately 50%–80% (Fig. 4A).

CPB population size grew exponentially when the eradication was low and the quarantine was not employed, reflecting the lack of the density dependence in the model (Fig. 4C). One and two years of field quarantine were efficient in reducing the exponential growth of CPB population over the whole range of eradication efficiencies. There was no difference in efficiency of one and two year quarantine either in the proportion of infected fields or the CPB population size.

When eradication, quarantine and replanting of infected fields with Bt-potato were used as an integrated control strategy, the percentage of infected fields and CPB population size both decreased with increasing eradication efficiency (Fig. 4B and D). Quarantine length affected only percentage of infected fields so that it was higher with one or two years of field quarantine than with zero years of quarantine (Fig. 4B). Replanting of Bt-potato right after CPB eradication seemed to be the most efficient control method. Quarantine length did not have an effect on CPB population size (Fig. 4D).

Life history characteristics and CPB ability to spread

All CPB life history characteristics we modelled had an effect on the percentage of infected potato fields, but their effect was small when Bt-potato was cultivated (Fig. 5). Increase in CPB immigration rate (from $\lambda = 0.001$ to $\lambda = 0.1$) from source populations outside the modelled landscape increased the percentage of infected fields from 0.01% to nearly 1% with conventional potato (Fig. 5A). Effect was similar with Bt-potato, but the percentage of infected fields was slightly lower (Fig. 5B). Quarantine length did not have an effect on CPB ability to spread within either plantation strategies.

The percentage of infected potato fields had a sigmoid relation to the number of offspring produced within conventional potato plantation strategy (Fig. 5C). CPB ability to spread increased exponentially after number of offspring increased to approximately 30, and then saturated when number of offspring reached approximately 60. One and two years of field quarantine were efficient in controlling the CPB spread after the number of offspring increased to approximately 25. With Bt-potato plantation strategy CPB ability to spread with increasing offspring number was not so evident and applying one or two years of field quarantine, even increased the beetle ability to spread within potato fields (Fig. 5D).

Both the percentage of the beetle dispersal and the number of dispersal steps (i.e., maximum dispersal distance) had no clear effect on the percentage of potato fields infected and this result was the same in the cultivation of conventional and Bt-potato (Fig. 5E, F, G, H). However, when conventional potato was cultivated, increased dispersal ability of the beetle seemed to have a slight decreasing effect on the percentage of potato fields infected. The use of one or two years quarantine decreased the beetle infection only when dispersal probability was low or beetles did not disperse at all (Fig. 5E and G).

Increased winter mortality decreased the percentage of infected fields. Quarantine was effective in the controlling of CPB when winter mortality with conventional potato plantation strategy was higher than approximately 75% (Fig. 5I). In addition, two years of field quarantine was more efficient than one year when winter mortality was lower than approximately 40%. If quarantine was not employed and winter mortality was low, the percentage of infected fields was higher than 1%. With Bt-potato plantation strategy the increase in winter mortality decreased the CPB ability to spread more efficiently than with conventional potato but the application of quarantine reduced the effect of Bt strategy (Fig. 5J).

Life history characteristics and CPB population growth

Change in CPB life history characters had similar effect on population growth as on the percentage of potato fields infected (Fig. 6). However, the increase in the number of offspring and the decrease in winter mortality led to largest population size growth when conventional potato plantation strategy was used (Fig. 6C and I). Field quarantine of one or two years was effective to control CPB population growth in

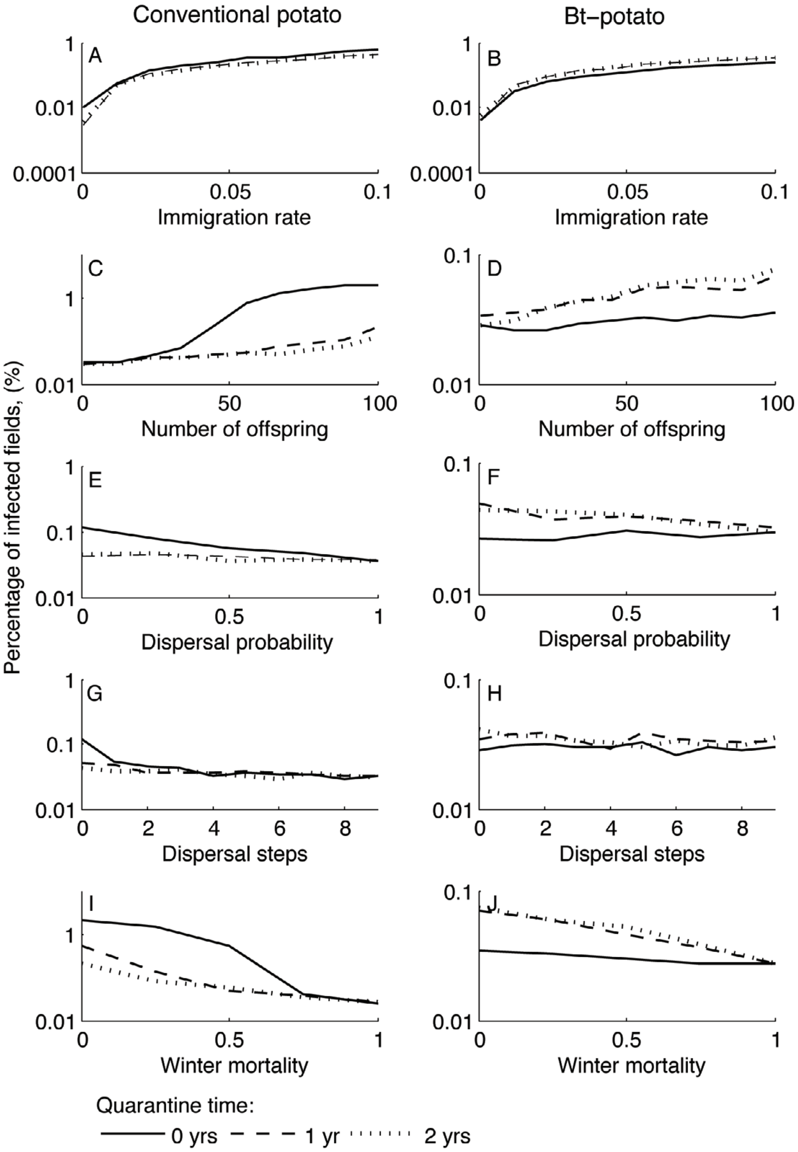

Fig. 5. Sensitivity analysis of the percentage of the infected potato fields with (**A**, **B**, **C**, **D**, **E**) conventional and (**F**, **G**, **H**, **I**, **J**) Bt-potato plantations with respect to Colorado potato beetle invasion pressure, number of offspring, dispersal probability, length of dispersal and winter mortality rate.

other scenarios except when the immigration rate increased (Fig. 6A). Bt-potato plantation strategy was effective to control the CPB population growth with increasing dispersal ability or decreasing winter mortality (Fig. 6F, H, J), but could not totally inhibit it when CPB immigration rate or number of offspring increased (Fig. 6B, D). Quarantine did not have any effect on CPB population growth when applied in combination with Bt-potato plantation strategy.

Discussion

CPB control in current climate

Within the control methods we considered, the two most effective for preventing the establishment of the Colorado potato beetle at Finnish potato fields in the current climatic conditions are an effective eradication of the detected beetles, and the use of quarantine after eradication. The exponential growth of CPB population at lowest eradication efficiencies reflects the high

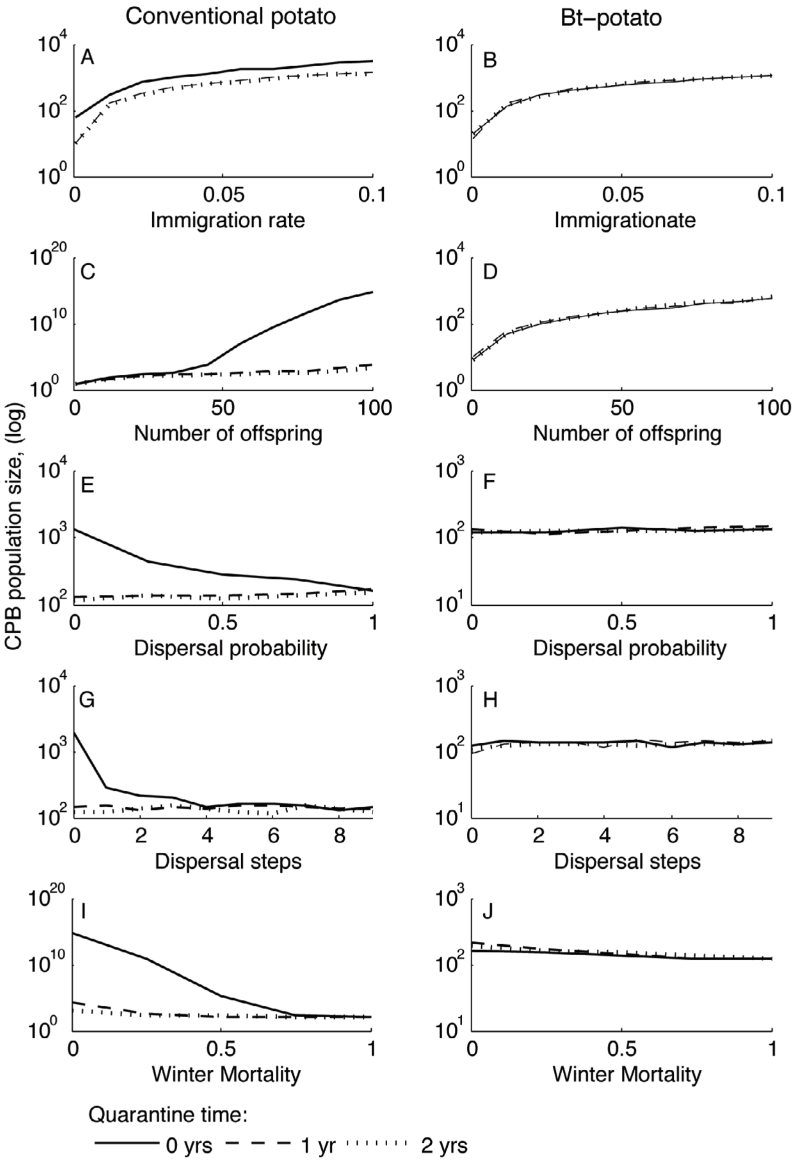

Fig. 6. Sensitivity analysis of the beetle population size in (**A**, **B**, **C**, **D**, **E**) conventional and (**F**, **G**, **H**, **I**, **J**) Bt-potato plantations with respect to Colorado potato beetle invasion pressure, number of offspring, dispersal probability, length of dispersal and winter mortality rate.

growth potential of CPB and the lack of density dependence in the model. For example, when eradication efficiency is as high as 90% it is efficient enough to inhibit CPB population growth and the population size is kept approximately at the same level as the yearly immigration rate is. However, when eradication efficiency decreases to 70% CPB population size may start to increase (increase may be rapid due to lack of density dependence in the model) and beetles start to disperse locally. Our results on the importance of pre-emptive control support the previous findings that prevention is more effective than attempting to remove already widely spread pest or other invasive alien species (Heikkilä & Peltola 2003, CBD 2007).

Estimated number of invading beetles with fixed immigration rate ($\lambda = 0.01$) is approximately 150 beetles per year in the modelled part of Finland. However, observations made in 1995–2005 in Finland show that the invasion densities vary greatly from year to year from zero to several hundred individuals per year (Evira 2008). This makes an accurate prediction of the establishment of the permanent CPB population difficult, since it has been shown that invasion success (establishment) of an alien species depends highly on the number of immigrating individuals (Green 1997, Memmott *et al.* 2005, Drake & Lodge 2006). Our assumption of constant immigration rate over the simulated landscape may lead to a slight overestimation of the number of invading beetles; however, for a single field (or other habitat cell) the number of immigrants varies between years. On the other hand, a large proportion of modelled immigrants ends up in the non-viable habitat and dies. Also, the numbers of beetles observed by Evira (2008) may be an underestimate, since only the beetles ending up in the vicinity of the potato fields are likely to be found.

Our model for integrated CPB management strategy consists of four separate parts: (1) the detection of the beetles from the fields, (2) control of the detected beetles (eradication of the beetles), (3) quarantine and (4) the plantation strategy after quarantine (conventional or Bt-potato). We assume a fairly high detection probability (50%) in the model, but it can be a realistic estimate for Finland, where awareness among professional farmers is high and beetles are intensively searched during the most critical period in July (Evira 2008). In addition, both the larvae and the adult CPB are highly visible due to their bright coloration. Also the eradication efficiency of the detected beetles from infected fields is high (90% in our model) as the eradication may involve the destruction of all potato plants within a field when found necessary (except for the trap plants) and it is conducted by plant protection authorities (Evira 2008). We found that high detection and eradication efficiencies together with one-year field quarantine is an effective control strategy in reducing beetle ability to spread in the landscape and the population growth.

The combination of effective eradication of beetles from infected fields and the planting of Bt-potato is a more effective control strategy than eradication and field quarantine method with the cultivation of conventional potato. However, in Bt-potato cultivation the quarantine method loses its power and it is no more beneficial to use. The effectiveness of the quarantine as a control method is a consequence of the lower proportion and increased isolation of conventional potato fields. It is thus more probable that dispersing individuals do not find viable habitat and die as a consequence. Quarantine is inefficient with Bt-potato since Bt-fields are also almost non-viable habitats for CPB and turning to Bt-plantation strategy increases the isolation of viable habitats permanently, where quarantine phases give no additional benefit. According to these results, plantation of the Bt-potato instead of conventional potato controlled with quarantine after CPB infection could be profitable for farmers since there would be no losses in yield due to the quarantine period.

The use of genetically modified Bt-potato in large-scale commercial cultivation includes many concerns and it is not currently in commercial use (Boiteau 2005). Probably the most serious ecological problem with Bt-potato use in the CPB control is the evolution of resistance against Bt-toxin, which is expected since it has been shown to occur when beetles are exposed to Bt sprays in laboratory studies (Ferré & Van Rie 2002). The efficiency of Bt-potato as a control strategy may thus deteriorate over time. Future studies should consider the development of the resistance against Bt-potato within the CPB population. Socio-economic issues, such as the contamination of the conventional potato varieties by genetically modified potatoes, should also be part of planning of any transgenic varieties on the farming practices.

CPB control after beetle adaptation or global warming

Changes in CPB life history characteristics by the global change or CPB's adaptation to colder climate may lead to establishment and even outbreaks in Finland, regardless of effective detection and eradication systems. Our results indicate that an increase in reproductive capacity and decrease in winter mortality rate are the life history characteristics that have the greatest effect on beetle invasion.

While CPB is very efficient in reproduction and a single female may produce even 2000 eggs per breeding season (EPPO/CABI 1997) only a fraction of the offspring survive to the overwintering adult stage. We varied the number of viable offspring around the estimated 30 individuals and already an increase to 50 offspring per adult individual lead to population outbreak in 30 years. The exponential population growth we see is a real possibility which may be realized if the immigrated individuals are able to escape detection and eradication processes and reproduce freely (Evira 2008). Our model predicts one year field quarantine to be sufficient to reduce the population growth even if offspring production is as high as 100 per adult. Quarantine is effective since a field becomes non-viable if at least one beetle is found. Another effect comes from the mortality of those individuals that escape detection and eradication but are killed if they can not disperse to another potato field. An increased isolation of potato fields would have a similar effect.

Winter mortality has pronounced effect on the CPB population size and ability to spread (as percentage of infected fields) but also on the choice of the control strategy. Decrease in the beetle winter mortality increases the proportion of the landscape infected by the beetles and also the population size, in which case detection and eradication of detected beetles should be efficient. In addition, if winter mortality decreases as predicted due to global warming or beetle adaptability to colder climate, the one-year quarantine strategy will no longer be effective. According to the model's predictions, at least two years of field quarantine will be needed if winter mortality decreases below 50%. Extending the quarantine time to several years has also economic consequences, since fields would not be cultivated for a longer time. Bt-potato may also increase the winter mortality of the beetle and force beetle to disperse. Nault (2001) found that winter mortality of the beetles that had fed on Bt-potato fields was more severe than the beetles that fed on conventional potato fields. Only 0.5% of beetles that fed on Bt-potato survived over winter.

Currently, the rate of winter mortality of the CPB in Finland is not accurately known but is expected to be high. For instance, in summer 2002 over 300 potato fields were infected by immigrating beetles, however, none of these fields were recorded to have beetles in the next summer (Evira 2008). This observation suggests that either eradication was extremely effective or the winter survival of the beetles was low. In Estonia, winter mortality of the beetles was highly variable between years depending on both the winter temperature and the type of the soil where the beetles hibernated (Hiiesaar *et al.* 2006). In the winter 2002/2003 when temperatures were low (–30 °C) for a long period, the mortality varied between 88% and 100% but during milder winters mortality varied between 12% and 57.6% (Hiiesaar *et al.* 2006). Diapause is thus one of the critical phases of the CPB life cycle restricting its spread (Hiiesaar *et al.* 2006). In southern Finland in 1900–2000 the mean winter temperature of the coldest month (January) varied between –16.5 °C and +1.4 °C (mean –7.8 °C) and in central Finland between –19.9 °C and –1.0 °C (mean –13.6 °C) (http://www.fmi.fi/saa/tilastot.html). Global warming scenarios predict the mean temperature in Finland to rise from 2 to 7 °C by the 2080s (Jylhä *et al.* 2004), making the region vulnerable to CPB establishment by increasing winter survival and larval maturation in summer.

An increased CPB immigration from the Baltic-State and Russian source populations could increase the risk of beetle establishment in Finland but population outbreaks are not expected when detection and eradication methods are efficient. Increased immigration of the beetles from source populations will, however, hinder the efficiency of eradication method in Finland since it would also be very difficult and costly to detect all local populations and individuals once the population is established and widely spread (Wittenberg & Cock 2005). Long-distance dispersal, like immigration from a source population to Finland, is mainly a random event, meaning that the beetles are not able to decide where to land. Dispersal is, therefore, risky and beetles usually disperse only when they suffer from lack of food plants or overcrowding (Sandeson *et al.* 2002). Nonetheless, even rare events of long distance dispersal can be crucial in population spread (Kot *et al.* 1996, Hastings *et al.* 2005, Nathan 2006), and its importance in expansion of invasive species is still greatly underestimated (Trakhtenbrot *et al.* 2005).

A quite unexpected prediction of our model is that local dispersal of the beetles recorded as the probability to disperse and the number of dispersal steps taken, has no clear effect on beetles' ability to spread or beetle population size in Finland. Dispersal has been shown to be an important factor in CPB invasion, and spread behaviour to occur by either walking or flying up to several kilometres (Boiteau 2001). Most of those beetles that are able to disperse several steps in our model will still stay quite close to their natal patch since the direction of dispersal is random to all four neighbouring cells. This means that only a small proportion of these highly mobile individuals end up to long distances from their natal patches. Since the potato fields are relatively isolated in Finland, there is a high probability that the beetle end up in an empty area in the matrix instead of the potato field. This could explain the effect of local dispersal on beetle ability to spread in the landscape.

The predictive power of our model could be improved by superimposing it with a climate model (like CLIMEX) like the CPB invasion risk is modelled for the UK (Jarvis & Baker 2001a, 2001b). Since the use of climate models requires a lot of weather and also phenology data of the CPB we do not have for Finland, we decided to simplify the effect of climate change with dispersal gradient and varying beetle life history parameters.

Conclusions

The spatially realistic simulation model developed here could serve as a tool to predict the future invasion potential of the CPB in cold-temperature regions on landscape level, since we have detected the life history variables that are likely to affect the beetles' population dynamics. However, even marginal differences in the life history traits, the behaviour of the beetle, the development of resistance to Bt-toxin and the changes in the climate may crucially change the population dynamics of the CPB.

Acknowledgements

We would like to thank Johanna Mappes and Leena Lindström from the University of Jyväskylä for providing us the first hand knowledge on the Colorado potato beetle life history in Finland. We also thank the anonymous referee who provided valuable comment on the earlier version. The Information Centre of the Ministry of Agriculture and Forestry in Finland for the environmental provided us the data of potato fields in commercial cultivation in Southern Finland. This research was funded by the Academy of Finland, Ministry of Agriculture and Forestry and Ministry of the Environment in Finland as a part of research programme on Environmental, Societal and Health Effects of Genetically Modified Organisms (ESGEMO) (http://www.mm.helsinki.fi/esgemo/english/).

References

Andow, D. A. & Zwahlen, C. 2006: Assessing environmental risks of transgenic plants. — *Ecology Letters* 9: 196–214.

Boman, S., Grapputo, A., Lindström, L., Lyytinen, A. & Mappes, J. 2008: Quantitative genetic approach for assessing invasiveness: geographic and genetic variation in life-history traits. — *Biological Invasions*. [In press].

Boiteau, G. 2001: Recruitment by flight and walking in a one-generation Colorado potato beetle (Coleoptera: Chrysomelidae) environment. — *Environmental Entomology* 30: 306–317.

Boiteau, G. 2005: Recruitment of adult Colorado potato beetles in Bt-transgenic potato fields. — *American Journal of Potato Research* 82: 379–387.

Cappaert, D., Drummond, F. A. & Logan, P. A. 1991: Population dynamics of the Colorado potato beetle (Coleoptera: Chrysomelidae) on a native host in Mexico. — *Environmental Entomology* 20: 1549–1555.

CBD 2007: *Convention on biological diversity. Invasive alien species. The IAS Portal — your information gateway on invasive alien species*. — Available at http://www.biodiv.org/programmes/cross-cutting/alien/default.shtml.

Cerda, H. & Wright, D. J. 2002: Could resistance to transgenic plants produce a new species of insect pests? — *Agriculture, Ecosystems and Environment* 91: 1–3.

Cooper, S. G., Douches, D. S. & Grafius, E. J. 2004: Combining genetic engineering and traditional breeding to provide elevated resistance in potatoes to Colorado potato beetle. — *Entomologia Experimentalis et Applicata* 112: 37–46.

Cooper, S. G., Douches, D. S. & Grafius, E. J. 2006: Insecticidal activity of avidin combined with genetically engineered and traditional host plant resistance against Colorado potato beetle (Coleoptera: Chrysomelidae) larvae. — *Journal of Economic Entomology* 99: 527–536.

Crowson, R. A. 1981: *The biology of the Coleoptera*. — Academic Press, London.

Drake, J. M. & Lodge, D. M. 2006: Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. — *Biological Invasions* 8: 365–375.

EPPO/CABI 1997: *Leptinotarsa decemlineata*. — In: Smith, I. M., Scott, P. R. & Holderness, M. (eds.), *Quarantine* *pests for Europe*, 2nd ed. *Data sheets on quarantine pests for European Union and for the European and Mediterranean Plant Protection Organization*: 352–357. CABI International, University Press, Cambridge

EU 2002: *EU Commission Directive 2002/28/EC of 19 March 2002 amending certain annexes to Council Directive 2000/29/EC on protective measures against the introduction into the Community of organisms harmful to plants or plant products and against their spread within the Community*.

Evira 2008: *Koloradonkuoriaisesiintymät Suomessa 1998–2005*. — Available at http://www.evira.fi/attachments/kasvintuotanto_ja_rehut/kasvintarkastus/karanteenituhoojat/kolorado/koloradonkuoriainen_1998_2005.pdf.

Ferré, J. & Van Rie, J. 2002: Biochemistry and genetics of insect resistance to *Bacillus thuringiensis*. — *Annual Review of Entomology* 47: 501–533.

Grapputo, A., Boman, S., Lindström, L., Lyytinen, A. & Mappes, J. 2005: The voyage of an invasive species across continents: genetic diversity of North American and European Colorado potato beetle populations. — *Molecular Ecology* 14: 4207–4219.

Green, R. E. 1997: The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. — *Journal of Animal Ecology* 66: 25–35.

Harding, C. L., Fleischer, S. J. & Blom, P. E. 2002: Population dynamics of the Colorado potato beetle in an agroecosystem with tomatoes and potatoes with management implications to processing tomatoes. — *Environmental Entomology* 31: 1110–1118.

Hare, J. D. 1980: Impact of defoliation by Colorado potato beetle on potato yields. — *Journal of Economic Entomology* 73: 369–373.

Hare, J. D. 1990: Ecology and management of the Colorado potato beetle. — *Annual Review of Entomology* 35: 81–100.

Hastings, A., Cuddington, K., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B. A., Moore, K., Taylor, C. & Thomson, D. 2005: The spatial spread of invasions: new developments in theory and evidence. — *Ecology Letters* 8: 91–101.

Heikkilä, J. & Peltola, J. 2003: Conceptualising the economics of plant health protection against invasive pests. — *Agricultural and Food Science in Finland* 12: 67–81.

Heikkilä, J. & Peltola, J. 2007: Phytosanitary measures under uncertainty. — In: Oude Lansink, A. G. J. M. (ed.), *New approaches to the economics of plant health*: 147–161. Wageningen UR Frontis Series 20.

Hiiesaar, K., Metspalu, L., Jõudu, J. & Jõgar, K. 2006: Over-wintering of the Colorado potato beetle (Leptinotarsa decemlineata Say) in field conditions and factors affecting its population density in Estonia. — *Agronomy Research* 4: 21–30.

Hoy, C. W., Vaughan, T. T. & East, D. A 2000: Increasing the effectiveness of spring trap crops for *Leptinotarsa decemlineata*. — *Entomologia Expetimentalis et Applicata* 96: 193–204.

Huang, J., Hu, R., Rozelle, S. & Pray, C. 2005: Insect-resistant GM rice in farmers' fields: Assessing productivity and health effects in China. — *Science* 308: 688–690.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) 1998: *Retkeilykasvio*, 4th ed. — Luonnontieellinen keskusmuseo, Kasvimuseo. Helsinki.

James, C. 2006: *Global status of commercialized biotech/GM crops: 2006*. — ISAAA Brief No. 35, ISAAA, Ithaca, NY.

Jarvis, C. H. & Baker, R. H. A. 2001a: Risk assessment for indigenous pests: 1. Mapping the outputs of phenology models to assess the likelihood of establishment. — *Diversity and Distribution* 7: 223–235.

Jarvis, C. H & Baker, R. H. A. 2001b: Risk assessment for indigenous pests: 2. Accounting for interyear climate variability. — *Diversity and Distribution* 7: 237–248.

Jeffree, C. E. & Jeffree, E. P. 1996: Redistribution of the potential geographical ranges of Misteltoe and Colorado beetle in Europe in response to the temperature component of climate change. — *Functional Ecology* 10: 562–577.

Jylhä, K., Tuomenvirta, H. & Ruosteenoja, K. 2004: Climate change projections for Finland during the 21st century. — *Boreal Environment Research* 9: 127–152.

Kot, M., Lewis, M. A. & van den Driessche, P. 1996: Dispersal data and the spread of invading species. — *Ecology* 77: 2027–2042.

Losey, J. E., Rayor, L. S. & Carter, M. E. 1999: Transgenic pollen harms monarch butterfly. — *Nature* 399: 214–214.

McBean, G., Alekseev, G., Chen, D., Forland, E., Fyte, J., Groisman, P. Y., King, R., Melling, H., Vose, R. & Whitfield, P. H. 2005: Arctic climate: past and present. — In *Arctic climate impact assessment*: 21–60. Cambridge University Press.

Memmott, J., Craze, P. G., Harman, H. M., Syrett, P. & Fowler, S. V. 2005: The effect of propagule size on the invasion of an alien insect. — *Journal of Animal Ecology* 74: 50–62.

Nathan, R. 2006: Long-distance dispersal in plants. — *Science* 313: 786–788.

Nault, B. A. 2001: Survival and fecundity of Bt-susceptible Colorado potato beetle adults after consumption of transgenic potato containing *Bacillus thuringiensis* subsp. *tenebrionis* Cry3A toxin. — *Entomologia Experimentalis et Applicata* 101: 265–272.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. 2001: Economic and environmental threats of alien plant, animal, and microbe invasions. — *Agriculture, Ecosystems & Environment* 84: 1–20.

Pimentel, D., Zuniga, R. & Morrison, D. 2005: Update on the environmental and economic costs associated with alien-invasive species in the United States. — *Ecological Economics* 52: 273–288.

Romeis, J., Dutton, A. & Bigler, F. 2004: *Bacillus thuringiensis* toxin (Cry1 Ab) has no direct effect on larval on the green lacewing *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae). — *Journal of Insect Physiology* 50: 175–183.

Romeis, J., Meissle, M. & Bigler, F. 2006: Transgenic crops expressing *Bacillus thuringiensis* toxins and biological control. — *Nature Biotechnology* 24: 63–71.

Sandeson, P. D., Boiteau, G. & Le Blanc, J.-P. R. 2002: Adult density and the rate of Colorado potato beetle (Coleoptera: Chrysomelidae) flight take-off. — *Environmental Entomology* 31: 533–537.

Sandeson, P. D., Boiteau, G. & Le Blanc, J.-P. R. 2004: Effect of adult Colorado potato beetle density on dispersal under field conditions. — *Environmental Entomology* 33: 1421–1430.

Sexson, D. L. & Wyman, J. A. 2005: Effect of crop rotation distance on populations of Colorado potato beetle (Coleoptera: Chrysomelidae): Development of areawide Colorado potato beetle pest management strategies. — *Journal of Economic Entomology* 98: 716–724.

Shelton, A. M., Zhao, J.-Z. & Roush, R. T. 2002: Economic, ecological, food safety and social consequences of the deployment of Bt-transgenic plants. — *Annual Review of Entomology* 47: 845–881.

Sutherst, R. W., Maywald, G. F. & Skarrat, D. B. 1995: Predicting insect distribution in a changed climate. — In: Harrington, R. & Stork, N. E. (eds.), *Insects in a changing environment, 17th Symposium of the Royal Entomological Society of London 7–10 September 1993*: 60–88. The Royal Entomological Society of London, Academic Press.

Tauber, M. J. & Tauber, C. A. 2002: Prolonged dormancy in *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae): a ten-year field study with implications for crop rotation. — *Environmental Entomology* 31: 499–504.

Thomas, G. & Wood, F. 1980: Colorado potato beetle in the Channel Islands. — *EPPO Bulletin* 10: 491–498.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D. M. 2005: The importance of long-distance dispersal in biodiversity conservation. — *Diversity and Distribution* 11: 173–181.

Voss, R. H. & Ferro, D. N. 1990a: Phenology of flight and walking by Colorado potato beetle (Coleoptera: Chrysomelidae) adults in western Massachusetts. — *Environmental Entomology* 19: 117–122.

Voss, R. H. & Ferro, D. N. 1990b: Ecology of migrating Colorado potato beetles (Coleoptera: Chrysomelidae) in western Massachusetts. — *Environmental Entomology* 19: 123–129.

Weisz, R. Z., Smilowitz, Z. & Fleischer, S. 1996: Evaluating risk of Colorado potato beetle (Coleoptera: Chrysomelidae) infestation as a function of migratory distance. — *Journal of Economic Entomology* 89: 435–441.

Whalon, M. E., Mota-Sanchez, D. & Duynslager, L. 2004–2007: *Arthropod Pesticide Resistance Database (APRD)*. — Available at http://www.pesticideresistance.org/search/12/141/0/.

Weber, D. C., Ferro, D. N., Bounaccorsi, J. & Hazzard, R. V. 1994: Disrupting spring colonization of Colorado potato beetle to nonrotated potato fields. — *Entomologia Experimentalis et Applicata* 73: 39–50.

Wittenberg, R. & Cock, M. J. W. 2005: Best practices for the prevention and management of invasive alien species. — In Mooney, H. A., Mack, R. N., McNeely, J. A., Neville, L. E., Schei, P. J. & Waage, J. K. (eds.), *Invasive alien species*: 209–232. SCOPE, Island Press.