Effect of climate change on the potential spread of the Colorado potato beetle in Scandinavia: an ensemble approach

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ABSTRACT: The Colorado potato beetle \textit{Leptinotarsa decemlineata} is an insect pest that can cause a substantial reduction of the potato harvest if left uncontrolled. The aim of this study was to assess the impact of a warmer climate on the Colorado potato beetle in Europe, since temperature influences the beetles' activity and development from egg to adult, and thereby the potential distribution. The study focuses in particular on the potential northward spread in the Scandinavian countries. In this region, the current climate is not warm enough to sustain the completed development of one generation in all years, and the region does not host a permanent population. Temperature data for 1961–2050 from 4 regional climate models and gridded observed data for 1961–1990 (reference period) were used for model calculations. We simulated the earliest timing of completed development of the first and second generations of the Colorado potato beetle, and assessed the geographical and inter-annual variation in the number of generations per year. The model simulations indicated a shift in the northern limit for establishment of a permanent Colorado potato beetle population by 2020–2050 in comparison with 1961–1990. In particular, the model showed a substantial increase in the frequency of years in which the temperature requirement for development of one generation was fulfilled in the transient zone, i.e. the southern part of Scandinavia. In addition, 2 generations per year may occur more frequently at the current distribution border at 55°N, increasing the risk of northward migration to the Scandinavian countries.

KEY WORDS: Colorado potato beetle · Adaptation · Inter-annual variation · Migration · Regional climate model · Scandinavia · Scenario A1B

1. INTRODUCTION

The global mean temperature has increased by about 0.8°C since the early 20th century, and projections for the 21st century indicate an additional average increase of 1 to 4°C (IPCC 2013). A warmer climate will affect the European agricultural sector, as both crop growth and the risk of insect attacks are directly influenced by temperature (Olesen et al. 2011, Trnka et al. 2011, Fand et al. 2012). Northward migration of different insect species has already been found in monitoring studies (e.g. Parmesan et al. 1999, Boman et al. 2008, Bebber et al. 2013), and to mitigate the effects of a warmer climate in northern Europe, the agricultural sector has to develop climate change adaptation strategies. Current control measures may be less efficient in a warmer climate, thereby requiring altered management practice, such as introducing new varieties of crops (Olesen & Bindi 2002), earlier planting (Tauber et al. 1988), modified crop rotation schemes (Alyokhin et al. 2008), and longer quarantine times for fields that have been infested (Valosaari et al. 2008).

The Colorado potato beetle (CPB) \textit{Leptinotarsa decemlineata} Say is an insect pest that can cause substantial reductions to potato harvests if left uncontrolled (Alyokhin et al. 2008). Both larvae and adults feed on foliage (Ferro et al. 1985). The development
from egg to insect is temperature dependent, and the number of generations per year depends on ambient temperature, day length, and availability of host plants (Tauber et al. 1988). The CPB was introduced into Europe in the beginning of the 1920s (Johnson 1967), and has since been established in most parts of Europe (Hare 1990). However, the Scandinavian countries do not host a permanent population (EPPO 2013), although southern Sweden and Denmark experienced invasions of CPBs in 1972 and 1983 (Gransbo 1980, Gripwall 1993), and Finland in 1998 and 2002 (Ooperi & Jolma 2009). These occasions have been associated with warm weather and southerly winds, triggering mass migration of beetles from Poland and Germany over the Baltic Sea (Gransbo 1980). Massive eradication measures were undertaken to prevent the establishment of a permanent population.

Climate impact modeling can be employed to estimate the development and potential spread of the CPB (Jönsson et al. 2013), and to assess the effect of different management strategies (Valosaari et al. 2008). CLIMEX was one of the first modeling tools used to determine the risks associated with the distribution of CPB in Europe (Sutherst et al. 1991, Baker et al. 2000, Rafoss & Saethre 2003, Kocmankova et al. 2010, Kocmankova et al. 2011), along with phenological models based on daily temperature to project the risk of northward spread of the CPB under climate change (Jarvis & Baker 2001, Ooperi & Jolma 2009, Jönsson et al. 2013).

The quality of climate impact model projections is influenced by the choice of climate data, as climate model data are associated with uncertainties. The genuine (non-reducible) uncertainties about the future global development are represented by different emission scenarios (Nakicenovic & Swart 2000). Knowledge gaps create uncertainties in model parameterizations, and failure to represent important processes can cause model biases. The performance of both global climate models (GCM) (Deque et al. 2012) and regional climate models (RCM) used for downscaling of GCM data (Fowler et al. 2007) are influenced by these kinds of uncertainties (epistemic), which are propagated onto the impact model simulations. An ensemble approach, using data from more than one climate model, has been suggested as a suitable measure to reduce the epistemic uncertainty (van der Linden & Mitchell 2009). The recommendation from the EU-FP7 research project ENSEMBLES was to focus on RCM simulations, rather than GCMs or emission scenarios, up to about the year 2050, since the differences in projected temperature increase are relatively small among the scenarios (van der Linden & Mitchell 2009).

The aim of this study was to assess the impact of a warmer climate on the potential distribution of CPBs in Europe. The analysis focuses on the Scandinavian countries, a region that does not host a permanent population and in which the current climate conditions do not allow for completed development of one generation in all years. Temperature data for 1961–2050 from 4 RCMs and gridded observed data for 1961–1990 (reference period) were used for model calculations. We simulated the earliest timing of completed development of the first and second generations of the CPB, and assessed the geographical and inter-annual variation in the occurrence of 0, 1 and 2 generations per year. The performance of the 4 ensemble members were evaluated at both regional and local scales, and compared with observed climate data to assess the uncertainties in the estimation of the frequency of the first and second generations in northern Europe.

### 2. METHODS

#### 2.1. Climate data

Daily temperature time series from 4 RCMs were used in this study as input to the CPB model runs for the period 1961–2050. The RCMs (RCA3, HIRHAM, RACMO and REMO; Table 1) had all been forced by one global climate model (ECHAM5-r3), representing the A1b emission scenario (Nakicenovic & Swart 2000). All 4 climate model runs using the rotated ENSEMBLES projection with a spatial resolution of 0.22 × 0.22° (approximately 25 × 25 km) that are available

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<tr>
<td>RCA3_Echam5_A1b</td>
<td>SMHI (Swedish Meteorological and Hydrological Institute)</td>
<td>Kjellström et al. (2005)</td>
<td>CPB_SMHI</td>
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<td>RACMO_Echam5_A1b</td>
<td>KNMI (Royal Netherlands Meteorological Institute)</td>
<td>van Meijgaard et al. (2008)</td>
<td>CPB_KNMI</td>
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<td>REMO_Echam5_A1b</td>
<td>MPI (Max-Planck Meteorological Institute)</td>
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<td>CPB_MPI</td>
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<td>DMI-HIRHAM_Echam5_A1b</td>
<td>DMI (Danish Meteorological Institute)</td>
<td>Christensen et al. (1996)</td>
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from the EU-FP7 research project ENSEMBLES were selected in order to assess variations across different models within the northern European region. The resulting impact model runs were denoted CPB_SMHI, CPB_DMI, CPB_KNMI and CPB_MPI (Table 1).

For evaluation of model performance, we used E-OBS gridded observed temperature data (version 8) with a daily time step and the same spatial resolution as the climate model data (Haylock et al. 2008). The impact model run driven by this data set, covering the control period 1961–1990, was denoted CPB_EOBS. Daily mean temperature and daily maximum temperature were extracted from all climate data sets, and used as input to the CPB model.

2.2. CPB model

A CPB model, driven by gridded temperature data with a daily temporal resolution, has been developed to analyze the climate change impact on the potential number of generations of the CPB (Jönsson et al. 2013). The model uses the daily mean temperature to calculate thermal sums, expressed as degree-days above a thermal threshold (DD) to calculate the CPB phenology. In a population of CPBs, individual variations in the thermal requirements can be found (Boman et al. 2008). Uncertainties associated with model parameterization were quantified in an earlier study (Jönsson et al. 2013). In the present study, the CPB model simulation focuses on the individuals with a low developmental threshold and short developmental time, as those are the ones most likely to establish new populations further north, where the climate is colder (Jönsson et al. 2013). The model developmental temperature threshold was set to +10°C, for calculating the following temperature sums: (1) 60DD for emergence from winter hibernation, starting from 1st January (Ferro et al. 1999), (2) an additional 51DD is required for feeding, mating, and egg laying, with flight initiation for dispersal set to a maximum temperature of 2±15°C (De Kort 1990, Alyokhin & Ferro 1999), and (3) 300DD development from egg to mature beetle, corresponding to the earliest developed individuals (Boman et al. 2008).

The model calculates one grid cell at a time. When the model has registered the day number for completed development of one generation (step 3), the model continues by checking whether the day length conditions for the initiation of reproductive diapause and winter hibernation are met. If so, the model ends the current year calculations, and continues with step 1 for the next year. If not, the model continues with steps 2 and 3 for the next generation. When a generation was initiated but not completed, the date of completed development was set to ‘not a number’.

The day-length threshold for triggering diapause is only known for a few European CPB populations (Sutherst et al. 1991, Kocmankova et al. 2011), and the CPB model has been developed to account for natural selection caused by regional climate conditions (Jönsson et al. 2013). The CPB model was parameterized according to the hypothesis that cold years leave footprints in the population genetics, as individuals with a too-short triggering day length will reproduce in autumn but fail to produce viable offspring as only mature beetles survive winter. The model-generated thresholds for diapause induction, based on grid-cell-specific 30 yr climatology, correspond approximately to 12 h in southern Europe, 15 h in mid-Europe and 18 h at the northern distribution limit (Jönsson et al. 2013). These values correspond to values reported from experimental studies, including beetles from the Netherlands (mid-parts, 15 h) (de Wilde et al. 1959), and beetles from a northern marginal (18 h) and a southern European (12 h) population (Lehmann et al. 2012).

2.3. Analyses of the CPB model simulation

Data from the 4 CPB model simulations were divided into three 30 yr time periods: 1961–1990 (control period), 1991–2020 (current conditions), and 2021–2050 (near future). In a first step, the number of years with completed development of 1 and 2 generations was summarized for each grid cell and time period. An ensemble average (CPB_AVG) was calculated as the average of CPB_SMHI + CPB_DMI + CPB_KNMI + CPB_MPI, excluding missing values. The performance of the CPB_AVG1961–1990 was evaluated by comparison with CPB_EOBS. The climate change signal was evaluated by comparing CPB_AVG1961–1990, CPB_AVG1991–2020, and CPB_AVG2021–2050.

In a second step, the performance of the individual ensemble members was compared to assess regional variations in number of years with 0, 1 or 2 generations caused by uncertainties in climate model data. To account also for the model-specific biases in timing of completed development, 6 grid cells were selected in different European agro-climatic zones (Bouma 2005; Fig. 1). Three grid cells were chosen in the Maritime zone (one each in the Netherlands, Denmark and Sweden), along with one grid cell in the North-East zone (Poland). In addition, 2 grid cells were selected in eastern and southern Europe, where the
climate is warmer and the beetle can produce 2−3 generations per year (Sutherst et al. 1991, Kocmankova et al. 2010, Kocmankova et al. 2011), one in the Central zone (Romania), and one in the Mediterranean zone (Italy). To evaluate the inter-annual variability in timing of completed development of the first generation, the 10th percentile (warm years), median, and 90th percentile (cold years) were calculated for each site and time period. Additionally, the transient model simulations were compared for all sites and ensemble members to visualize the inter-annual consistency in model biases. Finally, we used the CPB_EOBS simulation for Poland, Denmark, and southern Sweden to evaluate the model performance in relation to observations of CPB activity in southern Scandinavia during 1961−1990.

3. RESULTS

3.1. Number of years with 1 and 2 generations

3.1.1. CPB_EOBS

According to the CPB_EOBS simulation, the temperature conditions in southern and central Europe allowed for the completed development of at least one generation of CPB per year in 1961−1990 (Fig. 2A). Further north, in the region that currently does not host a permanent population, some of the years were too cold to sustain the development from egg to adult insect. This transient zone occurred approximately at latitudes between 55 and 65°N in the western, maritime part of Europe and at latitudes above 60°N in the region east of the Baltic Sea, which has a more continental climate. The CPB_EOBS simulation also indicated that at least 2 generations could develop in warm years in the region that currently hosts a permanent population (Fig. 2B).

3.1.2. Ensemble average

The CPB_AVG ensemble, representing the average of 4 CPB model runs driven by data from different RCMs, projected a geographical pattern for 1961−1990 that was similar to that of CPB_EOBS. Some regional differences can, however, be detected by visual comparison. In the region east of the Baltic Sea, the transient zone with 0 to 1 generation per year was estimated by the ensemble approximately 5° further south (Fig. 2A). The CPB_AVG also indicated a more general occurrence of at least 2 generations per year in lowland regions at latitudes below

Fig. 1. The 6 grid cells used in this study to analyze model biases in timing of completed development of the first and second generations of the Colorado potato beetle during 1961–2050
50°N, and the border between bivoltinism and monovoltinism around 53°N was more distinct than in CPB_EOBS (Fig. 2B). The future projections of the CPB_AVG ensemble indicated a gradual increase in bivoltinism for the periods of 1991–2020 and 2021–2050, but not any pronounced shift towards the north. The occurrence of monovoltinism was also projected to increase in the transient zone. Single years allowing for the development of one generation will occur 2–3° further north in 2021–2050.

3.1.3. Individual ensemble members

The geographical extension of the transient zone varied between the 4 individual ensemble members, due to differences in the model description of regional climate conditions in the Scandinavian countries and in northern Russia (Fig. S1 in the supplement at www.int-res.com/articles/suppl/c062p015_supp.pdf). CPB_DMI was the coldest ensemble member (at least for this region), and CPB_SMHI was the warmest, closely followed by CPB_KNMI and CPB_MPI. That is, CPB_DMI indicated that the temperature conditions for one generation were fulfilled in less than 10 yr in Denmark during 1961–1990, and not at all in the other Scandinavian countries. CPB_SMHI, in contrast, indicated a potential for successful reproduction during all years in Denmark and the coastal regions of southern Sweden, and for some years in southern Finland and southern Sweden. The differences among the individual ensemble members persisted in the simulations of 1991–2020 and 2021–2050, e.g. CPB_DMI indicated that very few years would be suitable for the CPB in southern Sweden and southern Finland, whereas CPB_SMHI indicated that most years would allow for the development of one generation in this region. The differences between ensemble members in model estimates of the border between bivoltinism and monovoltinism, varying between 50 and 55°N, were much less pronounced (Fig. S2 in the supplement).

3.2. Site-specific timing

3.2.1. Completed development of the first generation

The calculated, site-specific timing of completed development of the first generation varied between model simulations. In Denmark, a first generation

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<td>Second Generation (B)</td>
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Fig. 2. Number of years when the temperature requirement for completed development of (A) 1 and (B) 2 generations of *Leptinotarsa decemlineata* are fulfilled according to a model simulation with gridded observed climate data (CPB_EOBS) and an impact model ensemble (CPB_AVG) comprising 4 runs with input data from different regional climate models (Table 1).
could reach the adult stage in warm years, mainly during July and August according to CPB_SMHI, CPB_KNMI and CPB_MPI, whereas the CPB_DMI simulation indicated a later timing (Fig. 3A). In general, the CPB_DMI simulation resulted in much lower frequency of completed development than the other ensemble members. The CPB_SMHI, CPB_KNMI and CPB_MPI simulations indicated a substantial shift in timing of the completed development between 1961–1990 and 1991–2020. This was particularly pronounced in the relatively cold years, responding to the 90th percentile, indicating a shift in time from the end of October to the end of August.

In mid-Sweden, most of the years will be too cold according to all CPB model runs. However, a first generation could reach the adult stage in warm years, mainly during August and September (Fig. 3B). The estimated timing in 1991–2020 was 1–2 weeks later compared with the other 2 periods. That is, the impact of a gradually warmer climate will first be detected as an increased number of years with completed development late in the season. With an additional temperature increase, a shift towards an earlier date of completed development can be expected.

For the Netherlands, the ensemble members generally projected a few days earlier date of completed development in response to a warmer climate, corresponding to a shift from the end of July to mid-July (Fig. 3C). The 90th percentile of the CPB_DMI model simulation provided an exception, with later dates in 2021–2050. All ensemble members indicated a general trend towards earlier timing in Poland, Italy, and Romania, from mid-July to the end of June (Fig. 3D–F).

A comparison with CPB_EOBS indicated a cold bias for all 4 CPB_SMHI, CPB_DMI, CPB_KNMI and CPB_MPI simulations in Sweden and Denmark, and for CPB_DMI in the Netherlands (Fig. 3). All model runs were close to that of CPB_EOBS in Poland, with a tendency to overestimate the effect of warm years. All ensemble members indicated a warm bias in Romania. For the Italian grid cell, CPB_SMHI had a cold bias, whereas CPB_MPI and CPB_DMI overestimated the effect of warm years. For the individual sites, the ensemble members were consistent over time in projecting a relatively early or late timing of completed development (Fig. S3 in the supplement). The inter-annual variation was consistent among the model runs, since all RCMs had been forced by data from the same GCM. For individual years, however, the CPB_DMI often indicated a late timing when the

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Fig. 3. Model calculations of completed development of the first generation of *Leptinotarsa decemlineata*, from egg to mature insect, are influenced by the choice of climate model data. The subplots, representing 6 regions with different agro-climatic conditions (Fig. 1), show the results from 4 Colorado potato beetle (CPB) model runs driven by different regional climate model climate data sets. Each line contains information for 3 time periods: (P1) 1961–1990, (P2) 1991–2020 and (P3) 2021–2050. The climate change signal can be interpreted from the slope of the lines. For each model run, the thicker solid lines represent average conditions. The thin solid lines represent the 10% warmest years (lower lines, earlier timing) and the 10% coldest years (upper lines, later timing). Missing lines correspond to cold years, not sustaining the completed development of one generation. The horizontal dotted lines show the corresponding values calculated by CPB_EOBS (1961–1990), and model biases are depicted as deviations from these lines.
other models indicated an early timing, and vice versa. The CPB_EOBS simulation was used to illustrate the development of the CPB from initiation of the first generation to completed first and second generation in Denmark, southern Sweden, and Poland for the period 1961−1990 (Fig. 4). The thermal conditions for initiation of the first generation were often fulfilled a few days earlier in Poland than at the Swedish and Danish sites. The timing of the completed development of the first generation showed a similar tendency. In Sweden and Denmark, the temperature requirements for development of the first generation were fulfilled before September when the initiation was completed before July. A cold year (e.g. 1962) with late initiation of the first generation increases the probability of unsuccessful regeneration, i.e. the new generation does not reach maturity before winter. In Poland, early onset of spring activity in combination with warm summer weather allowed the CPB to produce a second generation in some years, whereas this was not the case in Denmark or Sweden.

4. DISCUSSION

Ongoing climate change will have consequences for the agricultural sector, affecting both the regional production capacity and the risk of damage to production. A warmer climate will lead to a longer growing season, which can have a positive effect on crop production, particularly in northern Europe (Olesen et al. 2011). Many insect pests will, however, also be favoured in this region, since global warming stimulates northward migration (Bebber et al. 2013). This will lead to an increased risk of production losses caused by insect attacks, eventually leading to higher costs of countermeasures (Roos et al. 2011). The CPB is currently listed as a quarantine species in the Scandinavian countries, i.e. it should be prevented from establishing a viable population (EPPO 2013). In this study we compared the future period 2020−2050 with 1961−1990, and the model simulations indicated a substantial increase in the occurrence of years in which the temperature requirement for the development of one generation will be fulfilled at the current northern distribution limit.

An ensemble approach has been put forward as a way of handling the uncertainty associated with climate modeling that is inherent in climate change impact studies (Taylor et al. 2012). The basic idea is that some models produce overestimates while others produce underestimates, and all models are ultimately wrong (Gleckler et al. 2008). By capturing different parts of reality, however, the average performance of several models represent the true conditions better than any individual ensemble member (van der Linden & Mitchell 2009). The final size of an ensemble is commonly determined by the availability of potential ensemble members and the computing time of the impact model. In this study we used
an ensemble based on 4 members to quantify uncertainties associated with model projections of regional climate conditions. Being interested in the temperature conditions promoting a northward establishment of the CPB, we selected climate data with a relatively high spatial resolution, i.e. a grid of 0.22 degrees instead of 0.44 degrees, which has been more commonly used. Since the study focused on the near future up to 2050, the ensemble was selected to quantify the variation in dynamic downscaling among RCMs, instead of the variation between GCMs or emission scenarios (van der Linden & Mitchell 2009). The DMI and SMHI data sets had a cold bias, approximately 1.5°C for 1961–1990 in comparison with observed temperature data for Scandinavian regions (van der Linden & Mitchell 2009). KNMI and MPI were approximately 0.5°C warmer than the E-OBS data for the same period. This is in line with our findings when evaluating the impact model runs. We did not employ any bias correction method, due to difficulties in assessing the outcome in terms of uncertainty reduction (Ehret et al. 2012).

Climate change projections based on insect phenomenology models are useful for the planning of adaptive measures, but a discussion on how to handle model uncertainties is needed. When working with impact models, such as the CPB model, the uncertainties are highly dependent on the species-specific requirements (Porter et al. 1991, Boman et al. 2008, Jönsson et al. 2013, Kiritani 2013). This was also found in the present study, shown as a large variation among ensemble members in projecting the geographical extension of the transient zone with 0 to 1 generation per year. Since these regions would benefit from having relevant climate information to support eradication strategies and control measures, the uncertainties associated with impact modeling and the use of climate scenario data must be handled. One way is to rely more on the ensemble average than the individual ensemble members. Another approach would be to rely more on the ensemble member showing the earliest date of completed CPB development (Figs. S1 & S2 in the supplement), in order to develop more precautionary strategies.

The CPB model was parameterised to simulate the earliest timing of completed development of the first and second generations, i.e. with the precautionary principle in mind. However, due to local climate conditions, not all CPBs in a local population will reach maturity at the same time. In addition, natural selection will influence the population characteristics over time, a process that is particularly pronounced in marginal populations. That is, the parameter settings used in this study represent the CPB population at latitudes of approximately 50–55°N, but the model assumptions may not hold true for newly established populations in Scandinavia as northward migration has been shown to alter the thermal adaptation of the CPB (Boman et al. 2008, Lytinen et al. 2009, Lytinen et al. 2012). Also, the regulation of diapause is under strong selection in northern boundary populations, as they face a shorter summer season and have to respond to cues from longer days to prepare for the cold season. However, the selection pressure on already established populations, for instance in mid Europe, may change in response to a gradually warmer climate, favouring migrating individuals with a lower threshold of day length response (Jönsson et al. 2013).

Policies on how to handle invasive insect pests may have to be adjusted in response to climate change, as methods that are suitable today may become less effective in a warmer climate (Carrasco et al. 2010). Regions in which the CPB is already established will experience an increased frequency of 2 generations in response to a warmer climate, and this may enhance the northward migration. The CPB_EOBS simulation indicated that the years with an invasion of CPB from northern Poland to southern Sweden and Denmark, i.e. 1972 and 1983, were the third warm years in a row (Fig. 4). In 1970–1972 and 1981–1983, the temperature conditions for completed development of 2 generations were fulfilled in Poland, which most likely had a positive effect on the CPB population size (Piekarczyk & Lipa 1985). The occurrence of strong southeasterly winds at the timing of flight activity was a triggering factor for the mass migration (Gransbo 1980). In contrast, years with a substantial decrease in CPB in southern Sweden (1974 and 1984) were colder than normal, which may have hampered the development of the first generation. Since 1979, more intense control measures have been implemented in Poland (Pruszynski & Wegorek 1991), and no mass invasion of CPB has been reported in Sweden or Denmark after 1983. The Baltic Sea acts as a dispersal barrier for southern Sweden, and in this region the migration may depend on southeasterly winds. The ongoing northward migration in Finland (EVIRA 2014) is, however, most likely influenced by other meta-population processes, as the CPB is established in neighboring countries. A colder climate provides protection, but temperature conditions for completed development of at least one generation may not have to be fulfilled in all years since the CPB can survive in a dormant stage for more than 1 yr (Tauber & Tauber 2002). However, the
potato can grow at temperatures above +2°C (Koo- 
man & Haverkort 1995) whereas the CPB is active at 
temperatures above +10°C. At the northern distribu-
tion limit, the main period of CPB activity will there-
fore occur rather late in the potato-growing season. 
The model simulations indicate initiation of the first 
generation around midsummer, at a time when the 
early potato varieties are harvested in Scandinavia. The CPB may therefore become less harmful in this 
region than further south, at least initially.

5. CONCLUSIONS

This study indicated a shift in the northern limit for 
potential establishment of a permanent CPB popu-
lation by 2020−2050 in comparison with 1961−1990, 
and the simulations showed a substantial increase in 
the frequency of years in which the temperature 
requirement for the development of one generation 
was fulfilled in the southern part of Scandinavia. In 
addition, 2 generations per year may occur more fre-
quently at the current distribution border, increasing 
the risk of northward migration to the Scandinavian 
countries. The geographical extension of the tran-
sient zone with 0 to 1 generation per year varied 
among ensemble members, and a common way to 
handle uncertainties associated with the use of clima-
te model data is to rely more on the ensemble 
average than on individual ensemble members. 
However, a more precautionary strategy, required 
for policy development when the stakes are high, 
would be to rely more on the ensemble member 
showing the worst outcome.

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LITERATURE CITED

Alyokhin AV, Ferro DN (1999) Reproduction and dispersal of 
summer-generation Colorado potato beetle (Coleoptera: 
Chrysomelidae). Environ Entomol 28:425−430

beetle resistance to insecticides. Am J Potato Res 85:395−413

Baker RHA, Sansford CE, Jarvis CH, Cannon RJC, MacLeod A, Walters KFA (2000) The role of climatic mapping in 
predicting the potential geographical distribution of non-
indigenous pests under current and future climates. Agric Ecosyst Environ 82:57−71

Bebber DP, Ramotowski MAT, Gurr SJ (2013) Crop pests 
and pathogens move polewards in a warming world. Nat 
Clim Change 3:985−988

siveness: geographic and genetic variation in life-history 
traits. Biol Invasions 10:1135−1143

Bouman ER (2005) Development of comparable agroclimatic 
zones. OEPP/EPPO Bull 35:233−238

Carrasco LR, Baker R, MacLeod A, Knight JD, Mumford JD 
(2010) Optimal and robust control of invasive alien 
species spreading in homogeneous landscapes. J R Soc 
Interface 7:529−540

Christensen JH, Christensen OB, Lopez P, van Meijgaard E, 
Botzet M (1996) The HIRHAM4 regional atmospheric clima-
tic model. Danish Meteorologica Institute Scientific 
Report 96−4, DMI, Copenhagen

De Kort CAD (1990) 35 years of diapause research with the 
Colorado potato beetle. Entomol Exp Appl 56:1−13

de Wilde J, Duinjtjer C, Mook L (1959) Physiology of dia-
pause in the adult Colorado beetle (Leptinotarsa decem-
lineata Say). I. The photoperiod as a controlling factor. 
J Insect Physiol 3:73−85

Deque M, Somot S, Sanchez-Gomez E, Goodess CM, Jacob 
amongst ENSEMBLES regional scenarios: regional cli-
mate models, driving general circulation models and 
interannual variability. Clim Dyn 38:951−964

Ehret U, Zehe E, Wulfmeyer V, Warrach-Sagi K, Liebert J 
(2012) Should we apply bias correction to global and 
regional climate model data? Hydrol Earth Syst Sci 16: 
3391−3404

EPPO (European and Mediterranean Plant Projection Organiza-
tion) (2013) Leptinotarsa decemlineata - EPPO A2 list 
of pests recommended for regulation as quarantine pests. 
www.epppo.int/QUARANTINE/listA2.htm (Accessed 20 
September 2013)

EVIRA (Finnish Food Safety Authority) (2014). Före kom sterna 
av koloradoskalbagge 2013. Available at www.evira.fi/
portal/se/vaxter/odling+och+produktion/vaxtsjukdomar+och+
skadedjur/farlaga+vaxtsjukdomar+och+skadedjur/
koloradoskalbagge/förekomster+2013/ (Accessed on 10 
February 2014)

pose serious threat to crop pest management: a critical 
paper-1112/ijsrp-p1109.pdf

potato beetle (Coleoptera, Chrysomelidae) temperature-
dependent growth and feeding rates. Environ Entomol 
14:343−348

Ferro DN, Alyokhin AV, Tobin DB (1999) Reproductive sta-
tus and flight activity of the overwintered Colorado 
potato beetle. Entomol Exp Appl 91:443−448

change modelling to impacts studies: recent advances in 
downscaling techniques for hydrological modelling. Int J 
Climatol 27:1547−1578

metrics for climate models. J Geophys Res D Atmos-
pheres 113:D06104, doi:10.1029/2007JD008972

Gransbo G (2010) Optimal and robust control of invasive alien 
species spreading in homogeneous landscapes. J R Soc 
Interface 7:529−540

Gripwall U (1993) Koloradoskalbaggen. Faktablad om växt-
skydd, jordbruk 37J Sveriges Lantbruksuniversitet, 
Uppsala
Kjellström E, Bärring L, Gollvik S, Hansson U and others (2005) A 140-year simulation of European climate with the new version of the Rossby Centre regional atmospheric climate model (RCA3). Reports Meteorology and Climatology No.108. SMHI, Norrköping

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