universität wien

DIPLOMARBEIT

Titel der Diplomarbeit

Modelling of population dynamics of the green oak leaf roller (*Tortrix viridana*) within oak-populations

angestrebter akademischer Grad

Magister der Naturwissenschaften (Mag. rer.nat.)

Verfasser:	Stefan Kapeller
Matrikelnummer:	0007453
Studienrichtung:	Zoologie (A439)
Betreuer:	Univ.-Prof. Mag. Dr. Konrad Fiedler

Wien, März 2009

This diploma thesis was performed at the

Federal Research and Training Centre
for Forests, Natural Hazards and Landscape

and was supervised by

Dr. Silvio Schüler

Abstract

The green oak leaf roller (*Tortrix viridana* L.) is a pest moth species in Central Europe which can cause complete defoliation of oaks during outbreaks. The present study used a spatiotemporally discrete simulation model to investigate and understand the population dynamics of the green oak leaf roller and the interaction with host trees of different qualities. Particularly, effects of dispersal range, tree-dependent mortality and tree preferences in oviposition were analysed. Therefore, a population equation of the Witting type, which allows creating realistic population cycles, was implemented in a spatiotemporal computer model (cellular automaton). For model parameterisation empirical data of a 30-year monitoring in Tellerman oak grove (Central Black Soil region in the European part of Russia) were used.

Variation of dispersal range had almost no effect on the population dynamics, whereas overall mortality had a great influence. High mortality lowers the population density and can lead to a selection pressure, which favours individuals with higher growth rate. The increasing population growth rate can not only compensate for the population decrease caused by mortality, but can even overcompensate it. Hence, in further consequence a high mortality can lead to higher average moth population levels through selection for population growth rate increase.

Keywords

green oak leaf roller, *Tortrix viridana*, population cycles, ecological modelling, herbivore-host interactions

Summary in German

Der grüne Eichenwickler (*Tortrix viridana* L.) ist ein wichtiger Forstschädling in europäischen Eichenwäldern. Aber nicht jeder Eichenbaum scheint gleichermaßen als Futterpflanze geeignet zu sein. Eichen unterscheiden sich zwischenartlich wie auch innerartlich genetisch hinsichtlich des Austriebszeitpunkts oder auch der inhaltsstofflichen Zusammensetzung. Um die Auswirkungen der qualitativen Zusammensetzung eines Eichenwaldes auf die Populationsdynamik des Eichenwicklers zu untersuchen, wurde ein räumlich-

zeitliches Simulationsmodell erstellt. Dieses Modell, basierend auf der Annahme dichteabhängiger Wachstumsraten und intraspezifischer Konkurrenz als wesentlichen Regulationsmechanismen, bildet realitätsnahe Populationsschwanken ab. Für die Parametrisierung des Modells wurden Daten einer 30-jährigen Freilandstudie herangezogen. Die computergestützte Modellierung ermöglichte die Durchführung zahlreicher Simulationsläufe mit variierenden Parametern. Insbesonders wurden Auswirkungen der Dispersalweite, baum-spezifischer Mortalität der Jugendstadien oder einer möglichen Eiablagepräferenz für bestimmte Baumtypen analysiert. Dabei erwies sich die Dispersionsdistanz als wenig bedeutsam, während hohe Mortalität (auf dem Umweg über eine Selektion für höhere Wachstumsraten) zumindest im Modell sogar zu stärkerem Anwachsen der Population führen kann.

Introduction

Figure 1: *Tortrix viridana*, larvae of 5th instar (photo by Hilke Schröder)

The model species - population biology, ecological and economical relevance

The green oak leaf roller (*Tortrix viridana* L., Fig. 1) is a serious forest pest species on oaks in Central Europe. During mass outbreaks the larvae of this moth can cause complete defoliation (Gasow, 1925; Rubtsov and Utkina, 2003). Since oaks have a high ability to recover, trees are not actually killed, but still there are serious effects on the trees fitness. Defoliated trees are more susceptible for secondary pests and pathogens. As another consequence of defoliation, the wood increment decelerates with economical consequences for the tree stock in commercial forestry (Rubtsov and Utkina, 2003; Baltensweiler et al., 2008).

T. viridana has a strictly annual life cycle throughout its distributional range in the western Palaearctic region. The flight period of adult moths is in late spring and early summer from May to June. Eggs are laid in pairs on the bark of twigs and hatch the following spring. Larvae enter the swelling buds and grow quickly during the period when young foliage is available. The population dynamics of *T. viridana* is similar to that of many other temperate-zone forest insects with very pronounced cycles (Berryman, 1996). Mass outbreaks occur in a periodic sequence every six to eight years (Horstmann, 1984). Calamities are very well documented in Germany and occur in Austria as well (Schröder and Scholz, 2005).

T. viridana is an oligophagous insect, which is limited to larval hostplants in the genus

Quercus (Gasow, 1925; Hunter, 1990; Du Merle, 1999). Within this plant genus, the quality of trees as forage plants is varying. Following observations of Schröder (2008a) pedunculate oaks (*Quercus robur*) are more strongly damaged than sessile oaks (*Quercus petraea*). Variation of plant quality traits, including secondary chemistry, is not only confined to trees among different oak species, but has also been detected within species. This may have profound influence on its herbivore population dynamics (Larsson et al., 2000; Helms and Hunter, 2005). Timing of budburst for example, determines the susceptibility of an oak for larvae of *T. viridana*. A close coincidence between budburst and larval eclosion has been reported in many studies (Gasow, 1925; Thalenhorst, 1951; Schütte, 1957; Schwerdtfeger, 1971) and has been linked with the cyclic population dynamics (Hunter, 1992; Du Merle, 1999; Ivashov et al., 2002). There have been several suggestions that late-flowering oak trees show a lower susceptibility than early-flowering individuals. Generally, asynchrony with plant phenology has a large impact on the dynamics of forest Lepidoptera, particularly in species with limited mobility (Forkner et al., 2008). The progressing climate change might distort the matching between larval eclosion and the time of budbreak, and therefore influence the number and intensity of outbreaks of forest pests (Logan et al., 2003; Karolewski et al., 2007; Forkner et al., 2008).

As long as the parameters responsible for mass outbreaks are still poorly understood, it is impossible to make predictions about future occurrences and spatial dynamics of the calamities.

Ecological modelling

Empirical research of insect-tree interactions is time-consuming and expensive. For one thing oaks grow slowly and it takes a long time until several outbreaks of *T. viridana* can be recorded. For another it is very difficult to distinguish different environmental effects and intrinsic population characteristics from observational data alone. Hence, a population simulation model seems to be a promising approach to study general processes of population dynamics. Such models can help to understand the impact of specific parameters as well as their interaction and correlation. If succesful, models may provide land managers with a method of predicting possible responses of species to changes in regional management strategies (Dunning et al., 1995). Within a simulation, parameters can be adjusted at will and a great many runs can be conducted. Models with a very limited number of parameters (usually labelled as 'strategic models') do not aim to reproduce or predict a concrete field situation, but to estimate range limits of possible

consequences for a certain set of simple assumptions (Czaran, 1998). Therefore, strategic models are helpful to understand the interaction of the chosen parameters, because unlike in real field situations the confounding influence of background variables can be left out.

Aims of this study

For a better insight into the interplay of some basic intrinsic and extrinsic parameters a spatiotemporal model was developed using a cellular automaton approach. This model was first used to rebuild the population dynamic of *T. viridana* as observed by Rubtsov (2003). Several simulation runs with varying parameters were then conducted to study the relation of early stage mortality, susceptibility of different oak species, preferences in oviposition and dispersal range. Specifically, the following questions will be addressed:

- Which parameters return a realistic dynamic behaviour?
- How does mortality influence the population dynamics?
- How does the composition of the forest regarding the tree quality influence moth population dynamics?
- How does a preference in oviposition influence the population dynamics?
- How does a variation of the dispersal range influence the population dynamics?

Methods

The cellular automaton for the simulations was developed with Delphi (CodeGear Delphi 2007), an object-orientated programming language. A regular lattice of cells represents a square-shaped forest of variable dimension with each cell standing for a tree. To avoid edge effects opposite edges are merged to a torus. At every discrete time t every cell has its own state configuration of variables, like moth abundance (N_t), moth abundance of the previous year (N_{t-1}), growth rate of this cells (trees) moth population (λ) or infestation from neighbourhood. The state of these variables in the next time unit (N_{t+1}) is determined by the state configuration of the neighbourhood cells (including the focal cell itself) and the model equation for population growth. Thus, every model run is a deterministic process and the output is completely depending from the initial state configuration.

The model

The underlying model equations define the model behaviour and the population dynamics. A well-known equation based on the concept of over-compensatory dynamics was formulated by Hassell (1976):

$$N_{t+1} = \lambda N_t (1 + aN_t)^{-\beta} \tag{1}$$

where N and N_{t+1} are the populations in successive discrete generations, λ is the finite net rate of population increase and a and β are constants defining the density dependent feedback term.

This equation, which can be found in almost any textbook on population ecology, is frequently used for modelling population dynamics of insects with discrete generations. However, over-compensation cannot explain cyclic dynamics with periods of more than two generations (Turchin and Taylor, 1992; Ginzburg and Taneyhill, 1994; Witting, 2000). Thus, another approach, allowing periods of more than two generations has been proposed by Witting (2000). He assumes selection pressures operating on density-dependent competitive interactions as ultimate reason for population cycles. These changes are either based on evolutionary changes in genotype frequencies or on phenotypic plasticity. Witting deduced a mathematical equation, which describes a realistic model behaviour. The basic idea behind this equation is that there is no constant reproduction rate, but a

variable, density-dependent population growth rate λ. High population density favours competitive traits and a low population growth rate, whereas a low population density causes a high growth rate, due to a higher environmental capacity and a shift to increased reproductive output. Mathematically, the dynamic population growth rate λ depends on the population abundance of the previous year N_{t-1}, the parameter γ, which defines the curvature of the density regulation function, and the additive genetic variance σ^2, which denotes the potential response of the growth rate to selection (see equations 2 and 3).

$$\lambda_t = \lambda_{t-1} N_{t-1}^{-\gamma} e^{\sigma^2} \tag{2}$$

The number of individuals can then be calculated as

$$N_{t+1} = N_t \lambda_t N_t^{-\gamma} \tag{3}$$

It is evident from equations (2) and (3) that the number of individuals N_{t+1} does not only depend on N_t but also on N_{t-1}.

Parameterisation

The operating population units in the model are cells (viz. trees). Therefore, it was necessary to find the order of magnitude of individual numbers for these subpopulations. Observations from own feeding experiments with *T. viridana* larvae were used for an estimate as to how many larvae can live per tree. These experiments were conducted in cooperation with Dr. Hilke Schröder (Federal Research Centre for Forestry and Forest Products, Großhansdorf, Germany) and aimed to estimate the number of larvae needed to cause complete defoliation of an average-sized oak tree. The number of leaves on trees is of course also variable, but based on Cecich and Larsen (1997) and own estimations, we proceeded with the assumption of 100 000 leaves per tree. Our feeding experiments showed that the amount of food, which is necessary for larval development, can vary a lot, but on average, one larva needs seven oak leaves until pupation (see Appendix). This reveals that there must be at least 14 000 foraging larvae on an average-sized oak tree for complete defoliation.

For the parameterisation empirical data from a 30-years monitoring provided by Rubtsov

and Utkina (2003) were used (Fig. 2). Rubtsov specified the moth density in his study as 'eggs per meter of branch'. However, the presented model is operating with 'individuals per tree' and therefore data had to be transformed, because the intrinsic forces on which Witting's paper (Witting, 2000) is based are expected to act at least on the level of a population of a complete tree. Rubtsov observed that complete defoliation can occur at

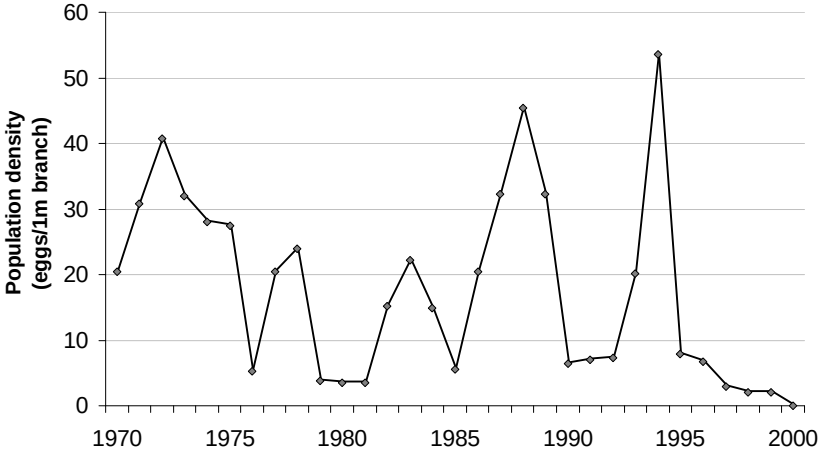

Figure 2: Population density in eggs per m branchlength. Data from a 30-years monitoring conducted at Tellerman oak grove (Voronezh oblast, Central Black Soil region of Russia) by Rubtsov and Utkina (2003) - modified. Peaks of outbreaks are very distinct and occur in consistent periods.

T. viridana densities of 40 eggs/m branchlength (Rubtsov 2003, p. 95, Fig. 5). Thus, we concluded that an egg density of $40m^{-1}$ is equivalent to 14 000 larval individuals per tree. For parameterisation Rubtsov's data were multiplied with $\frac{14\,000}{40} = 350$ in order to transform the data to 'individual per tree'-numbers.

For parameterisation of σ^2 and γ, empirical data were analysed by non-linear regression, as proposed by Witting (2000). Rubtsov conducted his studies on two separate sites (here referred as Series A and Series B). Data series from each site were used for several parameter estimation runs, both with the egg-density values and the transformed individual values (Table 2). Series B was analysed a second time (Series B*) with exclusion of the year 1999, when a very low density was observed.

Implementation of Witting's model

In order to implement Wittings equation for the population dynamics in a spatiotemporal model, three additional procedures were added: (I) Dispersal and calculation of N_{t-1}, (II) mortality (tree-dependent and tree-independent) and (III) tree preferences of

moths:

(I). Since the operating units of the chosen model are the cells and not single *T. viridana* individuals, a problem occurs when it comes to dispersal. The growth rate is a trait of the individual moth, but thinking of some hundred millions of moths flying around in a big forest, the calculation of the new density-dependent growth rate every year would demand formidable computer capacities and render a truly individual-based model impossible. Instead, the growth rate λ as well as N_{t-1} are stored for each cell. This approach is justified if assuming that the whole population on one tree is exposed to the same conditions and therefore will have (largely) equal characteristics. But since there is dispersal between trees, a population of one tree is actually a subpopulation in a metapopulation system. Therefore, the density (N_{t-1}) and the growth rate of each cell is calculated as the mean value of its neighbourhood cells. The number of neighbourhood cells to be considered depends on the dispersal range used in a particular model run. This approach allows the setup with variable dispersal range, and simultaneously the dispersal range also reflects the extent of genetic mixture. At the same time this way of calculating the growth rate is much faster than a truly individual approach.

All model runs were repeated with different dispersal distances ranging from one (dispersal only between neighbouring trees) to ten (also the tenth tree can be infested). Individuals are not distributed equally within the dispersal range. Disperser numbers are modelled as declining exponentially with the distance from the focus cell ('parent tree').

(II). In order to analyse the effects of different qualitative composition of forest, the introduction of another parameter was necessary. For this reason two types of 'mortality' were implemented. The 'tree-dependent mortality' could be individually regulated for two different types of cells: 'Quality A'-Trees and 'Quality B'-Trees. Quality means the susceptibility of the tree for larvae and affects the probability of survival during the larval stages. Another parameter, the 'tree-independent mortality' (overall mortality) regulates the mortality regardless of the qualitative type of the cell. It subsumes all other mortality agents, which do not depend on nutritional traits of the tree. This concerns mortality components during egg, pupal and adult life stages as well as other components, which do not dependent on tree quality, like predators or weather conditions. Each of these parameters may influence cyclic fluctuations of *T. viridana* populations profoundly, but are included in one term to keep the model simple and to get a clearer picture of the general role of mortality on population dynamics. Both types of mortality are in terms

of survival probability multiplied with the leaf roller abundance on every tree, before the next procedure of dispersal and the calculation of the growth function is applied. From a mathematical point of view, both types of mortality have the same effect on the population abundance, but they have been used in this study to analyse different aspects. The tree-independent mortality was used for analysing the general effect of mortality, irrespective of causal agents beyond the host plant. The tree-dependent mortality of 'Quality A'-Trees and 'Quality B'-Trees was used to analyse the effects of mixing different types of trees at the forest stand level. Therefore, these two types were randomly distributed within the simulated forest with varying proportions.

(III). To analyse effects of a possible oviposition preference, the parameter 'preference' had to be introduced. It allows to raise or lower the probability of dispersal to 'A'- or 'B'-trees. A preference of 1 means that all moths go on 'Quality A'-trees, whereas a preference value of 0 causes the opposite. The proportion of 'A'- and 'B'-trees in each dispersal-neighbourhood was also included in the calculation.

Simulation protocol

Table 1 gives an overview of all parameters and their values used in the presented simulation runs.

Table 1: Overview of all parameters, which were used for the simulation runs. 'Years'= timespan of a single run; 'Prop-B' = Proportion of 'Quality B'-trees; 'Pref-A' = Preference for 'Quality A'-trees (0 means high preference for B-trees, 0.5 means no preference, 1 means high preference for A-trees); 'Mort' = tree-independent mortality; 'Mort-B' = tree-dependent mortality on B-trees (0 means no mortality, 1 means high mortality on B-trees); 'Size' = Dimension of the simulated forest (number of trees/cells); 'Disp' = Dispersal range; 'γ' = period length; 'σ^2' = variation of growth rate; 'N_t' = initial number of individuals per tree in the year t=2; 'N_{t-1}' = initial number of individuals per tree in the year t=1

Altering parameters

	Years	**Prop-B**	**Pref-A**	**Mort**	**Mort-B**
Fig 3	31	0.5	0.5	0	0
Fig 4	20	0.5	0.5	0	0
Fig 5	200	0.5	0.5	0 - 1	0
Fig 6	30	0.5	0.5	0.2, 0.5, 0.8	0
Fig 7a	200	0.1	0.5	0	0 - 1
Fig 7b	200	0.5	0.5	0	0 - 1
Fig 7c	200	0.9	0.5	0	0 - 1
Fig 8a	200	0.1	0 - 1	0	0
Fig 8b	200	0.5	0 - 1	0	0
Fig 8c	200	0.9	0 - 1	0	0

Fixed parameters

Size	**Disp**	γ	σ^2	N_t	N_{t-1}
50x50	3	0.94	7.92	10805	7136

Results

Parameterisation

Estimations of the parameter γ, which affects the length of the period of population cycles, returned a value around 1 for series A and B* (1999 excluded) for parameter sets based on both egg density and individuals per tree (Table 2). In series B (without exclusion of the year 1999) γ is much lower (0.168). A low γ value returns a longer period length and would not create a realistic population cycle with the periodicity as known from the field (Fig. 3). Transformation of data did not affect the estimation results.

The estimations of the second parameter, the variation of the growth rate σ^2, showed very different results (between 0.04 and 8.3). A comparison with empirical data (Rubtsov and Utkina, 2003) revealed that a value of around eight returns a realistic amplitude of the model curve (Fig. 3).

Table 2: Results of different parameter estimation runs. Series A = floodplain oak stand; Series B = solonet oak stand; Series B* = data from site B but with year 1999 excluded. Data of each oak stand were analysed both with egg-density (eggs per meter of branch) and transformed to individuals per tree.

Series	based on	γ	σ^2
A	eggs	1.03	2.25
	individuals	1.03	8.29
B	eggs	0.17	0.04
	individuals	0.17	1.03
B*	eggs	0.94	2.4
	individuals	0.94	7.92

Taken together, the simulation of population cycles using the parameter estimates based on the data of series B* with individual numbers return a good approximation when compared with the empirical observations (Fig.3).

Model behaviour

A model run spanning 20 years is displayed in Figure 4. It shows the average abundance and the average population equilibrium of all trees. The population equilibrium is defined as $N^* = \sqrt[\gamma]{\lambda_m}$ (Witting, 2000). Therefore, the selection-induced changes in the growth

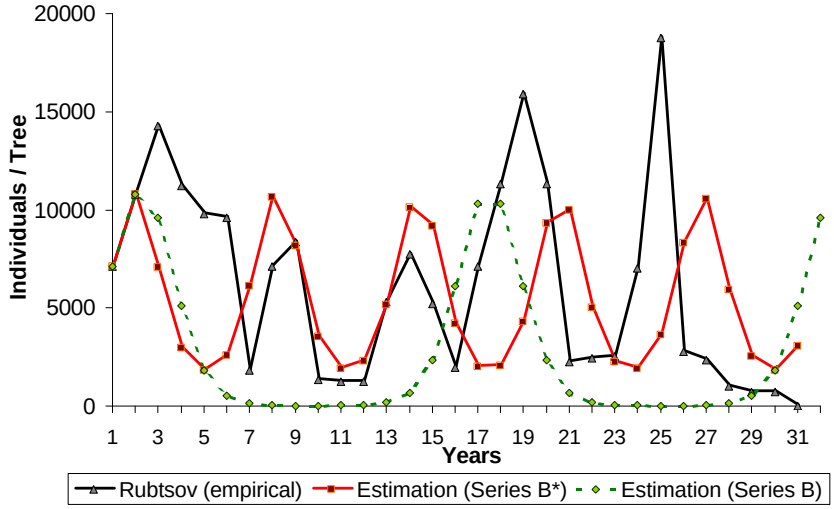

Figure 3: Simulation curve with parameters estimated from two datasets - Series B* ($\gamma = 0.94$ and $\sigma^2 = 7.92$) and Series B ($\gamma = 0.17$ and $\sigma^2 = 1.03$) - compared to empirical data from Rubtsov 2003.

rate λ are directly expressed in the cycle in the population equilibrium N^*. The population equilibrium is running synchronously one year in advance, while the abundance is following.

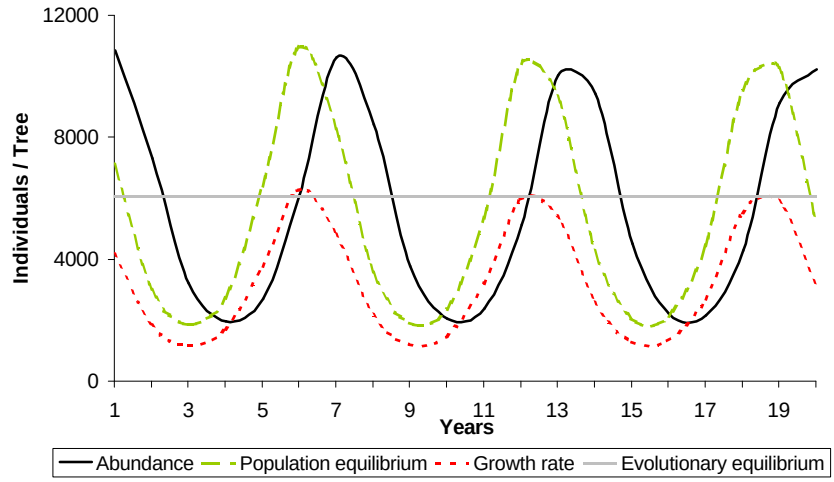

Figure 4: Average abundance and population equilibrium of a 20 year simulation run

A low population level induces a higher population growth rate. As a consequence the abundance increases until it reaches the level of the evolutionary equilibrium. This is the population level at the point of the highest population growth rate. If the population level is above the evolutionary equilibrium, the growth rate and thus the population equilibrium decrease again. Due to the model equations time delay, the population is still growing for one generation, but starts to decrease before reaching the peak level of the population

equilibrium. Hence, the curve of the population equilibrium has a larger amplitude than the curve of the abundance.

Figure 5 and 6 display the role of mortality for the population dynamics. An increasing overall mortality (due to parasites, predators or weather) induces an increase of the growth rate and can lead to a higher population level than in the absence of any mortality factors. High mortality reduces competitive interactions and favours selection for a high growth rate.

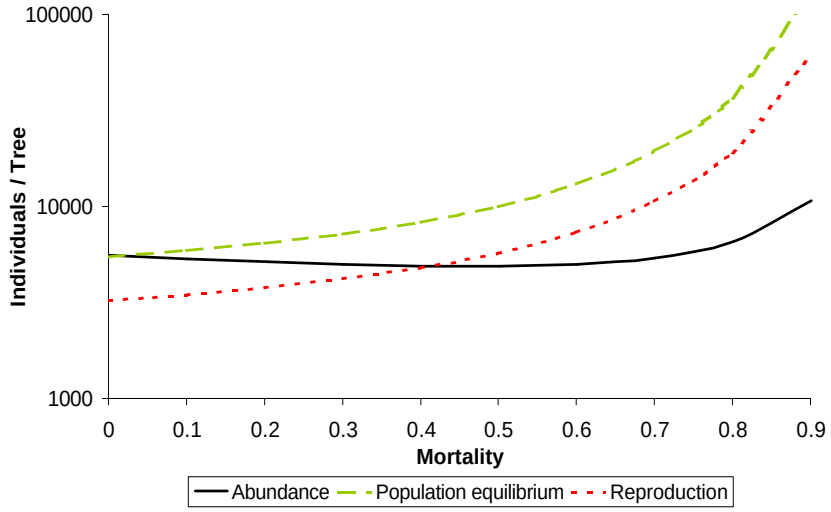

Figure 5: Average abundance, population equilibrium and population growth rate with increasing mortality on a logarithmic scale.

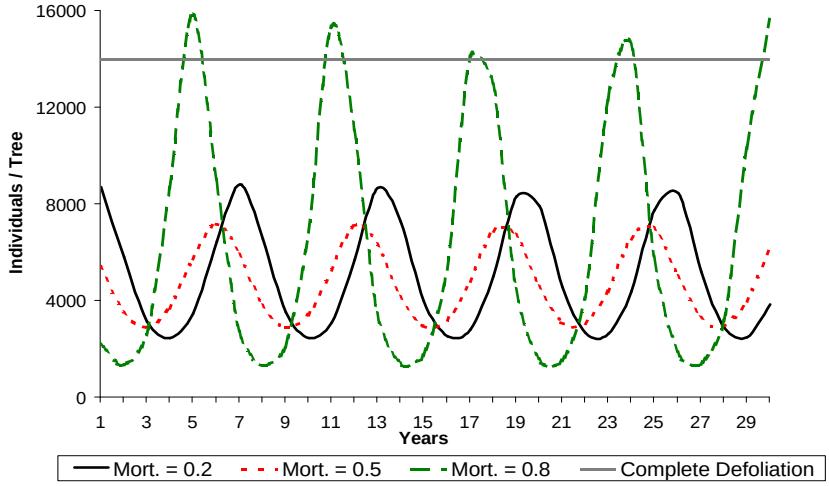

Figure 6: Average abundance of 30 year simulations with three levels of mortality. The horizontal line shows the population level at which complete defoliations can occur. Only a setup with high mortality (0.8 = 80% of larvae die) causes complete defoliations.

We find the lowest minimum and maximum abundances at a mortality of 0.5, which

means that 50% of individuals die during their development before they can reproduce. At this point the influence of the mortality is higher than the influence of the increased growth rate. But both effects are almost equal, since the population level is almost the same as with no mortality at all. Assuming a higher mortality, the effect of the raised growth rate counteracts the direct influence of the mortality. In our simulations, the level where complete defoliation occurs is only reached with a mortality higher than 0.8 (Fig. 6). However, high mortalities also increase the amplitude of population fluctuations, such that in the years between outbreaks abundances are particularly low.

Influence of dispersal range

All model runs were conducted with different dispersal distances ranging from one to ten. This variation did not have much effect on population dynamics. In none of the analyses, which are presented in this study, had the dispersal range any influence on abundance, temporal dynamics or population equilibrium.

Schröder and Degen (2008b) analysed the spatial genetic structure of *T. viridana* populations in North-Rhine-Westphalia (Western Germany) with AFLP markers. These studies revealed that the kinship between individuals within a range of up to 40m is higher than the kinship to individuals beyond this distance. A dispersal distance of 'three trees' approximates a distance of about 40m. Therefore, a dispersal range of three cells in our model is a realistic estimate of natural dispersal and was chosen for the documentation of the following results.

Influence of qualitative composition

Figure 5 shows the effect of mortality assuming that all trees are equally susceptible for *T. viridana*. Increasing mortality may actually raise the population abundance dramatically due to selection for higher population growth. The same underlying mechanism can be found, if a forest with a heterogeneous qualitative composition is simulated.
Figure 7 shows the results of three model runs with different qualitative compositions. In each model run the difference between 'Quality A' and 'Quality B'-trees is gradually raised by increasing tree-dependent mortality on 'Quality B'-trees from 0 to 1 in steps of 0.01. The mortality on 'A'-trees was kept constant at 0. Each of these hundred settings has been run in a model forest, where both types of trees were randomly distributed, for 200 years. The average abundance on both tree types (red dotted line and green

dashed line) and the total average abundance (black continuous line) are shown in Figure 7.

If we assume a forest with 10 % 'A'-trees (Fig. 7a), total average abundance is about 5 500 individuals per tree. Increasing mortality on 'Quality B'-trees will lead to lower abundances on this type of trees. Low abundances increase the population growth rate, but since there is dispersal, this higher growth rate feeds also back on near-by 'A'-trees. In those trees there is now a higher population growth due to the mortality on the neighbouring 'B'-trees. However, the average abundance remains at the same level.

When both tree types are present in equal proportions, this effect is even clearer (Fig. 7b). High mortality on one type of trees depresses its moth population. The effect of the increasing population growth rate is shared with adjacent trees due to dispersal.

If we assume a high proportion of 'B'-trees (Fig. 7c), we get a picture which resembles Figure 5. This is not surprising, since Figure 5 shows the results from a homogeneous forest with increasing mortality, while the model in Figure 7c relates to a high percentage (90%) of 'B'-trees with increasing mortality. Hence, this is almost the same scenario except for 10% randomly distributed 'A'-trees, where *T. viridana* does not show any mortality, but where the trees are highly affected.

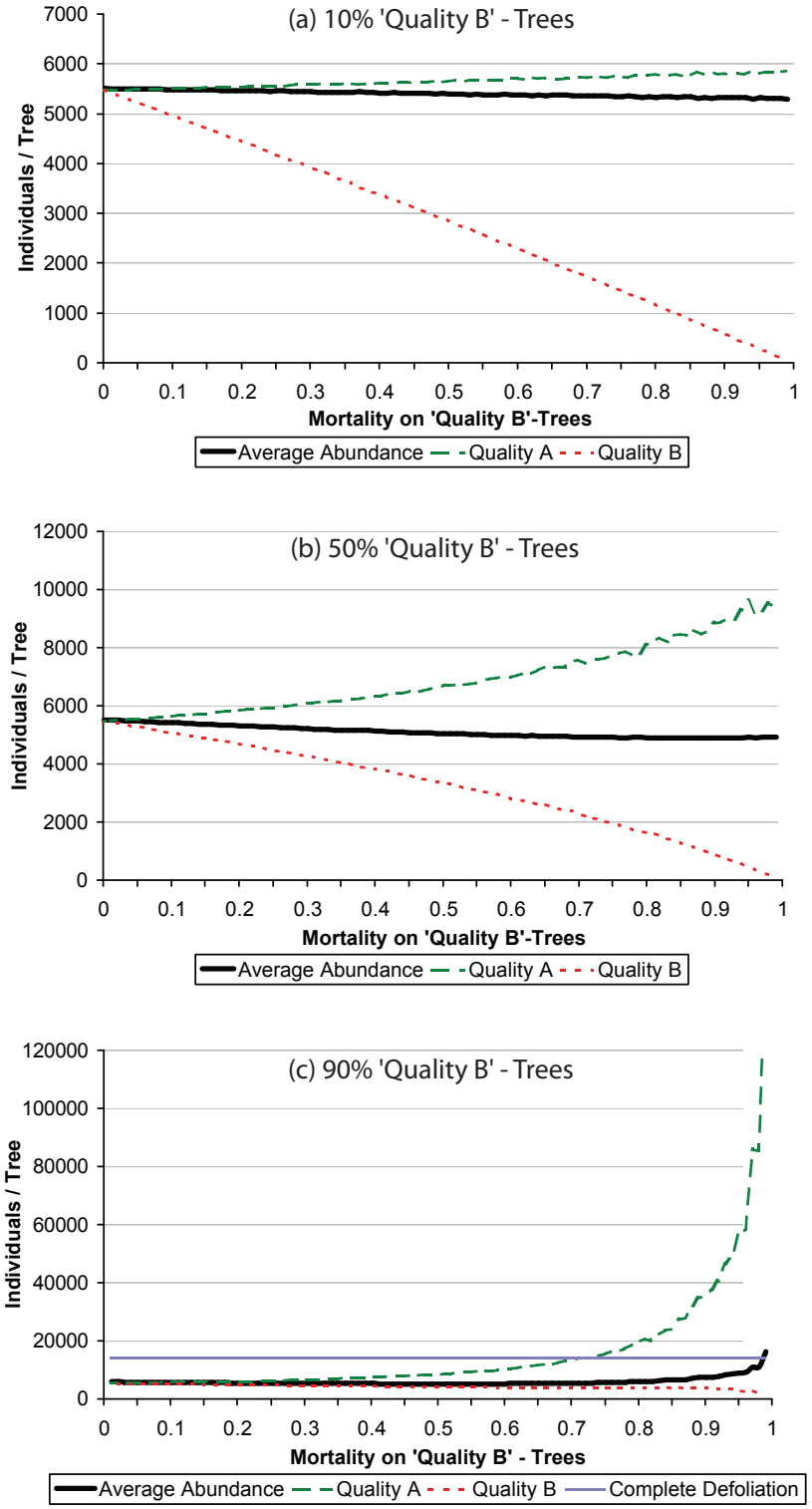

Figure 7: Average number of individuals per tree depending on mortality at 'Quality B'-trees is shown for three different qualitative compositions of the forest. 100 model runs with increasing mortality from 0 to 1 have been conducted. Each run simulated a time span of 200 years. The average abundances of these runs are shown in the figure. For values of other parameters see Table 1.

Variation of hostplant preference

The influence of a hypothetical preference in oviposition for one type of tree was analysed in a similar way as the qualitative composition on the stand level. The results of three model runs with different percentages of 'Quality B'-trees are shown in Figure 8. As a general trend, it can be observed that the abundance (individuals per tree) on 'A'-trees is continuously increasing as the preference for this type is raised from 0 to 1. A preference valued null means, that within the dispersal neighbourhood all eggs are laid on the other type of tree (A), whereas with a preference value of one, all other trees are being ignored. Even when very low or high preferences are modelled, there are numerous individuals on the 'avoided' type of tree. A preference value of 0.5 means that there is no preference for one type of tree at all. Figure 8b shows a scenario with equal numbers of both tree types. The result matches the intuitive expectation that a higher preference for one tree type leads to a higher number of individuals on this type, whereas the abundance on the other type is continuously decreasing. Figures 8a and 8c show the same model behaviour. The resulting curves for the two tree types are vertically mirrored due to the different proportion of those trees within the forest.

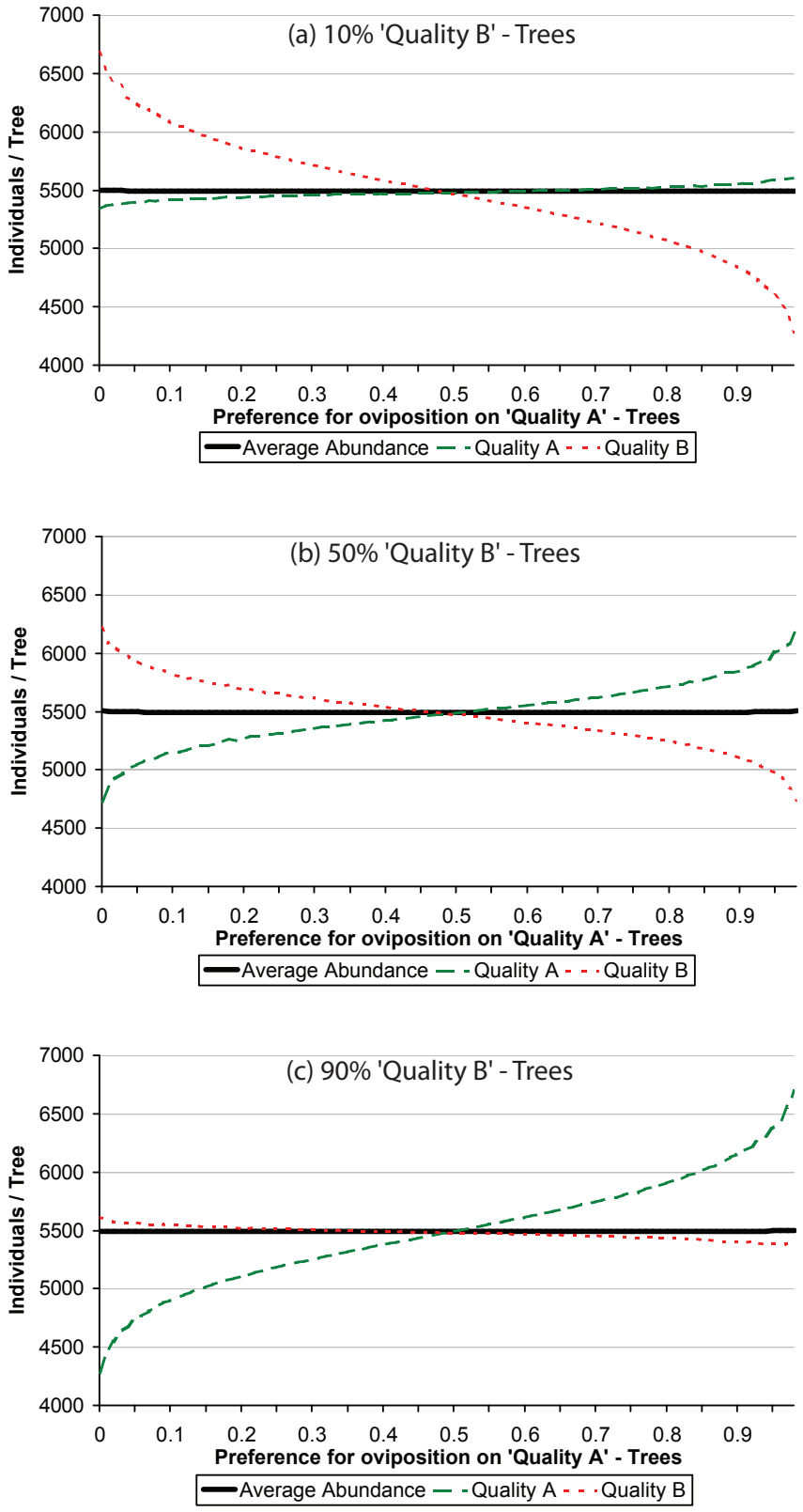

Figure 8: Average number of individuals per tree depending on preference for 'Quality A'-trees are shown for three different qualitative compositions of the forest. 100 model runs with increasing preference from 0 to 1 have been conducted. Each run simulated a time span of 200 years. The average abundances of these runs are shown in the figure. Preference 0.5 means no preference for one type of trees, 0 means strong preference for type A, 1 means strong preference for type B. For values of other parameters see Table 1.

Discussion

Suitability of Witting's equation for a spatiotemporal model

The present study used a spatiotemporal discrete simulation model to investigate and understand the population dynamics of the green oak leaf roller and the interaction with host trees of different qualities. Nedorezov and Sadykova (2008) tested the suitability of several mathematical models on the same data set as used in this study (Rubtsov and Utkina, 2003) and concluded that among all tested equations, a discrete logistic model fits best for describing *T. viridana*. There would be no need for more difficult models (like predator-prey or resource-consumer system dynamics (Nedorezov and Sadykova, 2008). Common logistic models can generate cycles through over-compensation, but not for periods longer than two generations. In order to generate long term cycles, which are typical for *T. viridana* and many other temperate-zone forest pest moths, Witting's model of density dependent competitive interactions was applied as a basis (Witting, 2000). This model is very appropriate for generating long-term cycles in abundance of animals with discrete, non-overlapping generations, like it is the case for many forest pest insects.

Many mechanisms have been hypothesised to be responsibly for the population cycles of forest defoliating insects, which occur typically in periods of 6-12 years (Kendall et al., 2005). Varying food quality (Helms and Hunter, 2005), parasitoids (Turchin et al., 2003) and maternal effects (Ginzburg and Taneyhill, 1994; Kendall et al., 2005) have received much attention. Spatial synchrony of population fluctuations among intra- and interspecific forest insect populations throughout large scales has been explained with dispersal among populations, spatially correlated weather conditions (Raimondo et al., 2004) or sunspot activity (Selas et al., 2004). Yet, there has been no conclusion as to which of the aforementioned hypotheses is most important. The impact of these mechanisms on population dynamics may be varying from species to species.

In contrast, Witting's model focuses on the role of intra-specific competition. It is able to generate realistic population cycles without extrinsic factors like weather, predator-prey or plant-herbivore interactions. This renders Witting's approach interesting for the use in spatiotemporal dispersal models and may be realistic at least for those herbivorous insect species which have a strong impact on their forage plant and may actually cause

complete defoliation. Most other forest pest species never occur at sufficiently high densities, where intra-specific competition were to play a decisive role. In most other forest pests, maximum population density is determind either by inter-specific competition, or predator-prey dynamics or other limiting factors. In contrast, the green oak leaf roller occurs during mass outbreaks in such high densities, that populations are mainly regulated through intra-specific competition. Earlier time-series analyses have shown that the population density of the previous year (N_{t-1}) explains more than 50% of variance in population growth rates (Hunter, 1998). This shows that intraspecific competition for food resources may really be the defining factor behind population cycles of *T. viridana*.

In the present study the role of density dependent changes in the average individual quality has been analysed, or in other words, the selection pressure through competitive interactions, which results in an across-generation change of population parameters. The basis of Witting's model is the assumption that population growth rate is not constant, but dynamic and density-dependent. The population density induces changes in life-history parameters through phenotypic plasticity, which are transmitted from parent to offspring.

The underlying assumption is that in phases of high population density limited food supply causes nutritional stress, which in turn induces a predictable change in the plastic phenotype. For the gypsy moth *Lymantria dispar* it is known that the nutritional environment of the parental generation influences the development time, fecundity and dispersal potential of offspring (Rossiter, 1991). A short development time is an important advantage, especially if resources are getting rare, but implicates lower pupal weights at the same time. Low pupal weights in turn cause lower fecundity. This traid-off between body-size and fecundity has been surveyed in detail for the autumnal moth *Epirrita autumnata* (Tammaru et al., 1996; Klemola et al., 2008). Contrary, in phases of low population density we assume a selection to slower larval development implicating higher fecundity of females. This results in faster population growth rate.

By suitable epigenetic mechanisms such changes in life-history parameters may be transmitted also to the next generation. Maternal effects, as one of many possible inherited environmental effects, have received much attention in that regard (Witting, 2000; Ginzburg, 1998; Raesaenen and Kruuk, 2007; Lazarevic et al., 2008; Zeh and Zeh, 2008). Indeed, Kendall (2005) analysed data from a pine looper moth *Bupalus piniaria* population in The Netherlands (Klomp, 1968) and found that pupal size positively affects

the larval survival of the offspring generation, which is a true maternal effect. Barbour (1980) found a negative relationship between pupal mass and population density two years previously.

Epigenetic mechanisms explain the occurrence of phenotypic variability even at small temporal scales without need to assume rapid changes in the insect's genotypes. Another way of 'handling' the density information would be possible through a shift of genotypic frequencies as a kind of balanced polymorphism. Assume there are two genotypes - one appears in moths with high reproduction rate but inferior competitive traits, the other one appears in moths with a slower reproduction but superior competitive traits. Fast larval development for example could be such an important competitive trait. A fast developing type of moths would have a huge advantage when resources are getting rare (at a high population density level), because they were probably able to pupate before complete defoliation occurs. As a trade-off they would have fewer offspring. The other type of moth, with slower larval development, would be more succesful if there are enough resources (at a low population density level), because they can produce more offspring. Both types do exist at any point in time of the model runs, but at different proportions, depending on the population density. A promising candidate for a polymorphic gene that might influence such insect population dynamics is phosphoglucose isomerase (Pgi), which was found to have significant effect on population growth of a butterfly species (Hanski and Ilik, 2006). However, whether density-dependent changes of growth rate are caused by phenotypic plasticity or different genotypes (balanced polymorphism), does not affect the results of the models explored here.

Model behaviour and parameterisation

The population dynamics of *T. viridana* according to the Witting model is basically influenced by two forces. One is the enhanced population growth rate when the population density level is low. The other one is the benefit of competitive traits when the population density level is high. This can be understood as a development-reproduction trade-off in terms of the r/K-continuum. A population equilibrium is reached when the two opposing forces are balanced against one another generating no overall selection. If the population is not at the population equilibrium, density dependent selection will change the average growth rate of the population. Actually, the population will never level out at the population equilibrium, because the process is time-delayed. For the calculation of next years abundance (N_{t+1}), not only data from this year (N_t), but also from the pre-

vious year (N_{t-1}) are needed. This distinguishes the model of Witting from many other models, which use only a delay of one generation. As a consequence, it is possible to generate cycles with a period length of many generations, dependent upon the magnitude of the population's response to selection (Fig. 4). This is of course an important asset of Witting-type models, since most population cycles of forest pest insects last for periods of more than two generations. Since the calculation of N_{t+1} is depending from both N_t and N_{t-1}, it is highly sensitive to the initial status. Small changes in the abundance of the first two generations can lead to very different amplitudes of every following cycle. In order to achieve an appropriate period length, it is important to have enough empirical data for the parameterisation. The data from Rubtsov (2003), who analysed the abundance of *T. viridana* over a period of 30 years, meet these requirements, but there is no other comparable dataset available. After all, Rubtsov investigated the population dynamics on two different sites and the parameterisation using non-linear regression returned very similar results (Fig. 2).

Influence of dispersal range

The estimates of dispersal in the model do probably not reflect the true dispersal behaviour of natural animals. As dispersal in nature is always a permanent process of decision making (whether to stay or not), it is not trivial to program realistic dispersal. Dispersal is a process, which can to some extent not be influenced by a moth itself. Passive dispersal through wind drift may play a certain role, especially for small moths flying above the forest canopy like *T. viridana*. But dispersal is also partly an active process, where the individual decides in which direction it should move. Many factors influence these decisions: Environmental conditions, population density (Hovestadt and Poethke, 2006), sex (Gros et al., 2008) and many more . For *T. viridana* it is known that females attract males with sex pheromones, as it is the case for most moth species. It is probably the males who accept a longer flight path in order to search for females. Simchuck reported that males mate first with females who hatched at the same tree and then they search for females at greater distances (Simchuk et al., 1999). Therefore, also the number of successful matings already carried out earlier in lifetime affects the dispersal decision. In this model an adjustable parameter specified the dispersal activity for each individual. In order to investigate the effect of various dispersal ranges, all model runs were conducted with several different dispersal settings. Surprisingly, the results did not change to a noteworthy extent. This shows that the patterns, which were found for the influence of

the qualitative forest composition and for the preference in oviposition, are very consistent and stable.

Influence of tree-independent mortality (overall mortality)

One of the key points of this study is that an additional mortality factor, which may act at any stadium of egg or larval development, may increase the population abundance. This seems to be counterintuitive, but can be explained through an increased reproduction rate at low population levels. A low density results in only few competitive interactions between *T. viridana* larvae and nutritional stress is low, which in turn favours selection of individuals with ability to produce more offspring. The population growth rate is increasing. High population densities lead to a selection pressure, which favours individuals with fewer offspring. The population growth rate decreases. If mortality is low the frequencies of both variants keep alternating, which leads to the typical stable population cycles, like it has already been explained previously.

High mortality reduces the density and induces selection for a higher population growth rate. If the response to selection for higher population growth rates is strong, it counteracts the immediate negative effect of mortality and may even lead to a population growth at a very high mortality level. The power of this force is quantified behind the value σ^2. Depending on how the changing growth rate is explained, the parameter σ^2 could be described as the additive genetic variance of the intrinsic population dynamic growth rate (Malthusian parameter r) or also as 'plastic response to inherited environmental effects' (Witting, 2000).

Influence of tree-dependent mortality and qualitative composition

T. viridana is foraging on any trees of the genus *Quercus*, but it seems that not all oak species are equally appropriate for larval development. At least, it has been observed that pedunculate oak trees (*Q. robur*) are suffering more from *T. viridana* moths than sessile oak trees (*Q. petraea*), even if the trees are standing right next to each other (Schröder and Degen, 2008a). Two ways are conceivable, how these observations can be explained. For one thing the female moths could have preferences when searching for the right place for

oviposition. This will be discussed in the following section. For another thing, there could be substantial differences between the two oak species, which cause an unequal fitness. Indeed, feeding experiments have shown that larvae need a little longer on *Q. petraea* until they pupate than on *Q. robur* (see Appendix). If these experimental results were transferable to field conditions, this could translate into a prolonged predation pressure and therefore a smaller survival rate. However, the differences in development between the two oak species, which have been revealed through these experiments, are not big enough to explain the aforementioned field observations on oak preferences. Still, they indicate differences in the chemical composition of the plants.

Mixing trees with different susceptibility for *T.viridana* affects the population dynamics dramatically (Fig. 7). In this scenario mortality is supposed to operate only on one type of trees ('Quality B'-trees), but the moth population is connected by means of dispersal. The consequences might be interesting also from a forestry point of view. Deliberately introducing trees of low quality as food plants of leaf rollers does not change average moth abundance nor their population dynamics. 'Quality B'-trees are indeed suffering less from foraging larvae, which is different from the scenario with only one type of tree and with tree-independent mortality. Now, the lower density on 'B'-trees favours the accumulation of fast reproducing moths, but those are dispersing randomly to other trees. As a result we have half the trees heavily damaged and half the trees little damaged. In contrast, in a forest with only one type of tree, all trees would suffer from equal defoliation.

Influence of oviposition preferences

As mentioned before, different oak species (*Q. robur*, *Q. petraea*) are not equally suffering from defoliation by *T. viridana*. Regarding food quality they are still both appropriate, but with minor restraints, since the larval development is slower on *Q. petraea* (see Appendix). However, the differences in defoliation intensities could also be caused through preferences in oviposition. It is conceivable that females prefer those trees where they expect a higher survival rate for their offspring. Host-plant selection by herbivorous insects is generally governed by volatile and non-volatile plant chemicals, as well as visual stimuli (Finch and Collier, 2000). The field of ovipostion preference of adult females and effects on larval performance of offspring is very controversially discussed in literature. Herbivorous insects very frequently show a preference for the host plant which is not the best for their offspring and often even reject those which are the best (Mayhew, 2001).

According to general life history theory, the effort put in searching for oviposition sites depends on age and physical condition of female adults (Singer et al., 1992; Tammaru et al., 1995; Javois and Tammaru, 2004). Little is known about oviposition preferences of *T. viridana*. Yet, it is unknown, whether female *T. viridana* can at all distinguish between different oak species. This could easily be tested with an experiment, where females can choose between branches of different oaks. Until now, such an experiment has not been conducted.

In the present study, theoretical consequences of an assumed preference have been investigated. The model behaviour is similar to what happened when introducing tree-dependent mortality, although what is going on behind is a little different: The preference for one type of tree causes a higher density (resulting in a lower reproduction rate) on this type. In contrast, the density is lower on the non-preferred trees (resulting in a higher reproduction rate). Hence, the overall population size remains the same, but again there are half the trees heavily damaged and half the trees suffer only little from defoliation.

Conclusions

A change of thinking towards natural, indigenous stock of trees is desirable and partly already taking place in forestry industry. Therefore, in Central Europe oaks will be increasingly cultivated in future in order to replace unnatural coniferous plantations. However, the ongoing climate change will affect intensity and frequencies of forest pest mass propagation and will lead to a growing necessity of understanding the population dynamics of these species. The results of the present study increase our knowledge on the population dynamics of the green oak leaf roller. The modelling results yield hypotheses to be tested in future experimental research. In the long run, such results could help to develop forest management measures to avoid complete defoliation and mass propagation of *T. viridana*. In view of the realistic model behaviour, the equation of Witting (2000) can be recommended for future use in spatiotemporal population models, as long as intraspecific competition and density-dependent variation in population growth rate can plausibly viewed as the major determinants of population dynamics.

Some findings of the present study based upon this model equation may be interesting for forestry praxis as well. The density-dependent change of the population growth results in some counterintuitive effects when combined with mortality factors. Mortality can be caused by natural regulation (predators, parasites, plant defence, etc.) but also by

chemical pest control. Considering the results of this study, one should be aware that a sudden decrease of population density can enhance the growth rate and actually induce mass propagations of *T. viridana*. However, it was shown that years of mass propagations are followed by years with a very low *T. viridana* density.

Mixing trees of different quality does not influence the average abundance of *T. viridana* in the whole forest, but may induce enormous population growth on the more suitable type of tree. This results in a spatially very heterogeneous damage. Complete defoliated trees may stand right next to hardly infested trees. This scenario has been observed naturally (Schröder 2008, personal communication) and can now be explained by use of the presented model.

It is arguable whether prevention of mass outbreaks is the only goal of forestry management. A heterogeneous forest with different types of oaks and different other tree species as well, may cause mass propagation of *T. viridana* on some trees. But these trees will be less damaged in subsequent years and they may even prevent defoliation on neighbouring trees. In forests consisting of only low quality trees (from the viewpoint of *T. viridana*), the population dynamics of *T. viridana* may behave as described above and induce an increasing population growth.

Acknowledgements

I would like to thank Dr. Silvio Schüler for excellent supervision of this study and many fruitful and interesting discussions.

Prof. Dr. Konrad Fiedler for many helpful comments on the manuscript.

Also Dr. Hilke Schröder (Federal Research Centre for Forestry and Forest Products, Großhansdorf, Germany) for facilitation of feeding experiments and the whole stuff from Großhansdorf for their cordial support.

Prof. Dr. Hans Joachim Poethke and Dr. Thomas Hovestadt from field station 'Fabrikschleichach' of the Julius-Maximilians-University Würzburg for help in programming and development of the simulation model.

Appendix - Feeding experiments

Experiments with *T. viridana* larvae were made in order to investigate, whether there are differences in food quality between leaves of *Quercus robur* and *Quercus petraea*. These experiments were conducted in the Federal Research Centre for Forestry and Forest Products, Großhansdorf (Germany). The results presented in Figure 9 and 10 are based on data from 137 larvae, which were separately fed with either leaves of *Q. robur* or *Q. petraea*.

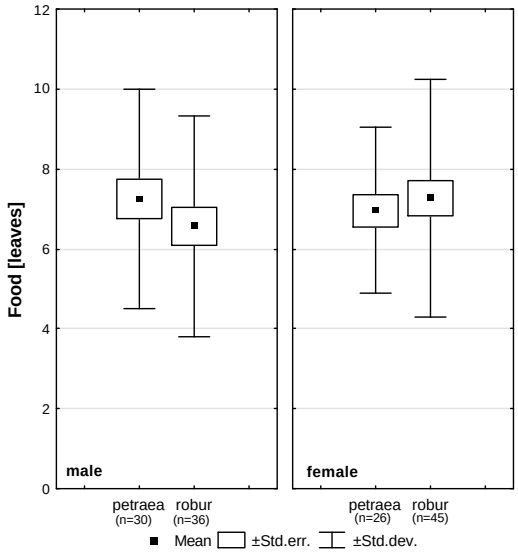

Figure 9: Food needed for larval development, calculated into amount of tree leaf-loss. Feeding damage of one bud is counted as a loss of six leaves.

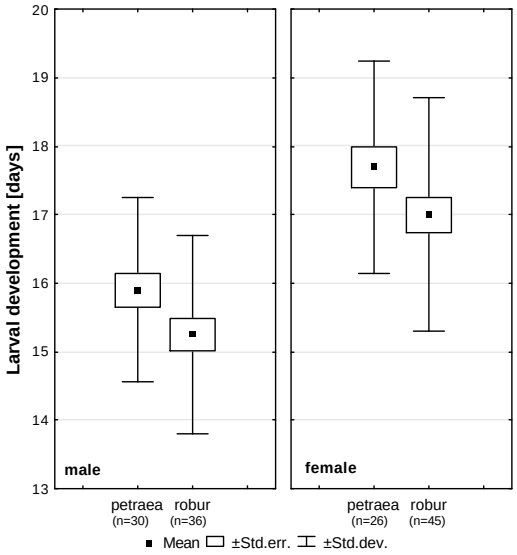

Figure 10: Duration of larval development, from egg hatching until pupation, on *Q. robur* and on *Q. petraea* for both male and female *T. viridana*.

Figure 9 shows the amount of leaf-loss for *Q. robur* and *Q. petraea* trees, which is caused by a single *T. viridana*. The given values are the sum of bud-damage of early larval stages and leaves eaten in later stages. One damaged bud is calculated as a leaf-loss of six leaves. This is the average number of leaves growing out of one bud.

There is a very high variation in the amount of leaves that have been eaten by a single larva, the mean value is about seven leaves per individual. No significant difference in the average amount of leaf-loss was found between both sex and oak species. However, the variances between *Q. robur* and *Q. petraea* were significantly different (Levene's test, $p<0.05$). This could be a hint that the substantial composition of *Q. robur* has developed a greater variability through co-evolution with its herbivores.

Figure 10 shows the duration of larval development on *Q. robur* and on *Q. petraea* for both male and female *T. viridana*. There is a significant difference between the mean duration of larval development between females and males and also between larvae on *Q. robur* and on *Q. petraea*. It is known that *T. viridana* larvae are proterandrous. This could be validated, as in our experiments male larvae pupated earlier than females as well (ANOVA, $p<0.001$). There is also a significant difference in mean duration of development between *Q. robur* and *Q. petraea* (ANOVA, $p<0.01$). This indicates substantial differences between these two oak species and also a different susceptibility as fodder plants for *T. viridana*.

References

Baltensweiler, W., Weber, U. M., and Cherubini, P. (2008). Tracing the influence of larch-bud-moth insect outbreaks and weather conditions on larch tree-ring growth in Engadine (Switzerland). *Oikos*, 117(2):161–172.

Barbour, D. (1980). *Population dynamics of the pine looper moth Bupalus piniaria (L.) (Lepidoptera, Geometridae) in British pine forests*. Ph.D. Thesis, University of Edinburgh, UK.

Berryman, A. (1996). What causes population cycles of forest Lepidoptera? *Tree*, 11:28–32.

Cecich, R. A. and Larsen, D. R. (1997). Bud demography and bifurcation in *Quercus alba* L., and *Quercus velutina* Lam. In *Diversity and adaption in oak species. Proceedings of the second meeting of WP 2.08.05, Genetics of Quercus, of the IUFRO*, pages 68–75. The Pennsylvania State University.

Czaran (1998). *Spatiotemporal Models of Population and Community Dynamics*. Chapman and Hall.

Du Merle, P. (1999). Egg development and diapause: ecophysiological and genetic basis of phenological polymorphism and adaptation to varied hosts in the green oak tortrix, *Tortrix viridana* L-(Lepidoptera : Tortricidae). *Journal of Insect Physiology*, 45:599–611.

Dunning, J. B., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H., and Stevens, E. E. (1995). Spatially explicit population models: Current forms and future uses. *Ecological Applications*, 5(1):3–11.

Finch, S. and Collier, R. (2000). Host-plant selection by insects - a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata*, 96(2):91–102.

Forkner, R. E., Marquis, R. J., Lill, J. T., and Le Corff, J. (2008). Timing is everything? Phenological synchrony and population variability in leaf-chewing herbivores of *Quercus*. *Ecological Entomology*, 33(2):276–285.

Gasow, H. (1925). Der grüne Eichenwickler als Forstschädling. *Arbeiten aus der biologischen Reichsanstalt für Land- und Forstwirtschaft*, 12:355–508.

Ginzburg, L. R. (1998). Inertial growth: population dynamics based on maternal effects.

In T. Mousseau, C. F., editor, *Maternal Effects as Adaptations*, pages 42–53. Oxford University Press.

Ginzburg, L. R. and Taneyhill, D. E. (1994). Population cycles of forest lepidoptera: A maternal effect hypothesis. *Journal of Animal Ecology*, 63(1):79–92.

Gros, A., Hovestadt, T., and Poethke, H. J. (2008). Evolution of sex-biased dispersal: The role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecological Modelling*, 219(1-2):226–233.

Hanski, I. and Ilik, S. (2006). Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biology*, 4:719–726.

Hassell, M. P., Lawton, J. H., and May, R. M. (1976). Patterns of dynamical behavior in single-species populations. *Journal of Animal Ecology*, 45:471–486.

Helms, S. and Hunter, M. (2005). Variation in plant quality and the population dynamics of herbivores: there is nothing average about aphids. *Oecologia*, 145(2):197–204.

Horstmann, K. (1984). Studies on the population-dynamics of the green Tortrix (Lepidoptera, Tortricidae, *Tortrix viridana* L) in lower Franconia. *Journal of applied entomology*, 98(1):73–95.

Hovestadt, T. and Poethke, H. (2006). The control of emigration and its consequences for the survival of populations. *Ecological Modelling*, 190(3-4):443–453.

Hunter, M. D. (1990). Differential susceptibility to variable plant phenology and its role in competition between 2 insect herbivores on oak. *Ecological Entomology*, 15(4):401–408.

Hunter, M. D. (1992). A variable insect-plant interaction: the relationship between tree budburst phenology and population levels of insect herbivores among trees. *Ecological Entomology*, 17:91–95.

Hunter, M. D. (1998). Interactions between *Operophtera brumata* and *Tortrix viridana* on oak: new evidence from time-series analysis. *Ecological Entomology*, 23:168–173.

Ivashov, A. V., Boyko, G. E., and Simchuk, A. P. (2002). The role of host plant phenology in the development of the oak leafroller moth, *Tortrix viridana* L. Lepidoptera: Tortricidae). *Forest Ecology and Management*, 157:7–14.

Javois, J. and Tammaru, T. (2004). Reproductive decisions are sensitive to cues of life expectancy: the case of a moth. *Animal Behaviour*, 68(Part 2):249–255.

Karolewski, P., Grzebyta, J., Oleksyn, J., and Giertych, M. J. (2007). Temperature affects performance of *Lymantria dispar* larvae feeding on leaves of *Quercus robur*. *Dendrobiology*, 58:43–49.

Kendall, B., Ellner, S., McCauley, E., Wood, S., Briggs, C., Murdoch, W., and Turchin, P. (2005). Population cycles in the pine looper moth: Dynamical tests of mechanistic hypotheses. *Ecological Monographs*, 75(2):259–276.

Klemola, T., Andersson, T., and Ruohomaeki, K. (2008). Fecundity of the autumnal moth depends on pooled geometrid abundance without a time lag: implications for cyclic population dynamics. *Journal of Animal Ecology*, 77(3):597–604.

Klomp, H. (1968). A seventeen-year study of the abundance of the pine looper (*Bupalis piniarius*). *Symposia of the Royal Entomological Society of London*, 4:98–108.

Larsson, S., Ekbom, B., and Bjorkman, C. (2000). Influence of plant quality on pine sawfly population dynamics. *Oikos*, 89(3):440–450.

Lazarevic, J., Nenadovic, V., Jankovic-Tomanic, M., and Milanovic, S. (2008). Genetic variation and correlations of life-history traits in gypsy moths (*Lymantria dispar* L.) from two populations in Serbia. *Archives of Biological Sciences*, 60(4):619–627.

Logan, J., Regniere, J., and Powell, J. (2003). Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, 1(3):130–137.

Mayhew, P. (2001). Herbivore host choice and optimal bad motherhood. *Trends in Ecology & Evolution*, 16(4):165–167.

Nedorezov, L. V. and Sadykova, D. L. (2008). Green oak leaf roller moth dynamics: An application of discrete time mathematical models. *Ecological Modelling*, 212(1-2):162–170. 5th European Conference on Ecological Modelling, Pushchino, Russia, Sept. 19-23, 2005.

Raesaenen, K. and Kruuk, L. E. B. (2007). Maternal effects and evolution at ecological time-scales. *Functional Ecology*, 21(3):408–421.

Raimondo, S., Liebhold, A., Strazanac, J., and Butler, L. (2004). Population synchrony within and among Lepidoptera species in relation to weather, phylogeny, and larval phenology. *Ecological Entomology*, 29(1):96–105.

Rossiter, M. (1991). Environmentally-based maternal effects - a hidden force in insect population dynamics. *Oecologia*, 87(2):288–294.

Rubtsov, V. V. and Utkina, I. A. (2003). Interrelations of green oak leaf roller population and common oak: Results of 30-year monitoring and mathematical modeling. *Ecology, Survey and Management of Forest Insects, Proceeding*, 311:90–97.

Schröder, H. and Degen, B. (2008a). Genetic structure of the green oak leaf roller (*Tortrix viridana* L.) and one of its hosts, *Quercus robur* L. *Forest Ecology and Management*, 256(6):1270–1279.

Schröder, H. and Degen, B. (2008b). Spatial genetic structure in populations of the green oak leaf roller, *Tortrix viridana* L. (Lepidoptera, Tortricidae). *European Journal of Forest Research*, 127(6):447–453.

Schröder, H. and Scholz, F. (2005). Identification of PCR-RFLP haplotypes for assessing genetic variation in the green oak leaf roller *Tortrix viridana* L. (Lepidoptera, Tortricidae). *Silvae Genetica*, 54:17–24.

Schwerdtfeger, F. (1971). Vergleichende Untersuchungen an der Kronenfauna der Eichen in Latenz- und Gradationsgebieten des Eichenwicklers (*Tortrix viridana* L.). *Zeitschrift für angewandte Entomologie*, 67:296–304.

Schütte, F. (1957). Untersuchungen über die Populationsdynamik des Eichenwicklers (*Tortrix viridana* L.). *Zeitschrift für angewandte Entomologie*, 40:1–36.

Selas, V., Hogstad, A., Kobro, S., and Rafoss, T. (2004). Can sunspot activity and ultraviolet-B radiation explain cyclic outbreaks of forest moth pest species? *Proceedings of the Royal Society B-Biological Sciences*, 271(1551):1897–1901.

Simchuk, A., Ivashov, A., and Companiytsev, V. (1999). Genetic patterns as possible factors causing population cycles in oak leafroller moth, *Tortrix viridana* L. *Forest Ecology and Management*, 113(1):35–49.

Singer, M., Vasco, D., Parmesan, C., Thomas, C., and Ng, D. (1992). Distinguishing between preference and motivation in food choice - an example from insect oviposition. *Animal Behaviour*, 44(3):463–471.

Tammaru, T., Kaitaniemi, P., and Ruohomaki, K. (1995). Oviposition choices of *Epirrita autumnata* (Lepidoptera: Geometridae) in relation to its eruptive population dynamics. *Oikos*, 74(2):296–304.

Tammaru, T., Kaitaniemi, P., and Ruohomaki, K. (1996). Realized fecundity in *Epirrita autumnata* (Lepidoptera: Geometridae): Relation to body size and consequences to population dynamics. *Oikos*, 77(3):407–416.

Thalenhorst, W. (1951). Die Koinzidenz als gradologisches Problem. *Zeitschrift für angewandte Entomologie*, 32:1–48.

Turchin, P. and Taylor, A. D. (1992). Complex dynamics in ecological time-series. *Ecology*, 73(1):289–305.

Turchin, P., Wood, S., Ellner, S., Kendall, B., Murdoch, W., Fischlin, A., Casas, J., McCauley, E., and Briggs, C. (2003). Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. *Ecology*, 84(5):1207–1214.

Witting, L. (2000). Population cycles caused by selection by density dependent competitive interactions. *Bulletin of Mathematical Biology*, 62:1109–1136.

Zeh, J. A. and Zeh, D. W. (2008). Maternal inheritance, epigenetics and the evolution of polyandry. *Genetica*, 134(1):45–54. Symposium on the Evolutionaly Ecology of Genetic Quality, Tours, France, July 26th, 2006.

LEBENSLAUF

STEFAN KAPELLER

Persönliche Angaben

Geburtsdatum	06. April 1982
Geburtsort	Linz
Wohnsitz	Grillparzerstraße 18
	2380 Perchtoldsdorf

Ausbildung

1992 – 2000	Gymnasium Petrinum Linz
seit 2000	Studium Biologie (Diplom) an der Universität Wien
seit 2004	Studienzweig Zoologie (Fokus Evolutionsbiologie)

Arbeitserfahrungen

Aug. 2002	Konrad Lorenz Institut Grünau
Jul. 2003	PULS-Praktikum des Alpenvereins in Lienz
Aug. 2003	Technisches Büro für Gewässerökologie Wels
Okt. 2003 – Okt. 2004	Zivildienst im Diakoniewerk Gallneukirchen
seit Okt. 2004	Ehrenamtliche Mitarbeit im Jane Goodall Institut - Austria (Koordination des Kinder- und Jugendprogramms Roots & Shoots)
Seit Sep. 2006	Besucherinformation im Tiergarten Schönbrunn (Kommentierte Fütterungen)
Jul. – Sep. 2007	Praktikum in der Bundesforschungsstelle für Wald, Landschaft und Naturgefahren (BFW)
seit Feb. 2009	Ökopädagogische Ausbildung des WWF

Stefan Kapeller
Grillparzerstraße 18
2380 Perchtoldsdorf
Mobil: 0650 4700119
Email: skape@gmx.at