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## A model of the European red mite (Acari, Tetranychidae) population dynamics and its linkage to grapevine growth and development

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### Abstract

A dynamic model for the development of the European red mite *Panonychus ulmi* (Koch) populations is presented and validated with four independent field data sets. It has the following characteristics:

1. Mite development, survival and reproduction are mainly driven by the daily temperature extremes and precipitation, modified by the food supply and nitrogen status of the host.

2. The population cohorts pass through egg, juvenile and adult life stages. Their development and aging occur above the stagespecific temperature thresholds and are modelled with the distributed delay method to account for the observed variance around the mean transit (development) time.

3. The link between the grapevine (*Vitis vinifera* L.) host plant and the European red mite population is modelled via the metabolic pool approach. The bitrophic relationship between the host and the herbivore has a quantitative and a qualitative component: the plant supplies food (dry matter) to the feeding mite stages, which conversely reduce the photosynthetically active leaf area. The qualitative aspect concerns the effect of the nitrogen concentration of the vine leaves on oviposition and development of the spider mites. The energy flow within and between trophic levels is expressed in dry mass equivalents [g].

4. The negative impact of rainfall is a significant component of the model. Precipitation affects oviposition and survival of the mites.

For the validation with four data sets all parameter values were kept constant except for fecundity which presumably varies among mite strains in different vineyards. The model successfully simulated the mite dynamics of different locations and years.

### 1 Introduction

A number of investigations have been made concerning various aspects of the biology of spider mites (HELLE and SABELIS 1985). From the life history parameters of individuals (such as developmental time, fecundity, mortality) under varying abiotic and biotic conditions, life tables can be compiled. Their analysis leads to life table parameters (such as intrinsic rate of natural increase,  $r_m$ ) which express the performance of a population under specific conditions (for a summary of recent research on spider mite life tables see WERMELINGER et al. 1990a, b, 1991b). These parameters are a measure of the population growth capacity under constant conditions, and are thus unable to represent the seasonal dynamics of spider mite populations with time-varying age structures under variable field conditions. Population growth depends on intrinsic factors and on environmental influences such as temperature and other climatic impacts, food availability, nutritional value of the host plant, feedback from injured host plant and predation. Analytical models have clear limitations in accounting for all these influences.

A simulation model allows the easy incorporation of all the above effects to obtain the structure of plant and herbivore populations at any point in time. The models on acarine systems were summarized by BAUMGÄRTNER et al. (1988). Many models on spider mite population dynamics especially focus on predator-prey relationships (RABBINGE 1976;

SHAW 1984; BERNSTEIN 1985; GENINI 1987; KLAY 1987; NACHMAN 1987; HAYES 1989) and lack adequate dynamic interactions between plant and spider mite populations (HERNE and LUND 1979; BAUMGÄRTNER and ZAHNER 1983; ZAHNER and BAUMGÄRTNER 1988; HARDMAN 1989; WOOLHOUSE and HARMSEN 1989). Other models concern specific microenvironmental interactions (TOOLE et al. 1984). All these models have in common that the nutritional base is poorly represented. This creates problems for simulating interactions between different trophic levels. Only one model considers the dynamics of host plant-mite interactions based on mechanistic principles (GUTIERREZ et al. 1988). This model is applied to the *Panonychus ulmi*-vine plant system.

In this work we present a model on the dynamics of the European red mite, *P. ulmi* (Koch) (Acari, Tetranychidae) which is closely linked to a comprehensive canopy model of the host plant. This quality enables the assessment of the role of nutrients in the dynamics of the plant-mite system. The model focuses on the population dynamics and is part of a comprehensive investigation (CANDOLFI 1991) on the role of spider mites in a vineyard ecosystem. It is parameterized largely from literature data and validated for Swiss conditions with four independent field data sets.

## 2 Material and methods

### 2.1 Model description

#### 2.1.1 Modelling approach

The spider mite model relies on a demographic model structure which is widely used for modelling population development and intertrophic relations. It includes the metabolic pool approach reviewed by GUTIERREZ et al. (1987) and GRAF et al. (1990). This approach has been used for both plant and herbivore models in general and for acarine models in particular. The linking of the two trophic levels is facilitated by the fact that the structure of the plant model (WERMELINGER et al. 1991a) is the same as the structure of the mite model detailed in this work. The model has a similar structure to that of the multitrophic cassava crop system (GUTIERREZ et al. 1988).

The main model features are briefly summarized here: The mite population is divided into four age-structured life stages, i.e. eggs, juvenile stages, adults, and winter eggs. Figure 1 depicts the flows of masses/individuals and their interactions with the host plant. SEVERINI et al. (1990) have demonstrated that a group of individuals born at the same time, i.e. a cohort, is the basic population unit. Furthermore a very general equation can be written to describe the flow of the individuals of a cohort through the system under study. Accordingly, the number of individuals in each life stage depends on the flow from one stage to another and the possible losses from each stage (fig. 1). These processes are temperature dependent and include a genetically controlled variability in developmental times. This complexity can be handled by time-distributed delay models with attrition (MANETSCH 1976; VANSICKLE 1977; SEVERINI et al. 1990). The reader is referred to these publications for mathematical details. Assuming linear developmental rates above a stage specific threshold in the naturally occurring temperature range (cf. WERMELINGER et al. 1990a), juvenile growth and aging, and the aging of adults, occur on physiological time expressed as degree-days ( $dd > 10^\circ\text{C}$  for eggs and juveniles,  $dd > 8^\circ\text{C}$  for adults). The metabolic pool requires the definition of a daily demand for resources. It is given by the energy need for respiration, development and egg production, and is expressed in leaf mass units [g]. Food acquisition is modelled per day and is not only driven by resource availability but also by the demand for the resources. The acquired food, i.e. dry matter, is distributed to the sinks according to the metabolic pool approach. The main driving variables are daily temperature extremes and precipitation. Development, reproduction and survival are modified by food supply and food quality, expressed by the N concentration of the leaves. Since the approach has been described several times before (MANETSCH 1976; GUTIERREZ et al. 1984; SEVERINI et al. 1990; WERMELINGER et al. 1991a), we will refrain from a detailed presentation of the mathematical structure and limit this work to the relevant components and relationships. The parameters are listed in table 1.

#### 2.1.2 Cohort development and aging

The hatching of the winter eggs and the development and aging of summer life stages are modelled via a time invariant delay process with a time step of one degree-day. Physiological units of age and time, expressed in degree-days [dd], are calculated by integrating a sine curve forced through daily

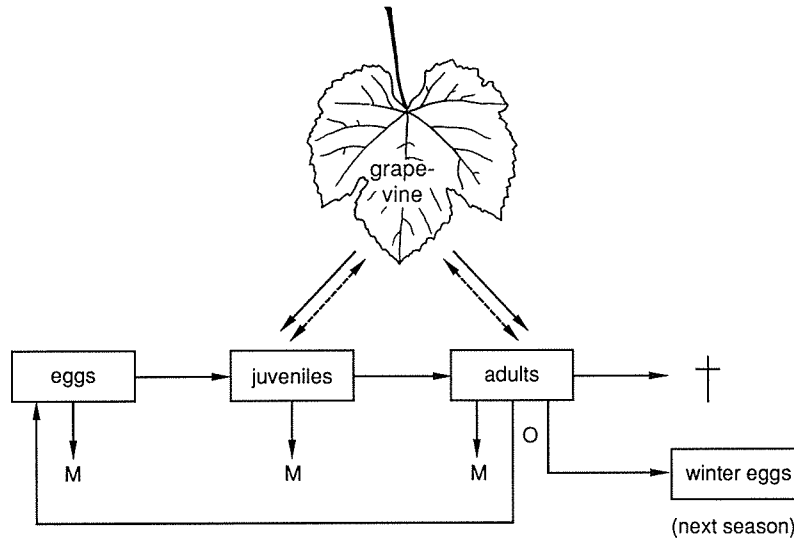


Fig. 1. Mass flows (solid arrows) within mite population and between mite population and the grapevine plant, and interactions (dashed arrows) between the two trophic levels as described by the model (M = mortality, O = oviposition, † = death at the end of the adult life span)

temperature extremes above the stage-specific developmental thresholds (FRAZER and GILBERT 1976). The different life stages have different development times *DEL* and are subdivided into *k* substages to account for the variability of the developmental times.

The population starts in spring with a number of surviving winter eggs given as initial, location-specific input values (table 2). Mean hatching time of winter eggs (*DEL<sub>w</sub>*) is 600 dd > 2.5 °C after 1 January (ZAHNER and BAUMGÄRTNER 1988). This procedure does not reflect the total development

Table 1. Parameter values of the *P. ulmi* simulation model  
(dd = degree-days; development and fecundity at standard N conditions, 3 % N)

Developmental threshold	winter eggs	2.5 °C (cf. text)
	eggs, immatures	10.0 °C
Oviposition threshold	adults	8.0 °C
Developmental time	winter eggs ( <i>DEL<sub>w</sub></i> )	600 dd > 2.5 °C from 1 January (cf. text)
	summer eggs ( <i>DEL<sub>e</sub></i> )	80.9 dd > 10 °C
Longevity	juveniles ( <i>DEL<sub>j</sub></i> )	87.6 dd > 10 °C
Preoviposition period	adults ( <i>DEL<sub>a</sub></i> )	187.0 dd > 8 °C
Number of substages	winter eggs <i>k<sub>w</sub></i>	25.7 dd > 8 °C
	eggs ( <i>k<sub>e</sub></i> )	30
	juveniles <i>k<sub>j</sub></i>	60
	adults ( <i>k<sub>a</sub></i> )	50
Max. fecundity ( <i>F</i> )	Stäfa	10
	Hallau, Zizers	54 eggs/♀ 32.4 eggs/♀
Juvenile growth rate ( <i>GR<sub>i</sub></i> , <i>i</i> = substage)		0.024 × weight × dd <sup>-1</sup>
Egg dry weight		1.5 µg
Female dry weight		4.0 µg
Sex ratio ( <i>SR</i> , proportion of females)		0.75
Respiration rate ( <i>R̄</i> )		0.24 d <sup>-1</sup>
Search rate ( <i>s</i> )		0.1
Conversion efficiency ( <i>c</i> )		0.3
Egestion rate ( <i>e</i> )		0.3

of winter eggs but is adequate to represent the time and the distribution of winter egg hatching. In the summer populations, the eggs produced by adults (except diapausing eggs) enter a vector of length  $DEL_e$  (expressed in dd) and containing  $k_e$  substages. After accumulating the heat sum required for the transit time, the hatching larvae leave this vector and enter subsequent vectors for juvenile development and adult longevity of length  $DEL_j$  and  $DEL_a$  and  $k_j$  and  $k_a$  substages respectively. The output from the last substage corresponds to the death of adult individuals. All data concerning stage durations at standard conditions (3% leaf N) originate from RABBINGE (1976). The developmental rate is proportional to the leaf N content (WERMELINGER et al. 1991b). This is accomplished by multiplying the daily  $\Delta t$  [dd] by the leaf N scalar  $v_l$  (see eqn. 7). The mortalities are discussed below.

### 2.1.3 Food demand

Total demand for food, i.e. leaf mass consumption, has the components juvenile growth, adult reproduction and respiration of both stages. The demand  $D_j$  per day for the growth of juveniles consists of the daily growth increment (the product of the maximum growth rate  $GR_i$  of each substage  $i$ , the number of individuals  $n_i$  therein, and the daily number of degree-days,  $\Delta t$ ) corrected for the conversion efficiency  $c$  of the incorporation of assimilated matter into body structure (eqn. 1).

$$D_j = \left( \sum_{i=1}^{k_j} GR_i \cdot n_i \right) \cdot \Delta t / (1-c) \quad (1)$$

Adult females have a demand  $D_a$  to produce eggs which is the number of individuals  $n_i$  in age class  $i$  times their oviposition rate  $OR_i$  (see eqn. 5i), multiplied by the physiological time  $\Delta t$  and the sex ratio  $SR$  of the population. It is again corrected for the conversion efficiency  $c$  of assimilated matter to eggs.

$$D_a = \left( \sum_{i=1}^{k_a} OR_i \cdot n_i \right) \cdot \Delta t \cdot SR / (1-c) \quad (2)$$

There is also a demand for juvenile and adult respiration. According to WERMELINGER (1989) about 1% of the dry weight of spider mites is respired per hour at 26°C, i.e. approximately one quarter of the body dry weight per day. Adult dry weight was assumed to be 4 µg (WERMELINGER 1989) and juvenile weight to increase exponentially from 0.5 to 4 µg. The respiration value is recalculated for daily recorded temperatures with a  $Q_{10}$  of 2.0 (temperature quotient indicating change of the intensity  $K$  of metabolic processes at a temperature  $T$  change of 10°C,  $Q_{10} = K_{T+10}/K_T$ ) and yields the respiration demand ( $R$ ) expressed in leaf dry mass (cf. eqn. 3).

The total demand  $D$  consists then of the assimilate demand of juvenile and adult stages and their respiration ( $R$ ), corrected by the egestion rate ( $\epsilon$ ):

$$D = (D_j + D_a + R) / (1-\epsilon) \quad (3)$$

### 2.1.4 Food uptake

Daily food acquisition ( $A$ ) is modelled by the modified function of FRAZER and GILBERT (1976), originally developed for predator-prey relations:

$$A = D \cdot (1 - \exp[-s \cdot M/D]) \quad (4)$$

where  $D$  is the total demand of the mite population for carbon resource, expressed in [g] dry matter (eqn. 3),  $s$  is the search rate, and  $M$  is the resource, i.e. the available leaf mass given by the plant model at this point in time. The acquired mass is distributed to the sinks to meet the demand of respiration with first priority, and then that of reproduction or growth. From the ratio between food uptake (supply) and food demand, an immediate daily scaling factor  $\rho_d$  ( $\rho_d \in [0,1]$ ) and a delayed mean scaling factor ( $\rho_m$ ) from the four most recent  $\rho_d$  are calculated. When food is limiting, these scalars affect fecundity (eqn. 6) and mortality (eqn. 9) respectively.

### 2.1.5 Reproduction

An age-specific oviposition rate (per dd) is attributed to each of the  $k_a$  adult substages. The oviposition rate ( $OR_i$ ) of substage  $i$  is the product of the relative oviposition rate ( $ROR_i$ ) and total fecundity ( $F$ ).  $ROR_i$  is the derivative of a function fitted to RABBINGE's (1976) data on cumulative fecundity and  $z$  is the female age [dd].

$$ROR_i = (0.015 - 0.00009 z) \quad ROR_i \geq 0 \quad (5i)$$

$$OR_i = ROR_i \cdot F \quad (5ii)$$

While RABBINGE (1976) reported  $F$  to be 27 eggs/female, it was calibrated according to the location under study, i.e. in Stäfa by a factor of 2.0 and in Hallau and Zizers by a factor of 1.2. This may be

attributed to different strains. Higher fecundity of Swiss mite strains was also suspected by ZAHNER and BAUMGÄRTNER (1988) in apple orchards. Daily oviposition ( $O$ ) (eqn. 6) of a population composed of  $n_i$  females in each age class  $i$  is scaled by the daily supply/demand ratio  $\rho_d$  as described in chap. 2.1.4 and by the nitrogen coefficient  $v_2$  (eqn. 7),  $\Delta t$  is the daily heat sum in dd.

$$O = \left( \sum_{i=1}^{k_i} OR_i \cdot n_i \right) \cdot \Delta t \cdot \rho_d \cdot v_2 \quad (6)$$

Thus, the time step of oviposition is 1 day. The oviposition period is preceded by a preoviposition period of 25.7 dd (RABBINGE 1976).

### 2.1.6 Leaf nitrogen effects

The nitrogen content of leaves is known to exert a significant impact on the development and reproduction of spider mites. The response of *Tetranychus urticae* Koch to leaf N (WERMELINGER et al. 1991b) was incorporated in the *P. ulmi* model. Linear scalars were used to model the effects of grapevine leaf N concentration on developmental and oviposition rates (see chap. 2.1.2 and eqn. 6)

$$v_1 = 0.63 + 0.12 N \quad (7)$$

$$v_2 = -0.75 + 0.58 N$$

where  $v_1$  and  $v_2$  represent the scalars affecting the development – via the number of daily accumulated degree-days – and reproduction respectively and  $N$  means leaf nitrogen concentration as calculated by the plant model (WERMELINGER et al. 1991a). At 3% leaf N both scalars are 1.0 giving standard developmental and reproductive values. In the heavily fertilized Stäfa plots the scalars had to be limited to  $v_1, v_2 \leq 1.0$ .

### 2.1.7 Rainfall effects

Very little information is available on the impact of rainfall on spider mites. For this model, data on precipitation effects on fecundity and mortality were adapted from HUI et al. (1985). Rainfall induced juvenile and adult mortalities ( $m_{r,j}$  and  $m_{r,a}$  respectively) are calculated as follows:

$$\text{if } 1 < \text{rain} < 20 \text{ mm/d} \quad m_{r,j} = 0.2 \quad (8)$$

$$m_{r,a} = 0.0$$

$$\text{if rain} \geq 20 \text{ mm/d} \quad m_{r,j} = 0.3$$

$$m_{r,a} = 0.3$$

Oviposition ceases at a precipitation  $> 1$  mm/d, i.e. practically as soon as rain occurs.

### 2.1.8 Other mortalities

An intrinsic per-day-mortality of  $0.01 \text{ d}^{-1}$  for eggs and of  $0.03 \text{ d}^{-1}$  for immatures is applied (RABBINGE 1976). Mortality due to starving ( $m_s$ ) is directly calculated from the four-day mean supply/demand ratio  $\rho_m$  described in chap. 2.1.4.

$$m_s = 1 - \rho_m \quad (9)$$

Pesticide mortality ( $m_{p,j}$ ,  $m_{p,a}$ ) per day is approximated by:

$$m_{p,a} = m_o \cdot (1 - [t/t_p]^2) \quad (10)$$

$$m_{p,j} = 1 - 0.8 \cdot (1 - m_{p,a})$$

where  $m_o$  is the initial mortality caused during the day of application,  $t$  is the time [d] elapsed since the application, and  $t_p$  is the efficiency time of the pesticide (average of 12 d; ZAHNER and BAUMGÄRTNER 1988). Survival of the juvenile stages is 80% of adult survival.

All these mortalities plus the above rainfall mortality are summarized in a proportional loss factor per degree-day and are incorporated in the model via attrition (VANSICKLE 1977).

Additional mortalities are caused by summer prunings and at harvest and correspond both to the proportion of leaves removed. This simple approach consciously disregards the spatial distribution and produces systematic errors. However, they are presumably too small to justify the incorporation of the spatial dynamics into this model.

### 2.1.9 Diapause

Induction of diapausing winter eggs is dependent on daylength ( $dl$ ) and temperature ( $T$ ) and may be modified by the nutritional quality of the food. A crude scheme for the proportion  $d$  of diapausing eggs was derived from a figure presented by VEERMAN (1985):

$$\begin{array}{ll} \text{if } dl \geq 13.5 \text{ h} & d = 0 \\ \text{if } dl < 13.5 \text{ h} & d = 0 \quad \text{for } T > 24^\circ\text{C} \\ & d = 0.6 \quad \text{for } 24 \leq T < 20^\circ\text{C} \\ & d = 0.8 \quad \text{for } 20 \leq T < 18^\circ\text{C} \\ & d = 1.0 \quad \text{for } T \leq 18^\circ\text{C} \end{array} \quad (11)$$

In fall, a leaf N concentration lower than 1.5 % induces the production of 100 % diapausing winter eggs ( $d = 1.0$ ).

### 2.1.10 Link to host plant

One of the advantages of the metabolic pool approach is the straightforward connection of different trophic levels (GRAF et al. 1990). It refrains from complex empirical interactions but relies basically on the simple fact that the gain of the upper-level assimilate pool by feeding is the loss of the lower-level pool. The relationship can be refined by adding qualitative effects such as leaf nitrogen influences. The model on the interactions between the grapevine plant (WERMELINGER et al. 1991a) and its associated spider mites follows these principles: *P. ulmi* affects the grapevine plant via the removal of leaf mass by food uptake. The consumption calculated in chap. 2.1.4 is subtracted in the vine model from the leaf mass. This reduces the available photosynthetically active leaf area. This is the only mite effect on the plant, since experiments in the field have revealed that, in contrast to *Tetranychus* species (WELTER et al. 1989; CANDOLFI 1991), *P. ulmi* has no direct influence on the photosynthetic rate of vine leaves, at least not at the mite densities investigated (CANDOLFI 1991). The influence of the lower trophic level, i.e. the grapevine, on the herbivores is given on the one hand by the leaf mass available for feeding (food quantity) and on the other hand by its N concentration (food quality).

## 2.2 Validation field data

The validation procedure consisted of a visual comparison between simulated mite populations and observed infestation patterns in differently managed vineyards. To facilitate the comparison between different locations and years, mite loads were defined as the mite densities multiplied by the feeding time in degree-days (table 2). The data on mite population development for the model validation were collected in three commercial vineyards in Switzerland from 1987 to 1989 with different cultivars, climatic conditions, soil and pest management: Stäfa, Canton of Zürich, in 1987 and 1988 on Riesling × Sylvaner; Hallau, Canton of Schaffhausen, in 1989 on Pinot Noir; Zizers, Canton of Graubünden, in 1989 on Gewürztraminer. Mite population per vine was estimated from mite densities of the most infested leaves of four shoots per vine using a previously defined scheme on mite distribution on main and lateral vine shoots (CANDOLFI 1991).

All vineyards were treated with pesticides, mostly fungicides. It proved difficult to discriminate mite toxic and non-toxic treatments, since no specific examination of pesticide-induced mite mortality was carried out. No toxic treatment was applied in Stäfa 1987, while Stäfa 1988 received a *Bacillus thuringiensis* treatment (Dipel®) on 22 July, which is reported to be harmful to spider mites (ROYALTY et al. 1990). In the Hallau 89 plot, the acaricide Remanex® (Tetradifon) was applied on 18 May to prevent excessive mite densities. In Zizers 1989 the simulations required a slight mortality on 28 August due to the application of the fungicide Drawifol® (Metomeclan), although no negative effect of this product on mites is reported. It is suggested that every pesticide application may have negative effects on spider mite populations due to mechanical sprinkling effects similar to rainfall. For more information on data collection and vineyard management the reader is referred to CANDOLFI (1991).

## 2.3 Evaluation of rainfall and N effects

The simulation model was used to evaluate the impact of rainfall and nitrogen on the population development of *P. ulmi* in Hallau. Four simulations were carried out: standard conditions, without rainfall effects on mortality, without rainfall effects on oviposition, and without leaf N effects.

### 3 Results

All mite parameters were kept constant for the simulation of the four data sets from different locations and years, except for the effects of pesticides and leaf nitrogen as discussed above and the fecundity in the Stäfa location. Figure 2 depicts the simulation of the total number of postembryonic stages of *P. ulmi* per vine plant and the corresponding

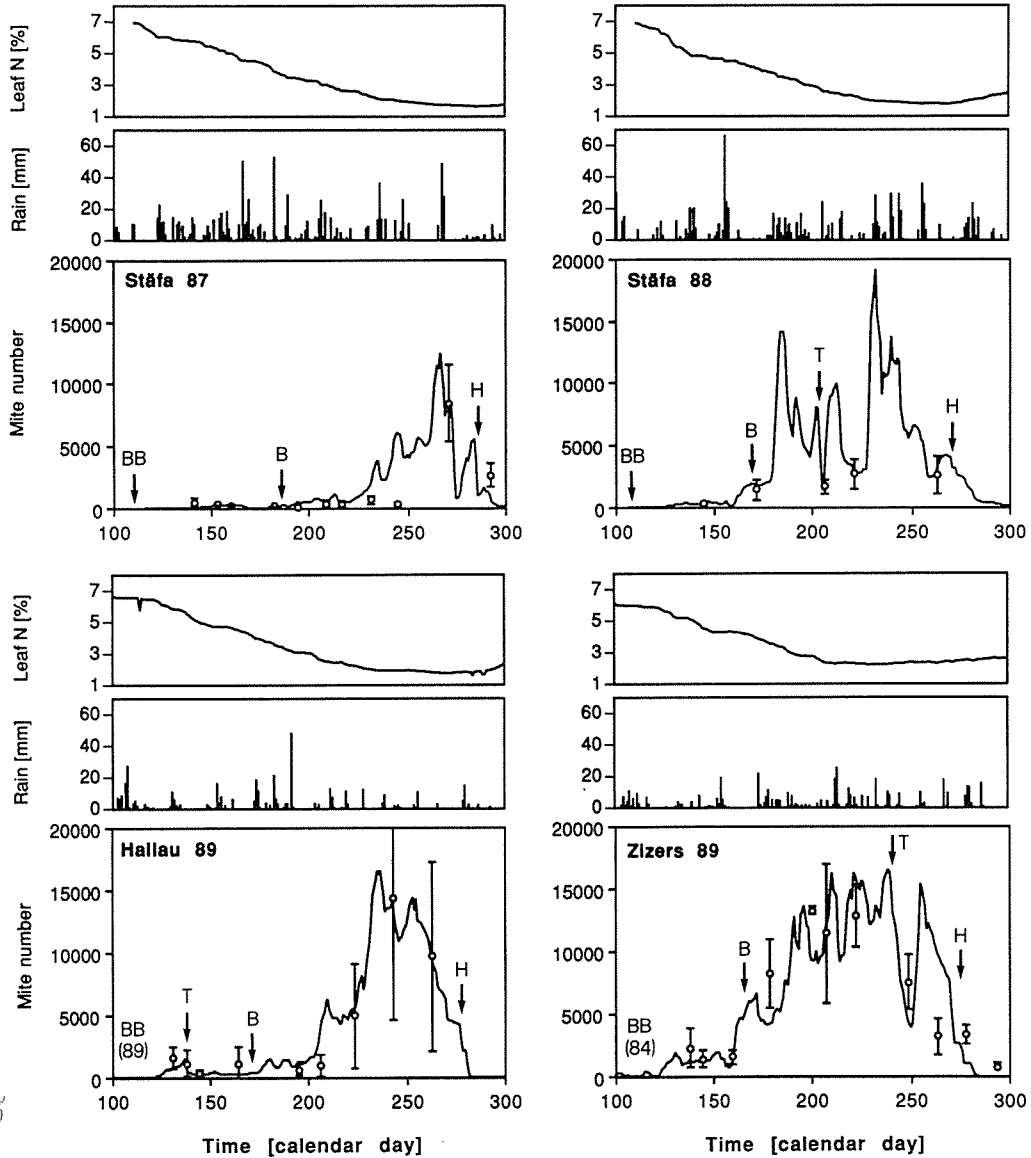


Fig. 2. Simulated seasonal dynamics of postembryonic stages of *P. ulmi* (symbols: field data, average number of individuals per vine  $\pm$  SD; B = bloom; BB = budbreak (number = day); H = harvest; T = detrimental pesticide treatment), observed rainfall pattern, and simulated dynamics of the average nitrogen concentration of grapevine leaves for four locations/years

field data, the standard deviation representing the variability of the counts on the most infested leaves. In addition, the seasonal patterns of rainfall and simulated leaf nitrogen simulated by the plant model (WERMELINGER et al. 1991a) are superimposed. The period represented in the graphs lasts from 10 April (day 100) to 27 October (day 300). Due to heterogeneous infestation levels of the 20 grapevine plants, the population means showed a large variation. In the Stäfa plot in 1987 the population remained low until the end of August. The population peaked no earlier than at the end of September. This was also reproduced by the model, but population build-up was simulated too early compared with the field data. The quality of the simulation in the same vineyard in 1988 is difficult to assess. Most of the few field counts turned out to coincide with minima of the simulated populations. On the one hand, the line perfectly matched the field data, on the other hand one could imagine a steady, slow increase of *P. ulmi* until about day 220, similar to the previous year, followed by the subsequent peak before day 260 or even without reaching a peak. This simulation was the most uncertain one of all locations.

The dynamics in Hallau 1989 could be well represented by the model. Although the field data showed considerable variation, the simulation closely followed the mean densities. After a small peak subsequent to budbreak (first mite generation, hatching from diapausing winter eggs), the population remained at a low level until mid July, and thereafter a large population developed for a period of two months.

The simulation of the spider mite dynamics in Zizers 1989 represented the general pattern observed in the field, although the last peak around day 260 is questionable since the field data may also suggest a gradual decline in September/October.

In the following analysis of the four simulation patterns the differences in population densities and dynamics are related to temperature effects, the negative impact of rainfall and different winter egg numbers (cf. also table 2). The comparison of the two years 1987/88 at Stäfa reveals significant differences in the total mite load (mite-days) as well as the dynamics pattern. Although starting with a higher number of winter eggs, the population in 1987 was lower throughout much of the season, possibly due to more frequent rainfalls in the early season than in 1988. Moreover, the spider mites accumulated more heat units in 1988. In 1989 the growth season started earlier than in 87/88. The two locations Hallau and Zizers had the highest total mite load and obtained the smallest amount of rainfall of all locations. Zizers with the highest mite load obtained a higher heat sum (degree-days) than Hallau with comparable rainfall. The different shapes of the population development can be explained by rainfall and temperature. At the beginning of the season Hallau had more rainfall and lower temperatures than Zizers, and in addition it received an acaricide treatment. This explains the relatively slow increase of mite numbers at Hallau. The number of winter eggs was equal in both sites.

Although the resulting mite loads were similar in Stäfa 88 and Hallau 89, the dynamics were different. Hallau started with a large number of winter eggs, but the hatching larvae were decimated by an acaricide treatment. In Stäfa 88 the temperatures were higher and therefore they accelerated population development, but rainfall apparently limited the

Table 2. Annual accumulated heat sum (degree-days > 10°C), rainfall, estimated number of surviving winter eggs and simulated mite load (postembryonic stages, [mite-days] of *P. ulmi* per vine plant at four locations

Location	Heat sum [dd]	Rainfall [mm]	Winter eggs	Mite load
Stäfa 87	1117.9	1374.8	1400	343'007
Stäfa 88	1249.4	1458.1	1000	677'298
Hallau 89	1166.2	751.9	6600	730'642
Zizers 89	1225.8	690.1	6400	1'096'082

population growth. The two contrary effects of temperature and rainfall are most evidenced by the comparison of the number of mite-days in the Stäfa 87 data (low heat sum, high precipitation) and Zizers (high heat sum, low precipitation), leading to a higher mite load in Zizers (table 2). Additionally, the higher winter egg number in Zizers also contributed to the larger population.

The evaluation of rainfall and nitrogen effects on the populations of *P. ulmi* in Hallau is illustrated in fig. 3. It shows that rainfall mortality exerted the most prominent effect on

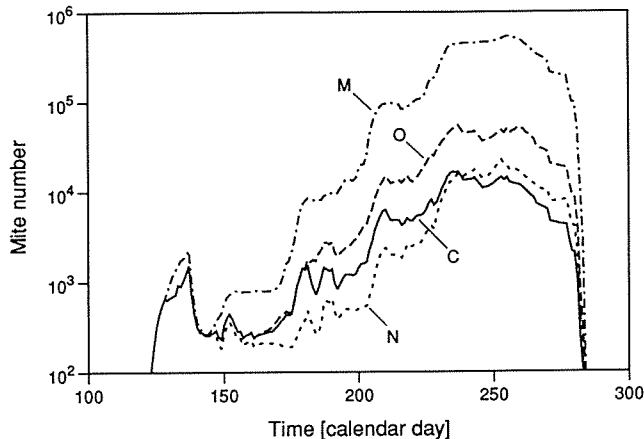


Fig. 3. Evaluation of the influence of rainfall and leaf nitrogen on the population development of *P. ulmi* at Hallau 1989 (M = simulation without mite Mortality caused by rainfall; O = without rain effect on Oviposition; N = without leaf N effect; C = Check, including all above effects)

the population pattern. Without this mortality (M in fig. 3) the simulated peak was 30 times larger than the control (C) and the population was larger throughout the whole season. Retaining rainfall mortality in the model, but omitting the negative effect of rain on oviposition (O) still yielded a considerably higher population peak than the standard simulation. The divergence of this curve from the standard occurred later in the season than the one of the no-mortality simulation. When the effect of leaf N was omitted (N), the populations remained lower until mid August. This was caused by the lack of young leaves rich in N favoring population development. At the end of the season the exclusion of N effects led to higher mite numbers than the standard, due to the missing detrimental effects of old, low-N leaves that export nitrogen to the reserves in the woody structures. Over the whole season, omitting the N effect overestimated the total mite load (expressed in mite-days) by 7%.

#### 4 Discussion

It has to be emphasized that the purpose of these simulations was to represent infestation patterns rather than to predict mite densities, and to assess the role of rainfall and nitrogen in the host-herbivore interplay. The pattern of the mite populations is similar in all locations: the populations remain on a low level until approximately the end of June, and then follows a more or less extended phase of high populations. As indicated already by the field data, the simulation confirms the remarkable fact that the population peaks occur only late in the season in August or even September. This curtails the importance ascribed to spider mite infestations during the sensitive phase of pre-bloom/bloom vine development (cf. CANDOLFI-VASCONCELOS and KOBLET 1990; CANDOLFI 1991). As an exception

Stäfa 88 showed two peaks, the first in late June. This simulation, however, is difficult to assess because of the unfortunate coincidence of the simulation minima with the field data. This emphasizes the need for a more frequent sampling schedule.

In this model the population dynamics are basically driven by temperature and rainfall. In contrast to temperature, only little attention has been directed to rainfall effects. This topic was addressed by a small number of studies, and in general they found a negative impact on spider mites (review by VAN DE VRIE et al. 1972; SIMPSON and CONNELL 1973; HUI et al. 1985; YANINEK et al. 1989). The effect may be direct by increasing mortalities, or via unfavorable humidity or elevated risks of disease to the mites (SIMPSON and CONNELL 1973). On the other hand, a recent publication by KLUBERTANZ et al. (1990) reported no significant effect of rainfall on *T. urticae* densities. In contrast to *P. ulmi* this mite species produces more webbing and preferentially inhabits the under side of the leaves. As a consequence *T. urticae* may be better protected against precipitation.

The simulation of the spider mite dynamics stressed the importance of the impact of precipitation. YANINEK et al. (1989) described a rainfall mortality function for high precipitation intensities in the tropics. This function proved unsuitable for our conditions and the data of HUI et al. (1985) were chosen for the model. Although these mortalities may appear exaggerated, they represented the rainfall effect in a satisfactory way. More detailed data on the relationship between mortality and short term rain intensities rather than rainfall per-day are needed to clarify this point. The second effect of rainfall on the ovipositional behavior of females needs to be further examined as well. In any case, precipitation does have negative consequences for spider mite egg production (HUI et al. 1985; YANINEK et al. 1989).

The evaluation of rainfall and nitrogen impact showed that the inclusion of nitrogen effects in the model is of minor importance compared to the dominant role of temperature and precipitation. Leaf nitrogen affects the infestation pattern rather than the total seasonal mite load. Since *P. ulmi* shows limited preference for leaf age classes during much of the season (CANDOLFI 1991) the incorporation of preferences for certain leaf age classes with different N concentrations appear here not to be worth-while – though easily feasible from the modelling point of view (cf. GUTIERREZ et al. 1988).

This modelling approach covers the plant-mite interactions more extensively than previous models. It permitted the identification of gaps in our knowledge of the system such as the realistic assessment of rainfall and pesticide effects. Thus, it is considered as a substantial component in the on-going analysis of the spider-mite/vineyard system.

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### Zusammenfassung

#### *Populationsdynamisches Modell der Roten Spinne (Acari, Tetranychidae) unter Berücksichtigung der Weinrebenentwicklung*

Ein dynamisches Modell der Populationsentwicklung der Roten Spinne *Panonychus ulmi* und dessen Validation mit vier unabhängigen Datensätzen werden beschrieben. Das Modell weist folgende Grundzüge auf:

1. Die wichtigsten Steuervariablen der Milbenentwicklung, Mortalität und Reproduktion sind die täglichen Temperaturextreme und die Niederschläge. Sie werden zusätzlich durch Nahrungsangebot und Stickstoffverhältnisse der Wirtspflanze beeinflusst.

2. Die Populationskohorten durchlaufen Ei-, Juvenil- und Adultstadien. Ihr Wachstum und die Alterung oberhalb einem stadienspezifischen Entwicklungsnullpunkt werden mittels der Methode des „distributed delay“ modelliert, welche eine Streuung der mittleren Entwicklungsdauer beinhaltet.

3. Der „metabolic pool“ Ansatz bewerkstelligt die Verknüpfung der Weinrebenpopulation (*Vitis vinifera* L.) mit derjenigen der Roten Spinne. Die Beziehungen zwischen den zwei trophischen Stufen Wirt und Phytophage besitzen eine quantitative und eine qualitative Seite: Die Pflanze liefert den saugenden Milben die Nahrung, was umgekehrt einen Verlust der assimilierenden Blattfläche bedeutet. Der qualitative Aspekt betrifft den Einfluß der Stickstoff-Konzentration der Rebenblätter auf die Eiablage und Entwicklung der Spinnmilben. Der Energiefluß zwischen den trophischen Stufen wird in Trockensubstanz-Einheiten [g] ausgedrückt.

4. Die negative Wirkung des Niederschlags ist ein wichtiger Bestandteil des Modells. Der Regen übt einen starken Einfluß auf die Eiablage und Mortalität der Milben aus.

Für die Validation des Modells mit vier Datensätzen wurden alle Parameterwerte konstant gehalten mit Ausnahme der Fekundität, die möglicherweise bei Milbenstämmen in verschiedenen Rebbergen schwankt. Das Modell war imstande, die Milbendynamik in verschiedenen Orten und Jahren nachzuvollziehen.

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