

## Chapter 3.1 Aspects of Damage Assessment

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 Spider Mites their Biology, Natural  
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### INTRODUCTION

Phytophagous mites are potentially a major pest of the main food, fibre and ornamental crops (Pritchard and Baker, 1955). This potential for damage has become increasingly evident during the last few decades. Spider mites may cause severe damage which results in very heavy losses in such crops as citrus, avocado, beans, cotton, apples, pears, plums and many other horticultural and ornamental crops. The damage caused by spider mites has commonly been so obvious (to the extent of complete 'burning' or leaf abscission) that only a limited effort has been made to document the physiological nature of the losses or to determine precisely under what conditions, what levels of density, and in relation to what species, those losses actually occur (Van de Vrie et al., 1972). It is known, however, that spider mites do not commonly cause widespread damage in agroecosystems where productivity is far below its potential. Two complementary explanations for this phenomenon are usually found in the literature.

The first and most common explanation is that in agroecosystems where productivity is far below its potential, regulatory factors such as diseases and predators (parasites are unknown) control the spider mite populations. In agroecosystems where production levels are high broad-spectrum pesticides are usually used. The pesticides have a more adverse effect on the enemies of the spider mites (predators) rather than on the spider mites themselves, thus enabling an outbreak of the latter.

The second explanation is that crops which are grown at near-optimal levels, i.e. where growth is not limited by water or nutrients, form an excellent food source for parenchyma-cell-sucking organisms such as spider mites. Under these conditions, regardless of the influence of agronomical measures on mite enemies, the development rate, fecundity, reproduction rate and lifespan are all positively affected and enhance the increase in mite populations which can in turn result in occasional outbreaks (Van de Vrie et al., 1972).

Another, not often mentioned reason for the importance of spider mites in highly productive ecosystems concerns man's concept of damage. Well defined economic injury levels (EIL) are normally absent or based on specialists' estimates. Detailed and well performed field experiments to determine damage relations are virtually absent (Van de Vrie et al., 1972). Many detailed studies of the various effects of spider mites on tissue and individual plant plots have been carried out under controlled conditions (Tomczyk and Kropczynska, Chapter 1.4.7), but the consequences of these observations for crops grown under field conditions are rarely evaluated.

The belief that a well functioning crop should be free of visible symptoms of spider mite attack is still one of the major components for the definition of economic injury levels. Although this may be valid for ornamental crops which are sold for aesthetical purposes, this is certainly not true for the food and fibre crops. These crops have the capacity to tolerate some degree of spider mite attack (Van de Vrie et al., 1972). More fundamental field experiments which study the spider mites and crop physiological relations are necessary if the economic injury levels are to be placed on a solid basis. However, such studies are virtually absent as combined efforts of crop agronomists and entomologists to define damage relations are seldom found and thus a large gap exists between laboratory studies and field experiments. Simulation models may help to bridge this gap between the detailed laboratory studies on mite damage described by Tomczyk and Kropczynska (Chapter 1.4.7) and the economic injury level needed for the supervision of pest and disease control in acarine systems. This will be illustrated in this chapter.

#### CROP PRODUCTION LEVELS, SPIDER MITE INJURY AND DAMAGE

The introduction of the EIL concept for control in economic entomology in the early 1960s was an important step forward in the development of field, crop and pest specific thresholds (Stern et al., 1959). It was felt necessary to distinguish between different factors that affect the expression of yield loss and damage effects (Stern, 1973). Crop production levels can influence these damage effects. It is, therefore, helpful to distinguish four production levels (de Wit, in Penning de Vries and Van Laar, 1982).

Production level 1: growth occurs under conditions of ample plant nutrients and water. Growth and yield are determined by weather conditions and crop physiological characteristics. Growth rates of  $C_3$  plants under these conditions amount generally to 200 kg dry matter  $ha^{-1} day^{-1}$  and for  $C_4$  plants depending on latitude they vary between 200 and 400 kg dry matter  $ha^{-1} day^{-1}$ . Potential yields are approached under these conditions.

Production level 2: growth is limited by shortage of water at least part of the time, so that growth rates are reduced by the ratio between the actual and potential transpiration. Growth rates under these conditions are in general much lower than their potential value and vary between 100 and 200 kg dry matter  $ha^{-1} day^{-1}$ .

Production level 3: growth is limited at least part of the time by shortage of water and nitrogen and this results in growth rates which are generally lower than 100 kg dry matter  $ha^{-1} day^{-1}$ .

Production level 4: growth occurs under conditions where water or nutrients are limiting during the major part of the growing period so that growth rates vary usually between 12 and 50 kg dry matter  $ha^{-1} day^{-1}$ . Yields are generally not much higher than 1000 kg dry matter per hectare per growing season.

Unfortunately, most agricultural production ( $> 60\%$ ) takes place at production level 4 and only ca. 1% of the world's agricultural crops are classified as production level 1. Very few field crops belong to this group; only the intensive arable cropping situation in Western Europe approaches these circumstances. Many horticultural crops and some of the cash crops also fall into this production level. Most field crops and pastures are at production levels 3 and 4 and a minority fall into production level 2. At all production levels pests and diseases may play a role as yield-reducing factors. Spider mites, as indicated earlier, are only of importance in crops achieving production levels 1 and 2.

Spider mites seem to be specific for horticultural crops and high value and very intensively produced field crops. This is highlighted in the extensive review of the biology, ecology and pest status, and host-plant relations of Tetranychids by Van de Vrie et al. (1972); of 20 crops suffering from spider mite damage only 2 were field crops, i.e. cotton and soy beans. The crops suffering most from spider mite damage are: fruit orchards such as apple, pear, peach, almond, apricot and citrus; glasshouse crops such as beans and ornamental crops; and horticultural crops such as strawberries and snap beans. Crop conditions which are characterized by high and intensive production favour yield loss due to spider mites. This is due to the effect of the host crop condition on the population dynamics of spider mites and on the damage relation.

Many authors have demonstrated increases in population densities of spider mites associated with the application of pesticides (insecticides and fungicides). This is due to a direct effect of some insecticides such as DDT on the physiological stimulation on spider mites and indirectly due to the considerable effects of pesticides on the natural enemies of spider mites (Huffaker and Spitzer, 1950; Van de Vrie et al., 1972). The absence of control by natural enemies due to their death by pesticides causes a considerable increase in spider mite populations. The consequence of this increase in population numbers is in many cases amplified by the physiological effect on the host plant—spider mite relation, partly due to pesticide effects and mainly due to improved crop condition as a result of agronomical measures. Many laboratory studies have demonstrated an increased response in the host plant when well fed. Not only the tolerance is affected but changes also occur in plant-physiological parameters (Tomczyk and Kropczynska, Chapter 1.4.7). However, the quantitative evaluation of such effects at crop level is normally absent. Field experiments are difficult and very time consuming and are normally carried out under poor and variable environmental and agronomical circumstances. Soil condition, cropping history and agronomical measures are often not defined and they may be highly variable.

As a result of this, their conclusions are very specific and general guidelines cannot be based on such experiments. Economic injury levels based on these experiments are more estimated than based on the detailed plan physiological studies described by Tomczyk and Kropczynska (Chapter 1.4.7) as is the integration of this knowledge from proper field studies. Consequently the literature data on the conditions under which damage due to spider mites most clearly occurs is very conflicting. For the fruit tree red spider mite (*Panonychus ulmi* (Koch)) on apple, for example, Kuenen (1946, 1949) demonstrates that the damage due to this organism is more severe in hot dry years than in other years, whereas Jary and Austin (1937) report that damage is particularly severe in cool wet weather.

Similar results can be cited for the other damage/injury causing spider mites (Van de Vrie et al., 1972). Economic injury levels for the most important spider mite species (two-spotted spider mite, *Tetranychus urticae* Koch, fruit tree red spider mite or European red mite, *P. ulmi*, *Tetranychus pacificus* McGregor and *Oligonychus punicae* (Hirst)) are for this reason difficult to determine and are formulated for various crops by specialist meetings sponsored by F.A.O. instead of being formulated with well defined experiments which have been carried out under various but ill defined conditions.

## CROP LOSS ASSESSMENT

### Field experiments and economic injury levels (EIL)

To illustrate the difficulties in defining the economic injury levels based on ill-defined field experiments the experience with the fruit tree red spider mite on apple, one of the most studied host plant—spider mite relations, is given. In 1956 Van de Vrie showed in individual tree trials in The Netherlands, in a well kept, well fertilized and intensively controlled Beauty of Boskoop apple orchard, that a spider mite density of maximally 40 mites per leaf or 1–2 mites per  $\text{cm}^2$  or 1080 mite days per leaf or 54 mite days per  $\text{cm}^2$  caused a yield loss of 18% and a reduction of shoot growth of 30%. Avery and Briggs (1968a, b) in similar experiments in England using 2-year-old Lord Lambourne trees demonstrated that a mite density of maximally 2.5 mite/ $\text{cm}^2$  and 70 mite days did not result in significant differences ( $\alpha = 0.10$ ) in apple yield/ha or in shoot growth, dry weight of apples or the number of buds. In a detailed study from 1965 to 1971 at various sites in England, Light and Ludlam (1972) experimented in small plots situated in apple orchards. They used different spraying treatments to determine the immediate and delayed effects of the mites. Spider mite numbers were measured frequently and different pomological characteristics were recorded. The mite densities in their experiments varied from 800 mite days per leaf to 2000 mite days and densities of up to 40 mites per leaf were recorded. This experiment was statistically very well designed and should have picked up small significant differences. However, significant differences in yield could only be determined when the number of mite days per leaf exceeded 1350. In the year after the measured differences different pomological characteristics were recorded but in none of these parameters could significant differences be determined.

At Hood River Valley, Oregon (U.S.A.) a 4 year study using individual 10-year-old Newton and Golden Delicious apple was carried out by Zwich et al., (1976). The mite densities were observed at weekly intervals for various spider mite control treatments (timing and method of control). The trees were irrigated when necessary and nitrogen supply was abundant. Chemical control was in accordance with normal farming practice and the pruning was done chemically. Again, yield, fruit weight and various other pomological characteristics were measured. Maximum densities of 70 mites per leaf and maximally 1400 mite days were reached in these experiments. These high mite densities did not result in significant differences either in the yield or in other pomological characteristics. Only at the highest mite density was the chlorophyll content of the leaves significantly affected ( $\alpha = 0.10$ ). Effects on fruit growth, shoot length, number of buds and trunk diameter were absent in the year following the heavy infestation. Apparently the apple trees growing under 'optimal' conditions could tolerate high mite densities, up to 1900 mite days or a maximum density of 70 mites per leaf. These results led Zwich et al. (1976) to fix the economic injury levels of fruit tree red spider mites at 20–30 mites per leaf. This is ca. 10-fold the economic injury level proposed by the technical expert meeting of the F.A.O. in 1973. It seems impossible to explain these conflicting experimental results. Crop physiological parameters are however very loosely determined in all experiments described and the cropping history of the experimental orchards and crop agronomical measures are not given. Moreover the data on spider mite densities are often incomplete. The age composition of the spider mite population is not supplied and accuracy of the population density is not given. The way crop agronomical measures were

implemented is not described and the weather conditions during the experiments are not recorded. This lack of information makes the interpretation of data difficult.

Buth (internal report, 1977) performed field experiments in The Netherlands in a 4-year-old Winston-M9 apple orchard. The field was divided into 49 plots each plot consisting of 18 trees. Half of the experimental field was sprayed regularly with cyhexatin in order to keep it clear of spider mites (control). In both the treated and untreated blocks, subplots with different methods of soil coverage were examined. Mite densities were determined at 14 day intervals for 100 haphazardly taken leaves. The population densities reached maximally 96 mites per leaf or 2500 mite days per leaf. When this high density was reached the mites were controlled by a chemical treatment. For the control and treatment apple numbers per unit area did not differ, but slight differences between individual weights occurred. Differences in apple growth occurred before spraying and this difference did not alter after spraying (Fig. 3.1.1.). However, differences in yield between the treatment and control were not significant ( $\alpha \leq 0.05$ ). Differences in other agronomical measures, shoot length, trunk diameter and number of buds were not significant either.

Differences in treatment were absent in 1977 so that only after damage year effects could show up, however no differences occurred. Apparently the considerable mite load on the apple trees was not sufficient to cause noticeable damage. This may have been partly due to the abnormal weather conditions. In 1976 the growing season was dry and hot and apple orchards on the heavy clay suffered from water shortage. Since the plots were not irrigated the effects of water shortage were very clear in all treatments except for those where the undergrowth of weeds, etc. was completely prevented. Effects of the spider mites, when present, were completely overruled by effects of water shortage.

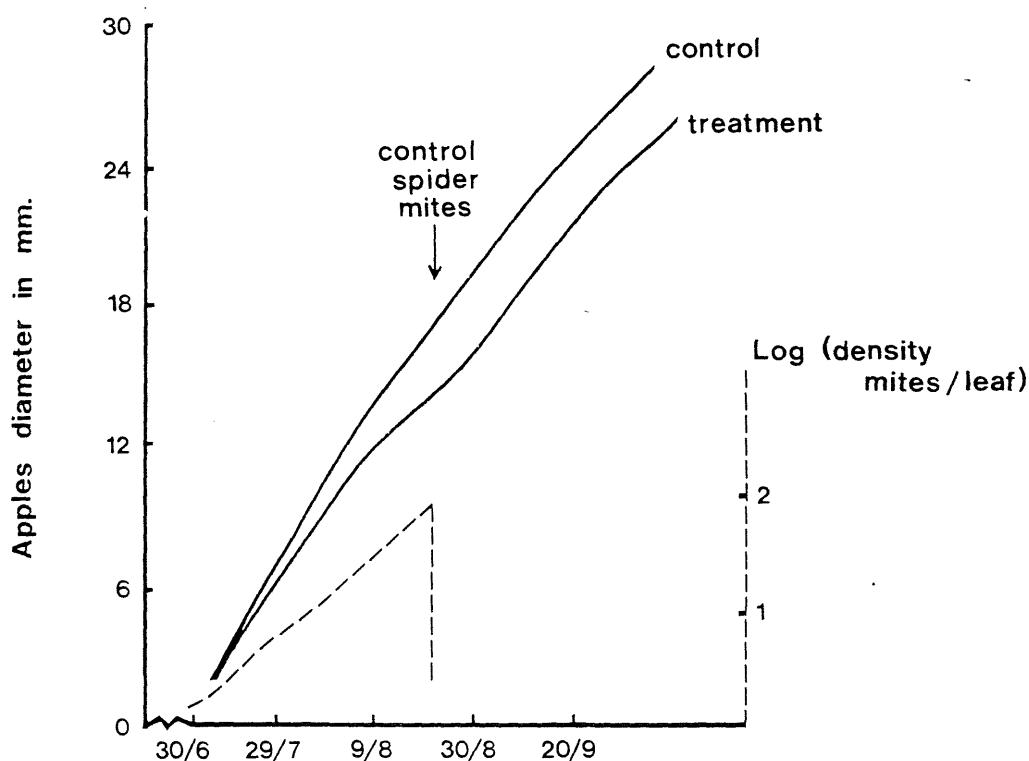


Fig. 3.1.1. Consequences of a heavy attack of fruit tree red spider mite on apple growth in a well kept apple orchard in The Netherlands (Buth, internal publication).

The studies presented above can be extended and in particular the studies of Hoyt et al. (1979) should be mentioned. However, from all these investigations it is not possible to formulate well defined economic injury levels. The results are conflicting. This may be partly due to the qualitative nature of many of these studies (Hoyt et al., 1979). Most of the studies compare trees with uncontrolled mite populations with trees having nearly complete control of mites, but some have treatments in which late or early attacks of mites are distinguished. This results in recommendations for injury levels which are variable in time (Van de Vrie, 1970; Hoyt et al., 1979). The proposed injury levels of Hoyt et al., (1979) are based on the mite day concept; they propose 2000–2500 mite days, which they consider to be on the 'safe side'. Late or early populations are in this case not distinguished. This level is much higher than the maximum densities of Van de Vrie (pers. communication), who proposes 2, 4 or 7 mites per leaf in the case of early, average or late spider mite attack. These densities correspond to 60, 120 or 180 mite days (Hoyt et al., 1979), respectively.

Tanigoshi (1975) takes an intermediate position. He considers 500 mite days as a reasonable economic injury level for fruit tree red spider mite. Apparently the conclusions of Smith (1966) referring to economic losses due to insects and mites are still valid: 'with a few exceptions, we have not established the economic threshold of insect injury'. Chant (1966) considered that economic threshold levels are almost invariably higher than expected. This statement may be confirmed by the different data given above and, more important, differences in proposed economic injury levels for spider mites are not shrinking but are increasing in size.

The considerable differences in economic injury levels proposed by different authors, apparently based on circumstantial evidence and the interpretation of their own field experiments, illustrates the need for experiments in which the specific conditions under which trials are carried out are well defined so that general guidelines may be formulated. However, it may be impossible to formulate general guidelines and more detailed experiments could add another millimetre of paperwork to that stack of experimental results which are difficult to interpret. The gap between the detailed observations in laboratory and glasshouse experiments described by Tomczyk and Kropczynska (Chapter 1.4.7) and the field data abundantly available in the literature seems too wide to bridge with one or two well defined experiments. The major reason for this is probably the great number of factors which are involved in the population growth of the spider mites and the host crop—spider mite relation. Therefore, damage relations based on field work only seem difficult to formulate.

#### Factors affecting yield loss

The basic interaction between mites and their host plants are affected by several abiotic and biotic factors. They may influence the population dynamics and the relation between yield loss (quantitatively or qualitatively) and number of mite units either in mite density or mite days.

Effects on population dynamics are widely described by many authors. Micro weather and nitrogen content of the host plant are generally considered to be the major factors (Van de Vrie et al., 1972). In detailed water culture experiments, Storms (1971) demonstrated the effect of nitrogen concentration of bean leaves on fecundity and development of two-spotted spider mites. He stated that not only nitrogen content but also age of the leaves is of importance. In similar detailed water culture experiments with apple seedlings and fruit tree red spider mite Rabbinge (1976) showed that

significant differences in fecundity are only present between leaves with a nitrogen content of 3.5 and 1.8%. Effects on development were only clear when leaves were suffering from nitrogen shortage. However at present, nitrogen levels in apple leaves in modern fruit orchards vary between 2.2 and 2.6% (Rabbinge, 1976), so that a direct effect of nitrogen on fecundity may be negligible. This is confirmed by the pot experiments of Van de Vrie and Delver (1979). For 2-year-old apple trees, Beauty of Boskoop on M<sub>2</sub> rootstock in pots they showed that when the nitrogen levels become extremely low a considerable effect on the population of spider mites could be demonstrated, however as soon as nitrogen levels exceeded 1.8% any difference in fecundity and population increase is absent.

During ageing of apple leaves nitrogen levels decrease considerably and this may have some effect on the total number of mite days in field experiments, but the size of these effects seems negligible when peak densities exceed 25 mites/leaf. Other spider mite-host crop relations have not been studied in that much detail so that conclusive remarks cannot be made. It seems clear, however, that nitrogen concentrations in leaves may affect the population parameters only when differences become considerable. This does not occur in crops producing at production levels 1 and 2 where most spider mite damage is found. Under these conditions maximal fecundities are normally reached.

In many crops the effect of micro weather on spider mites is generally complex; variations exist in temperature, sunlight, wind profiles, etc. Therefore, many authors (e.g. Van de Vrie et al., 1972) claim that micrometeorological observations are needed to understand the population dynamics of spider mites. Using experimental and modelling studies, Rabbinge (1976) showed that for the *Panonychus ulmi*-*Amblyseius potentillae* system in apple orchards, small oviposition rate changes have greater impacts on population dynamics than variations in micro weather. This conclusion does not hold when the spider mites have a clear preference for a particular place on the crop, e.g. the leaves at the outside of an apple tree. Before starting detailed microweather measurements it is therefore advisable to evaluate possible effects with population models (Welch, 1979).

The effect of crop condition on yield loss per unit of mite density has been poorly studied. Herbert and Butler (1973) have investigated the effect of spider mite populations on the nitrogen content of leaves. This may be considerable at high mite densities, which have been shown to promote ageing of the trees. These effects will become more severe when crops are producing at levels where the nitrogen is being redistributed and translocated to the harvested products (Vos, 1981).

However, more-detailed studies of these phenomena under field conditions are extremely scarce and would require a major effort from entomologists, crop physiologists and agronomists. The absence of quantitative information on the exact effect of crop condition on damage relations of spider mites is probably partly due to the lack of physiological knowledge about the crops which suffer most from spider mite damage. Perennial crops are physiologically much more difficult to understand than annual crops which have been studied very widely. Another approach is required to obtain more insight which may help to formulate economic injury levels.

## SIMULATION

### Experimental simulation

To study some of the consequences of spider mites and insects on the performance of crops Hall and Ferree (1976) measured experimentally the photosynthesis of apple leaves from which parts had been removed by cork borers. Losses in leaf area of up to 7.5% had no significant effect on net photosynthesis. Significant reductions in net photosynthesis were observed 1 day after treatment when losses in leaf area exceeded 10%. Increased circumference of the leaf area lost by simulated insect feeding increased the reduction in net photosynthesis. Injury to main side leaf veins significantly amplified the reduction in net photosynthesis compared with net photosynthesis values of leaves with interveinal injury.

Apple leaves can withstand a considerable decrease in leaf area. At crop level this phenomenon is even stronger. Perennial crops have in most cases Leaf Area Indices which exceed  $3 \text{ m}^2$  leaf area per  $\text{m}^2$  soil area so that complete light interception is found. In these situations leaf area reduction does not reduce the growth rate. Only when the crops are subjected to summer pruning or they are poor in leaf area for some other reason would the mutilation of leaf mass affect photosynthesis, and consequently the growth, considerably. Simulation studies of this type may be useful for insects that simply consume leaf mass, such as for example leaf beetles, but are inadequate for spider mites as leaf area is not removed but is initially physiologically affected and then killed without removal, making light interception still possible. Experimental simulations are then difficult to perform.

### Simulation with models

To study the consequences of spider mites on crop growth, combination models of the population dynamics of the mites and of the growing crop may be used. Such combination models have been developed for insect pests in specific crops, such as cotton, alfalfa, apple and wheat (Gutierrez and Wang, 1976; Rabbinge et al., 1981). In some cases, comprehensive simulation models have led to simplified economic models for decisions for spraying or spraying, but only in a very few cases is their reliability good enough to use them as management tools.

Multivariate regression models of the type developed by Thompson (1969), Pitter (1977) and Bridge (1976) are often more reliable for the average situation. With correct 'tuning', such models can accommodate better than average field conditions since historical data include the variations in plant stand, diseases and pests, and nutrients and water supply. Such regression models perform best in predicting the mean performance of a population of fields, whereas the dynamic models may work best with the individual field. Regression type models would not lead to better insight but to descriptions of the average situation which may be used for recommendations to individual farmers. However, the great variability, demonstrated above for the fruit tree red spider mite—apple crop system, would lead to an average which does not help the farmer as variability seems more normal than the mean responses.

To study the causes of these differences in mite—crop systems dynamic simulation models are needed and they may help to formulate the economic injury levels or rather economic injury *relations* that are field specific since they take into account the characteristics of site and host crop—spider mite relation. In this way dynamic simulation models form the bridge between

the detailed studies and factual knowledge of the effects of spider mites on morphological and plant physiological characteristics on one hand and the behaviour of an infested crop on the other.

Of the dynamic models, the explanatory ones should be used, as these integrate the underlying physiological and morphological processes which determine crop behaviour. By sensitivity analysis and simplification, summary models are developed which may be used in management systems (Rabbinge, 1983).

Thus we may distinguish 3 types of models which express different levels or phases of development, knowledge and insight. At the frontiers of knowledge, preliminary models are very common. They enable the quantification and evaluation of hypotheses and are useful as such, but seldom survive long. Many different hypotheses may be expressed quantitatively in these models and their consequences may be calculated and used for an evaluation. These models may help as guidelines in experimental research. Comprehensive models may be developed from these preliminary models as a result of scientific progress; more knowledge and insight becomes available and may promote the lucidity of the system studied. The third category of models comprises summary models. These models are derived from comprehensive models and serve as vehicles for communication, instruction and management. Since summary models are derived from comprehensive models, different forms of these may exist depending on the objective and interest of its user.

Combination models of crop growth and pests and diseases exist in each phase of model development. Combination models of mites and crops are however very scarce. To illustrate the approach a preliminary combination model of a spider mite population and a field crop will be discussed.

A summary model for potential growth (SUCROS) (Penning de Vries and Van Laar, 1982) is interconnected with a population model of spider mites. The summary model for crop growth comprises three modules. The first module comprises the computation of photosynthesis. De Wit's (1965) calculation procedure to compute photosynthetic rates for closed green crop surfaces is adapted and used to determine the gross photosynthesis rate of the crop. Daily total global radiation, LAI and photosynthetic parameters, light use efficiency and photosynthesis at light satiation are the only input parameters. The second module calculates the respiration of the crop. Growth respiration and maintenance respiration are distinguished. Growth respiration is needed for the construction of structural plant material as proteins, fats and carbohydrates out of the primary photosynthetic products. The conversion efficiencies computed by Penning de Vries (1975) are used to determine the amount of primary photosynthetic products needed to produce structural plant material. Maintenance respiration is needed for the maintenance of already existing structural plant material. Its structure must be maintained and this involves the turnover of protein and the sustaining of ionic gradients and membrane structure. Maintenance respiration is temperature dependent, whereas growth respiration is not.

The third module comprises development and partitioning. Development of a crop and morphogenesis is introduced through an empirical relation between development rate and temperature. Morphogenetic processes are not simulated as they are too poorly understood. Partitioning of structural plant material between the various plant organs is introduced through another empirical relation.

A full description of the summary model and the comprehensive model on which it is used can be found elsewhere (De Wit et al., 1978; Penning de Vries and Van Laar, 1982). The summary model can be applied to various crops

when the appropriate parameters and characteristic relations are introduced. Here it is applied to a field crop, wheat, and the two-spotted spider mite *T. urticae*. Coupling of this summary model to the population model of the spider mites is based on the nature of the interrelations. Plant mites inject their stylets through the epidermis into the parenchyma cells and swallow the content. The attached cells may die and the surrounding cells often show phenomena such as suberization of cell walls, decrease of photosynthetic activity and increased maintenance respiration. The summary model for the crop is changed at two places to introduce these effects.

Firstly the maintenance respiration is increased with a term that accounts for the mites. This respiration term is considered to be proportional to the mite density. Although this may be true at relatively low densities it overestimates the effects of the mites at high densities. Secondly, an effect of the mites on the photosynthetically active leaf mass is introduced. This effect is also mite-density-dependent, the basis of these effects being derived from measurements of Tomczyk and Van de Vrie (1982) and damage data of Sabelis (1981) on chrysanthemum and roses. The density of the mites is simulated by way of 8 age classes, lumping the different morphological stages together. A more realistic population model which may be combined with a comprehensive crop model should consider the different morphological stages and the sensitivity of development rate to temperature and food quality (Rabbinge, 1976; Sabelis, 1981). This effect, and that of temperature and other abiotic factors, on reproduction, mortality, etc., are not yet combined.

Computations with this preliminary (conceptual) model show that minor changes in the respiration rate due to the presence of the mites causes a major effect on the growth rate of the canopy; consequently yield is considerably affected. The same holds for the effect on leaf senescence; an increase in average leaf senescence of 4 days results in a yield loss of 500 kg wheat/ha. These processes and effects only occur when weather conditions are favourable: high temperature, fast crop development and limited radiation levels.

Further hypothesis testing may be carried out with this combination model. For example, effects of webbing, which appears earlier than injury symptoms (Sabelis et al., 1983), on assimilation rate, light use efficiency and/or assimilation rate at light satiation, may be evaluated. However, the reliability of such model computations is doubtful as too many descriptive relations on the system level are needed to run them and too many guestimates are required. Therefore, comprehensive models are needed in this process of hypothesis testing and gaining insight into the consequences of different effects of the spider mites on plant physiological parameters.

The ultimate aim of such studies is to manipulate the acarine system using the damage relations which are developed with these combination models.

#### CONCLUDING REMARKS

Evidence on mite-host plant relations is given by Tomczyk and Kropczynska (Chapter 1.4.7) and provides some possibilities which explain the probable interactions between mites and plants. Their factual data are however so patchy that a complete picture is difficult to draw.

Mechanical damage by piercing the tissues seems of minor importance although it may cause water loss which could cause water stress in the plant. This would, however, require very heavy attacks by spider mites.

Evaluation of such effects on crop level is virtually absent as the experimental conditions necessary to test such an hypothesis under field conditions are never satisfied. For that reason and to promote the efficiency of scientific efforts, combination models of growth of the host plant and the population of spider mite should help. Another reason for using the modelling approach is due to the complex nature of the effects spider mites may cause such as: changes in the concentrations of soluble sugars and amino acids; decrease in the water content of the crop; and an increase in the concentration of the first products of photosynthesis due to blockage of starch synthesis resulting from saliva injection.

The possibility of incorporating crop condition in such models makes an evaluation for various circumstances and growing conditions possible.

In that way the knowledge of the fundamental processes governing the spider mite—host plant relation may be used to gain insight into the behaviour of infested crops under various circumstances. Economic Injury Levels should be based on cooperative work of acarologists, crop agronomists and crop physiologists.

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#### REFERENCES

- Avery, D.J. and Briggs, J.B., 1968a. Damage to leaves caused by fruit tree red spider mite, *Panonychus ulmi* (Koch). *J. Hortic. Sci.*, 43: 463—473.
- Avery, D.J. and Briggs, J.B., 1968b. The aetiology and development of damage in young fruit trees infested with fruit tree red spider mite, *Panonychus ulmi* (Koch). *Ann. Appl. Biol.*, 61: 277—288.
- Bridge, D.W., 1976. A simulation model approach for relating effective climate to winter wheat yields on the Great Plains. *Agric. Meteorol.*, 17: 185—194.
- Buth, G.J.C., 1977. De invloed van de stikstofvoeding van appelbomen op de populatie ontwikkeling van de fruitspintmijt, *Panonychus ulmi* (Koch) en de reactie van de boom hierop. Doctoral verslag. Vakgroep Entomologie. Agricultural University, Wageningen, The Netherlands.
- Chant, D.A., 1966. Integrated control systems. In: *Scientific aspects of pest control*. National Academy of Science, Publication 1402, Washington DC.
- De Wit, C.T., 1965. Photosynthesis of leaf canopies. Agricultural Research Reports No. 663, Pudoc, Wageningen, The Netherlands.
- De Wit, D.T. et al., 1978. Simulation of assimilation, respiration and transpiration of crops. *Simulation Monographs*, Pudoc, Wageningen, The Netherlands, 148 pp.
- Gutierrez, A.P. and Wang, Y., 1976. Applied Population Ecology: Models for crop production and pest management. In: G.A. Norton and C.S. Holling (Editors), IIASA. Proceedings of a Conference on Pest Management.
- Hall, F.R. and Ferree, D.C., 1976. Effects of insect injury simulation on photosynthesis of apple leaves. *J. Econ. Entomol.*, 69: 245—248.
- Herbert, H.J. and Butler, K.P., 1973. The effects of European red mite, *Panonychus ulmi* (Acarina: Tetranychidae), infestations on N, P and K concentrations in apple foliage throughout the season. *Can. Entomol.*, 105: 263—269.
- Hoyle, S.C., Tanigoshi, L.H., and Browne, R.W., 1979. Economic injury level studies in relation to mites of apple. In: J.G. Rodriguez (Editor), *Recent Advances in Aracarology*, Vol. I, pp. 3—13.
- Huffaker, C.B. and Spitzer Jr., C., 1950. Some factors affecting red spider mite populations on pears in California. *J. Econ. Entomol.*, 43: 819—831.
- Jary, S.G. and Austin, M.D., 1937. Department of Entomology. *J. S.-east Agric. Coll. Wye* 39: 9—15.

- Kuenen, D.J., 1946. Het fruitspint en zijn bestrijding. *Tydschr. Plantenziekten* 52: 69—82..
- Kuenen, D.J., 1949. The fruit tree red spider mite (*Metatetranychus ulmi* Koch, *Tetranychidae*, Acari) and its relation to its host plant. *Tydschr. Entomol.*, 91: 83—102.
- Light, W.I.St. G. and Ludlam, F.A.B., 1972. The effects of fruit tree red spider mite, *Panonychus ulmi* Koch on the yield of apple trees in Kent. *Plant Pathol.*, 21: 175—181.
- Penning de Vries, F.W.R., 1975. The cost of maintenance processes in plant cells. *Ann. Bot.*, 39: 77—92.
- Penning de Vries, F.W.R. and van Laar, H.H., (Eds.), 1982. *Simulation of Plant growth and crop production. Simulation Monographs*, Pudoc, Wageningen, 308pp.
- Pitter, R.L., 1977. The effect of weather and technology on wheat fields in Oregon. *Agric. Meteorol.*, 18: 115—131.
- Pritchard, A.E. and Baker, E.W., 1955. A revision of the spider mite family *Tetranychidae*. *Mem. Ser. Vol. 2, San Francisco Pac. Coast Entomol. Soc.*, 472 pp.
- Rabbinge, R., 1976. Biological control of fruit tree red spider mite. *Simulation Monographs*, Pudoc, Wageningen, 234 pp.
- Rabbinge, R., 1983. How to use combination models in crop protection, *SROP Bull.*, 1983/VI/2, pp. 31—46.
- Rabbinge, R., Drees, E.M., van der Graaf, M., Verberne, F.C.M. and Wesselo, A., 1981. Damage effects of cereal aphids in wheat. *Neth. J. Plant Pathol.*, 87: 217—232.
- Sabelis, M.W., 1981. Biological control of two-spotted spider mites using phytoseiid predators. Part 1. Modelling the predator—prey interaction at the individual level. *Agricultural Research Report No. 910*, Pudoc, Wageningen, 242 pp.
- Sabelis, M.W. et al., 1983. Experimental validation of a simulation model of the interaction between *Phytoseiulus persimilis* and *Tetranychus urticae* on cucumber. *SROP Bull.*, 1983/VI/3, pp. 207—229.
- Smith, E.H., 1966. Advances, problems and the future of insect control. In: *Scientific Papers of Pest Control*. National Academy of Science, Washington DC, pp. 41—72.
- Stern, V.M., 1973. Economic thresholds. *Annu. Rev. Entomol.*, 18: 259—280.
- Stern, V.M., Smith, R.F., Van de Bosch, R. and Hagen, K., 1959. The integration of chemical and biological control of the spotted alfalfa aphid — Part I. The integrated control concept. *Hilgardia* 29: 81—101.
- Storms, J.J.H., 1971. Some physiological effects of spider mite infestation on bean plants. *Neth. J. Plant Pathol.*, 77: 154—167.
- Tanigoshi, L.K., Hoyt, S.C., Browne, R.W. and Logan, J.A., 1975. *Ann. Entomol. Soc. Am.*, 6: 972—986.
- Thompson, L.M., 1969. Weather and technology in the production of corn in the U.S. Corn Belt. *Agron. J.*, 61: 453—456.
- Tomczyk, A. and Van de Vrie, M., 1982. Physiological and biochemical changes in three cultivars of chrysanthemum after feeding by *Tetranychus urticae*. *Proc. 5th Int. Symp. Insect—Plant Relationships*, Wageningen, 1982, pp. 391—392.
- Van de Vrie, M., 1956. Over de invloed van spintaantasting op de opbrengst en groei van vruchtbomen. *Tydschr. Plantenziekten*, 62: 243—257.
- Van de Vrie, M. and Delver, P., 1979. Nitrogen fertilization of fruit trees and its consequences for the development of *Panonychus ulmi* populations and the growth of fruit trees. In: J.G. Rodriguez, (Editor), *Recent Advances in Acarology*, pp. 23—31.
- Van de Vrie, M., McMurtry, J.A. and Huffaker, C.B., 1972. Ecology of mites and their natural enemies. A review, III Biology, ecology and pest status, and host plant relations of Tetranychids. *Hilgardia* 41: 345—432.
- Vos, J., 1981. Effects of temperature and nitrogen supply on post floral growth of wheat: measurements and simulations. *Agricultural Research Report 911*, Pudoc, Wageningen, 164 pp.
- Welch, S.M., 1979. The application of simulation models to mite pest management. In: J.G. Rodriguez (Editor), *Recent Advances in Acarology*, pp. 31—41.
- Zwich, R.W., Fields, G.J. and Mellenthin, W.M., 1976. Effects of mites population density on 'Newton' and 'Golden Delicious' apple tree performance. *J. Am. Soc. Hortic. Sci.*, 101: 123—125.