

## 10.1 Systems analysis and simulation as an aid to the understanding of acarine predator-prey systems

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### INTRODUCTION

During the last decade systems analysis and simulation have gained increased interest in crop protection. In the Working Party on Integrated Control of Pests, these techniques were so far used mainly to analyse and understand biological control with mites.

The experience with introduction of endemic predatory mites and modified spraying schemes and products indicate that these predatory mites can reduce and maintain populations of fruit-tree red spider mite below the economic threshold. At present, predatory mites are coming into wide use in the control of spider mites in apple orchards, and a large proportion of the growers of vegetables in greenhouses are using predatory mites for control of spider mites in cucumber and sweet peppers. For sweet peppers the predatory mites can be used as an acaricide. A permanent control system is desirable for all crops but it is questionable whether it can be achieved. This study investigates the possibilities for such control in relation to prey and predatory mite species, their spatial distribution, webbing activity and behaviour. In the two crops, the changes with introduction of predatory mites have been measured, but the mode of control is still poorly understood. This understanding should be based on integration of the knowledge of the underlying ecological processes. Our study with simulation models aimed at such an integration and at closer insight in the acarine systems and their sensitivity to disturbance. It may thus pave the way for simple prescriptions on how to manage the prey-predator system in the course of time in relation to crop status and climate. Simplified models can thus lead to advice in sprayings and interventions with predatory mites or alternate prey; they may also help in planning observations during the monitoring phase.

### MODELLING TECHNIQUE

The models used in this study are of the state-variable type, and contain state variables, that characterize quantitative properties of the system, such as the number of eggs and females, the amount of biomass or the content of the predator's gut, rate variables that express the rate of change of the state variables, such as development rate, oviposition rate or the predator's digestion rate, and driving variables that characterize the influence from outside, such as macrometeorological variables.

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Often a hierarchical approach is used. It is based on the idea that only two levels of causal depth should be distinguished in a model. For example the rate of assimilation may be explained from knowledge of the stomatal behaviour, the physiology of cells may be explained from the underlying biochemical processes. However, a problem in using this principle is that in complicated systems the causal relations are so manifold that a relational diagram looks like a spider's web rather than a pyramid. Usually the causal connections are more numerous in some places than in others, so that it is sometimes possible with some skill and effort in modelling, to distinguish regions with relatively many relations inside and only a few outside. These regions are called submodels.

Often simplified and short mathematical relations based on calculations with these submodels are used in the higher-ordered models of the whole system. Models on walking behaviour of a predatory mite may, for example, constitute one of the models on subprocesses of the predation process, which in its turn is one of the elements of a model on the population dynamics of predacious and prey mites in a crop system.

#### POPULATION MODELS

For both prey and predator, population models are based on knowledge of the effect of humidity, temperature, daylength and food quality. Relations between rates of development, mortality, oviposition, ageing, diapause on one hand and temperature or other physical factors on the other hand are introduced based on data from the literature, on estimates and on laboratory experiments. To account for the different morphological stages, age classes are distinguished. The residence time in each age-class depends on the length of that development stage of the animals. Dispersion in time during development and ageing is also taken into account. For example eggs of one batch laid at the same moment hatch at different times. To do so, a special 'boxcar' routine is developed with which development through different stages is simulated. This subroutine mimics the dispersion in time during development and ageing and adapts the mimicked dispersion to external conditions. Basically this is done by distinguishing artificial age-classes within the morphological age-classes, which are passed at different rates.

#### PREY-PREDATOR INTERACTIONS

The core of the population models of prey and predatory mites consists of the interactions between the two populations. These interactions include functional responses of the predator to prey density and quantitative responses of the predator to increasing or decreasing prey densities. To grasp the complicated prey-predator relation, Fransz (1974) unravelled behavioral components of the predation process in detail. He found that the predator's behaviour was governed by the satiation level of the gut and that this induces changes in prey preference and prey utilization. Fransz's studies were done with the two-spotted spider mite and the predatory mite *Metaseiulus occidentalis*. The adult female predator (the most voracious stage) shows a strong preference for the younger stages of the prey, but this preference decreases when the predators are 'hungry'. To measure prey preference and prey utilization in relation to satiation level of the predator, the predation process was analysed in detail.

~~A time series of the predation process with all its elements was made. A searching predator encounters a prey and this may result in a killing. What happens depends on the satiation level of the predator. In hungry predators, the success ratio (number of successful encounters divided by the total number of encounters) is high and in satiated predators low. The handling or killing of the predator takes some time (handling time), after which the predator may start feeding. The length of the feeding period depends again on the satiation level of the predator since hungry predators may stay long with their prey, even after the prey's body content is completely consumed, whereas satiated predators may leave their prey before they are completely consumed.~~

#### SATIATION LEVEL OF THE PREDATOR

Apparently the satiation level (gut content) is one of the most important state variables in the system. Several ways to measure the satiation level are possible. For fruit-tree red spider mite and the predatory mite *Amblyseius potentillae*, gut content can be scored visually because well-fed predators are dark and reddish, while hungry predators are whitish and transparent. A colour scale was therefore developed that related the amount of leaf and animal pigments in the predator, which together constitute the colour, to the relative predation rate and prey utilization. These relations were introduced into the population models. Oviposition rate and development rate of the predator (quantitative response) also depended on the satiation level and temperature and were similarly introduced into the population model. If a visual characterization of the satiation level is impossible, the weight of the predators may be used as a state variable that governs predatory behaviour.

#### STOCHASTIC CHARACTER OF THE PREDATION PROCESS

Two events in the predation process show a clear stochastic character. These are the encountering and abandoning of the prey. Franz (1974) showed that because of the curvilinear relationships of the encountering rate and abandoning rate with the predator's satiation level, stochastic models have to be used. With linear relationships, the differences between deterministic and stochastic models were absent. Since the relations mentioned were non-linear, a stochastic model was necessary. This tedious affair required much computer time and so the development of other techniques was necessary. Especially for population models of prey-predator interactions, simplified models are urgently needed.

Franz (1974) therefore introduced a new simulation method called compound simulation. This was basically a deterministic simulation model for classes of individuals with a certain satiation level, which are iteratively reclassified in each time interval. When the number of classes is properly chosen, the results of this model scarcely deviate from the stochastic model and the computer time is considerably less.

Another way to account for the stochastic character of some elements of the predation process is to apply queuing theory, as proposed by Taylor (1976). In this approach, the predator is considered to be a service facility, for example a dentist, and the prey to be a client. This client may enter the waiting room (gut) at a certain rate in expectation of the service (digestion). To evaluate the mentioned predation models, i.e. deterministic,

~~stochastic, compound and queuing, their outcomes were compared with the results of experiments on the predation rate of *M. occidentalis* on eggs of two-spotted spider mite. The deterministic model gives erroneous results and the outcomes of the three other models fall within the confidence intervals of the measurements.~~

The model calculations further showed that if the number of two-spotted spider mites was kept constant with one standardized<sup>1</sup> *M. occidentalis* predator on a leaf disc, an equilibrium was reached within a few hours. In that situation, the degree of satiation of the predatory mite oscillates with a small amplitude at a level that depends mainly on predator and prey density and on the temperature of the system. In this steady state, unique relations exist between the predation rate and the density of prey and predator, so that simplified relations may be introduced in the population models. In the situation of the fruit-tree red spider mite the relative predation rate (predation rate divided by prey density in the steady state), and prey utilization expressing the degree of consumption of a prey are introduced as functions of the satiation level. Temperature affects both these relations and evidently also the rate of digestion and thus the decrease in satiation level.

#### MICROWEATHER

Since the mites operate in the small laminar layer around the leaf, they are exposed to the microweather there. To evaluate the effect of microweather on the biological parameters, a microweather simulator was coupled to the population models. For the fruit-tree red spider mite — predatory mite system, the result of this combined model calculation does not differ from the population model calculations in which air temperature was used as a driving force. Thus the wide variety of leaf temperatures is such that the few places with temperatures much higher than the air temperature must be cancelled out by a high number of leaves with temperatures slightly lower than the air temperature.

#### VALIDATION OF THE POPULATION MODELS

Evaluation procedures should be performed by comparing model output with the results of independent experiments on the population level. The simplest evaluation of the population models of prey and predator mites is by measurement of the population growth of prey and predator in the course of time in small ecosystems under controlled conditions in situations with and without predators. The results for the fruit-tree red spider mite are shown in Figure 1 and are reached with a model in which the difference in size of the system is introduced by simple extrapolation of the surface on which the predation process experiments are done (5.6 cm<sup>2</sup>) to the surface of the ecosystem. Although the results of this evaluation were reasonable, it was questionable whether such a simple extrapolation is permissible, since in many cases errors due to the heterogenous distribution of the prey and the specific walking pattern of the predator may counterbalance but also cause considerable deviations from the simulated pattern. For the two-spotted spider mite, this question was examined. In

1. The predatory mites used in the predation experiments were reared under constant conditions and are of a well defined age, gut content and food history.

that system, prey are distributed in clusters and interfere with the mobility of the predator by the production of a dense web. Within these webbed colonies, very high densities of prey, 20-100 cm<sup>-2</sup>, are reached. Outside and inside the colony, behaviour is quite different. Outside the colonies, the predators walk in fixed patterns, guided by leave fringes and veins, inside the colonies their walking pattern is more random. Not all morphological stages of prey and predator participate in the dispersal process. In the two-spotted spider mite, dispersal is mainly by the adult females before oviposition whereas in the predatory mites both adult females and males may be active in dispersal during their whole imaginal life, depending on food conditions. Therefore to evaluate the population models in these situations, a provision was introduced to account for the dispersal. The dispersal submodels of the predator and prey were developed from detailed studies of walking behaviour of both. Dispersal by wind was not considered for these situations, since the wind speed is too low to induce take off of the predatory (Johnson & Croft, 1977) and prey mites under greenhouse conditions. Basically these models were so constructed that population models were applied to different spatial unities coupled by different dispersal rates. These simulation models included the clear preference of the predatory mites *M. occidentalis* and *P. persimilis* for the webbed areas. Their effectiveness in searching behaviour outside the colonies guided by leave fringes and leave veins make their residence time outside the colonies negligible. This does not hold for other predatory mite species such as *Amblyseius potentillae* that cannot move around in the webbed areas and shows a clear preference for the thickest parts of the ribs, as a resting place.

Model calculations with population models in which these aspects of dispersion were considered showed that, in systems of limited size, regulation of the population of prey was possible, as in the experiments shown in Figure 2.

#### EVALUATION FOR THE FIELD SITUATION

To evaluate the simulation models under field conditions, the simulated fluctuations in population of fruit-tree red spider mite and the predatory mites was compared with the averaged results of some apple orchards. Figure 3 gives the observed average densities and the simulated densities for adult females of the prey and predator. The simulated functions are based on an initial number per 100 leaves of 4 prey females that have just matured, 1 predator female on 1 June, the observed surface of the leaves and the weather data of 1974 in the orchards. There was a good overall agreement between the simulated and measured results, especially for the maximum numbers of prey and predator, the time lag between these maxima and the density of prey and predator with respect to each other. Also the observed and simulated colour values (the indicator of satiation level) of the adult predator were in good agreement.

From the simulations, the number of generations can easily be deduced and, by changing parameters and structural elements in the model, their contribution to the behaviour of the system may be determined. None of the changes had a major effect on the behaviour of the acarine system in orchards. A wide range of prey-predator ratios may be tolerated in spring without leading to too high prey densities in the summer. The predation activity of the younger stages and the adult males of the predatory mite was relatively insignificant and

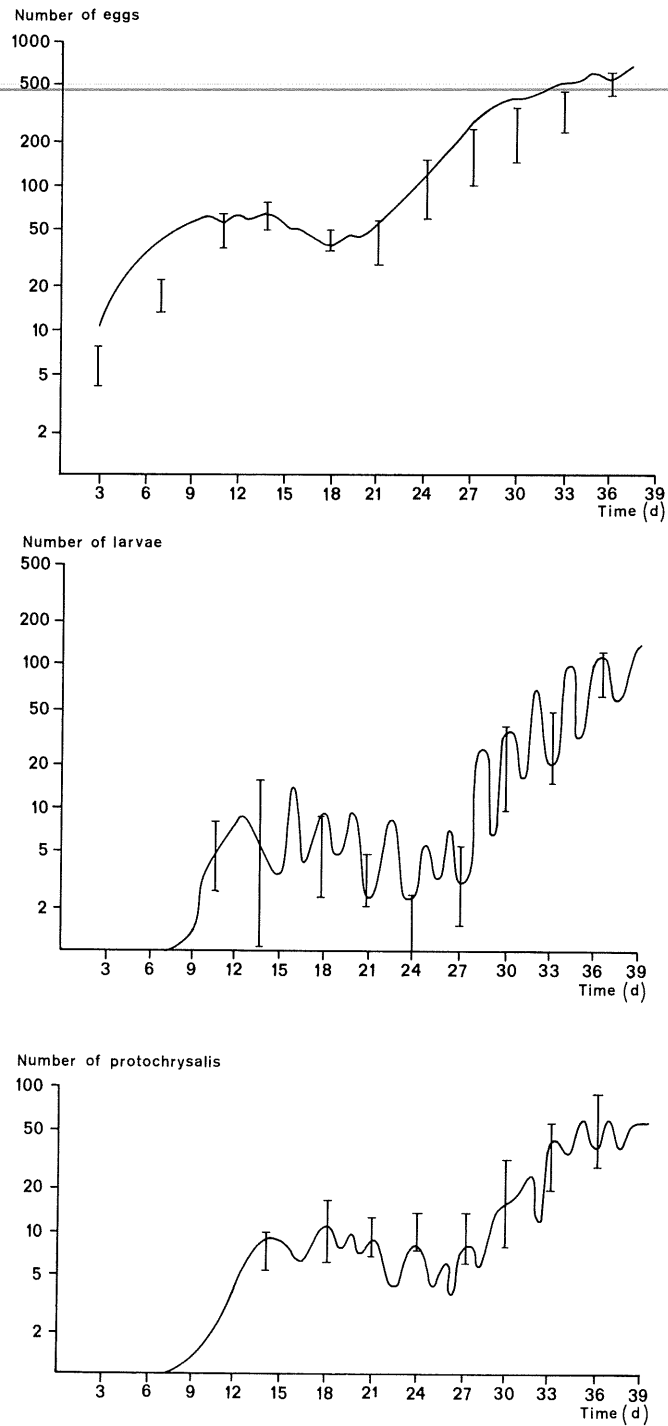


Fig. 1. Simulation of population dynamics of fruit-tree red spider mite and the predatory mite *Amblyseius potentillae* in a small apple ecosystem in comparison with the experimental outcomes (Rabbinge, 1976). Simulated numbers of the spider mite are given as drawn lines and measured figures as confidence intervals ( $\alpha=0.05$ ) (p. 286). Simulated numbers of the spider mite are given as dotted lines and measured figures as confidence intervals ( $\alpha=0.05$ ) (p. 287).

*Amblyseius potentillae*

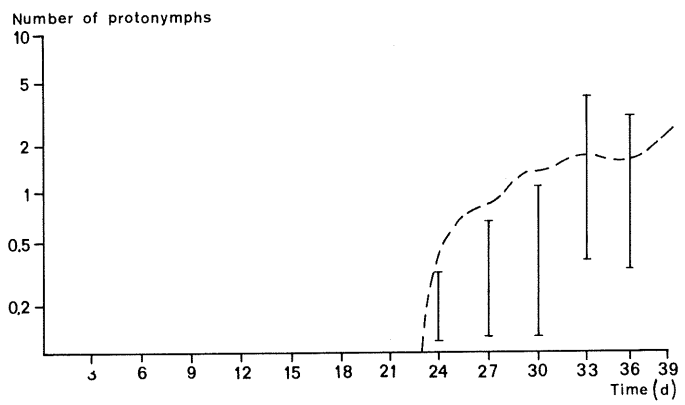
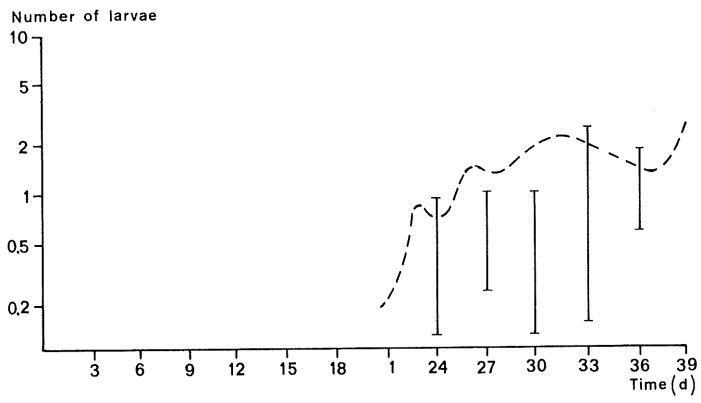
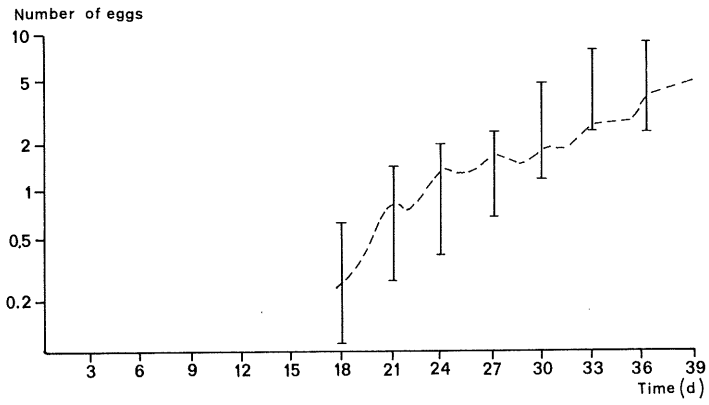
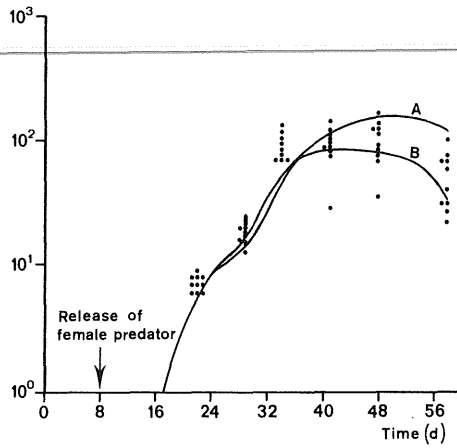


Fig. 1 continued.

Number of oviposition females



Tetranychus urticae

Number of eggs, larvae, nymphs, adult males and preoviposition females

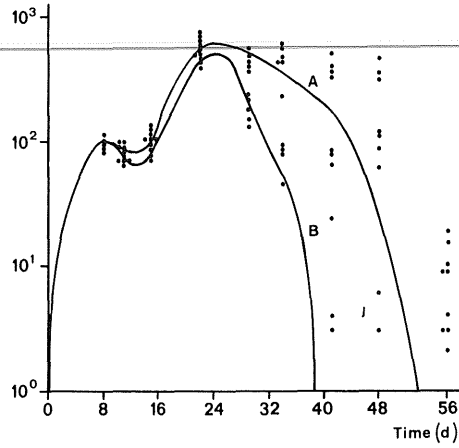
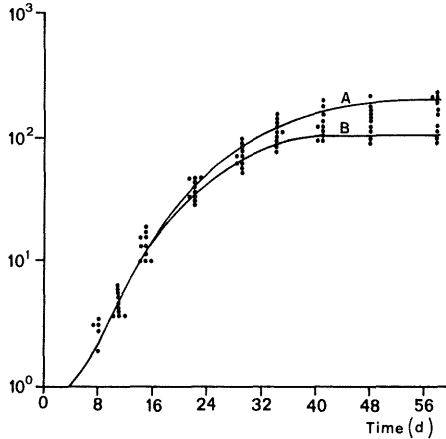
Webbed leaf area (cm<sup>2</sup>)

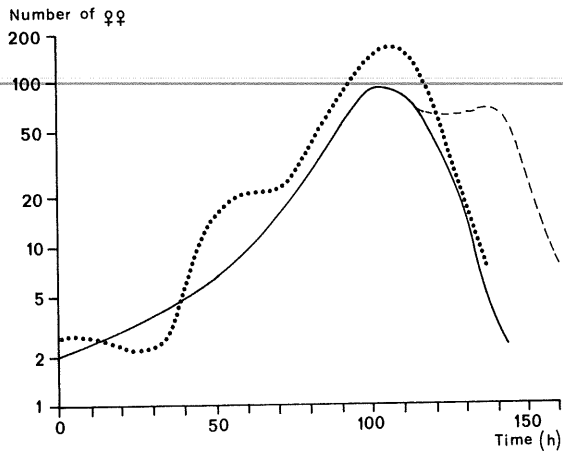
Fig. 2. Simulation of the population dynamics of two-spotted spider mite *Metaseiulus occidentalis* in roses in 8 leaf ecosystems (Sabelis, 1980).

a A twig with 8 spider mite colonies with effects of mutual interference on predation.  
 b A twig considered as one colony, without mutual interference effects and neglecting dispersal.

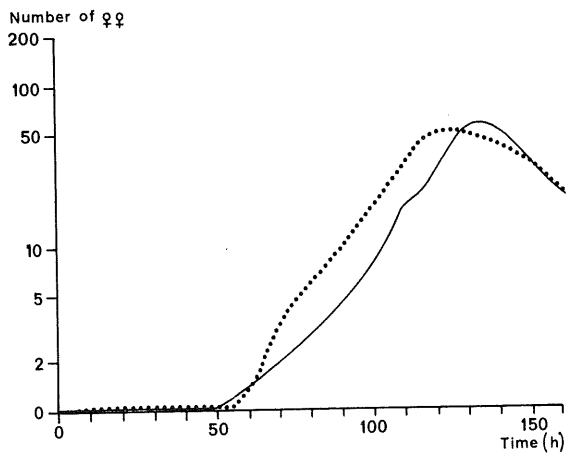
the adult female predatory mite was the major regulator because of its high predation capacity, its long life and its numerical response to increasing prey densities. The system was rather sensitive to length of the juvenile period of the prey and the delay in development of the predator if it was not sufficiently fed. The latter effects may be prevented if alternate prey like gall midges (Eryiophidae) or mildew spores and honeydew are present.

For the acarine system in roses, dispersal of the two-spotted spider mites and the predatory mites in the crop was of major importance. The simulations showed that dispersal of





*Amblyseius potentillae*



*Amblyseius potentillae*

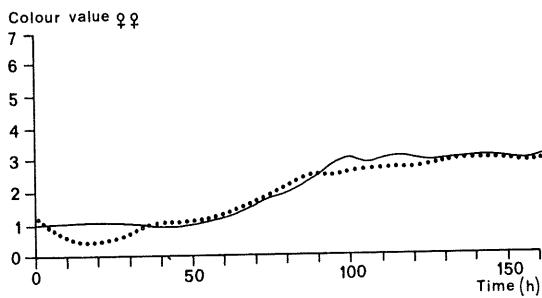


Fig.3. Simulated (dotted lines) and experimental results (drawn lines) of the population dynamics of fruit-tree red spider mite and the predatory mite *A. potentillae* in apple orchards (Rabbinge, 1976). Data are number of mites per 100 leaves.

~~the predators caused a considerable delay in the predator-prey interactions. This delay was partly due to the predatory mite frequently entering and leaving the colonies at low prey densities and also perhaps to the relatively high predator densities. As a consequence of this behaviour the variability in prey numbers increases considerably (Fig. 2).~~

#### MANAGEMENT AND PROSPECTS

For management, the models are too complicated and too time-consuming. Therefore other simplified relations are needed. This has been met for the fruit-tree red spider mite system by sensitivity analysis. Thus prescriptions were developed which show acceptable prey-predator ratios. The acceptable ratio of prey females to predator female was 10 on 25 May, and decreased to 3 on 15 August. Prescriptions of this type may be used by the extension services and the monitoring growers.

The model calculations with the two-spotted spider mite system showed that dispersal behaviour of the prey and predatory mites had a great effect on the behaviour of the system. So far only the dispersal of walking prey and predatory mites has been considered and it seems necessary to investigate the dispersal of prey and predatory mites by wind. Some knowledge of these effects is available (Johnson & Croft, 1977), but this information is still insufficient to gain more understanding of the dispersal of mites. In roses in greenhouses, dispersal by wind seems negligible since wind velocities are never high enough for departure. Other aspects that need more research are the possibilities for other food resources for the predatory mites to survive periods of food scarcity. The models showed that these alternate food sources were necessary in the orchard system since prey densities may reach very low levels. This is even more needed for clustered prey, for instance two-spotted spider mites in roses. The models were a help in formulating the conditions that had to be fulfilled to reach a reliable control system.

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