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# Ecology of Tetranychid Mites and Their Natural Enemies: A Review

## III. Biology, Ecology, and Pest Status, and Host-Plant Relations of Tetranychids

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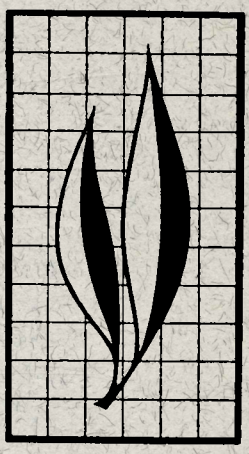

The literature pertaining to the bionomics of some of the most important tetranychids is reviewed. Considerable attention is paid to the possibilities of spider mites reaching pest levels as a result of environmental factors. It is concluded that more information is needed on economic injury levels of various species on different crops and under various climatic conditions. The influences of cultural practices and their interactions as related to population development of tetranychids also need more study. Furthermore, work is needed on the influence of climatic conditions on development of tetranychid mite populations together with possible predictability of outbreak situations. Finally, we need to know more about the fundamental relations between the host-plant quality and spider mite development, and the impact of spider mites on the development of their host plants.

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# III. Biology, Ecology, and Pest Status, and Host-Plant Relations of Tetranychids[1, 2, 3]

## INTRODUCTION

THE SPIDER MITES (Tetranychidae) have long been considered potentially serious pests of a wide variety of our major food and fiber crops and of our ornamentals (Pritchard and Baker, 1955), and the full realization of this potential has become increasingly evident since World War II. Spider mites may cause such severe injury that very heavy losses result, in such crops as citrus, avocado, beans, cotton, apples, pears, plums, tea, and a great many others. Effects have commonly been so obvious—to the extent of a complete "burning" or leaf abscission—that only a limited effort has been made to document the nature of the losses or to determine under precisely what conditions, what levels of density, and in relation to what species, those losses actually occur.

It is known, however, that spider mites do not commonly cause widespread damage in natural or seminatural environments little influenced by man. An extensive literature suggests two different explanations, both of which undoubtedly contain much truth. The most common view has been that in these undisturbed situations, natural factors, such as predators and diseases (parasites are unknown), commonly hold the mites in check. In environments where broad-spectrum pesticides are used, however, the enemies are more adversely affected than the spider mites, and an outbreak of the latter occurs. Much recent work has shown that some conditions, e.g., the use of fertilizers, better crop management, and, in fact, application of pesticides, enhance the intrinsic power of increase of the mites, and may occasion outbreaks, regardless of the influence on mite enemies.

Other vital ecological aspects of the problem include: the role of weather; interspecific as well as intraspecific competition for the food supply; and the important role of resistance in some spider mite species to the acaricides used against them. That weather and nutrition, as well as enemy action, affect spider mite abundance is self evident. The quality, quantity, and dispersion of nutritive material may be involved. Weather and nutrition are interrelated in that weather may have a direct effect on increases or decreases in the food supply, or an indirect effect through its influence on natural enemies. Jeppson *et al.* (1957) and Jeppson (1963*a*) describe certain cases in California involving the interrelationships

[1] Submitted for publication March 5, 1969.

[2] The survey of the literature pertaining to this review was completed in January, 1968; some publications that appeared during 1968 and 1969, however, were also included. The review was prepared as part of a broad program on the ecology and biological control of spider mites, of the Biological Control Working Group of the International Biological Program (IBP).

[3] See "Literature Cited" for citations referred to in text by author and date.

between nutrition and weather and the degree of control experienced from the use of acaricides. Force (1967) has recently illustrated how weather may alter the role of predatory phytoseiids in the control of particular prey species. The exclusion of a particularly capable enemy by climatic influence may eventually result in less efficient control of the pest.

## A NOTE ON ACARICIDES

Under modern agricultural and horticultural practices, possibilities for mite outbreaks have increased in recent years. Intelligent management of control methods depends on understanding the causes of such outbreaks. Since we do not propose, in this review, to treat in detail the problem of resistance to acaricides, we present the following resumé, and refer the reader to a definitive account, that of Helle (1965).

For a period of years, it was possible to control most species of spider mites by use of post-World War II acaricides. Those acaricides include the organophosphates and a number of specifics, such as Aramite (butylphenoxy isopropyl chloroethyl sulfite), chlorobenzilate (ethyl dichlorobenzilate), Fenson (para-chlorophenyl benzenesulfonate), Kelthane (bis (chlorophenyl) trichloroethanol) and DMC (dichloromethyl carbinol). Recently, however, many populations of mites have developed marked resistance.

The cross-resistance exhibited by a strain selected under repeated treatment with a given material is currently a subject of intensive investigation. Jeppson (1963*b*) states that ". . . mite strains selected with chlorinated hydrocarbon acaricides were resistant only to very closely related compounds, but were cross-resistant to many OP (organophosphorus) compounds even though there was no evidence of resistance to the chlorinated hydrocarbon acaricides used in the selection, . . . and mite strains . . . selected with OP acaricides were highly resistant to most of the available OP-type acaricides."

From a series of elegant experiments, Helle (1962) concluded that a single major gene can account for a large part of the resistance to parathion in *Tetranychus urticae* Koch, but that additional modifying hereditary factors are also involved. Resistance is transmitted dominantly by both sexes. Helle found that the backcrossed individuals (resistant × susceptible) × susceptible always sustained a mortality of about 50 per cent when treated with parathion levels of 50 to 1,000 ppm.

Overmeer (1966) showed that in developing resistance to the sulfone Tedion, two stocks of *Tetranychus urticae* developed substantial intersterility both between themselves and between either one and the unselected, wild stock. Thus, with the release of the selective pressure, such populations in the field would tend to drift back toward the original nonresistant state.

Some reports have been made on a reduction in the reproductive potential in OP-resistant strains. Lehr and Smith (1957) and Henneberry *et al.* (1960) found that OP-resistant *Tetranychus urticae* females deposited fewer eggs than did susceptibe females. Dittrich (1961), in a very detailed study, demonstrated that in four strains of *T. urticae* from the same genetic origin, but with different degrees of resistance to demeton, the fecundity was directly linked with the degree of resistance—high resistance correlated with low fecundity, and low resistance with high fertility. Watson and Hansen (1963) and Foott (1965*b*), however, found no correlation between fecundity and resistance.

The problem of resistance may eventually be solved by discovery of materials against which resistance will not develop, or by development of a nega-

tively correlated acaricide that is abnormally toxic because a strain is resistant to some other material. Steinhausen (1968) reported such a negative correlation of an acaricidal carbamate (Formetanate) in a pair of N- and R-strains of *Tetranychus urticae* of identical genetic origin. Dittrich's (1969) data strongly indicate a negative correlation of OP-resistance with chlorphenamidine, which has some structural affinity to Formetanate, in the Leverküsen N- and R- strain of *T. urticae*. If more of such types of acaricides could be found, the problem of resistance could probably be relieved.

# THE BIOLOGY OF TETRANYCHIDS

The life history and general bionomics of the tetranychids were reviewed by Boudreaux (1963). A review of the biology of Japanese species was made by Mori (1967). The morphology of *Tetranychus urticae* and of *T. atlanticus* McGregor has been extensively dealt with by Blauvelt (1945) and Baker and Connell (1963), respectively. Ehara (1960) dealt with the digestive and excretory mechanism of *Bryobia*; Anwarrullah (1962) described in detail the morphology and anatomy of *Panonychus ulmi*, *T. viennensis*, *Bryobia rubrioculus* and *B. kissophila*, while Dosse and Langenscheidt (1964) dealt with the morphology, biology, and histology of the *T. urticae-cinnabarinus*-complex, and their hybrids. Here, we shall treat only certain aspects important in the consideration of species pertinent to our understanding of the population ecology and natural control of the group.

The life cycle of tetranychids is a typical epimorphosis, the stages being egg, larva, protonymph, deutonymph, and adult. The three immature stages are each followed by a quiescent stage: nymphochrysalis, deutochrysalis, and teleiochrysalis, respectively. There is a marked difference between males and females in the rate of development. The early-maturing males locate and remain near the female teleiochrysalis until the females hatch. Copulation takes place almost immediately after hatching of the young female. This explains why, in a normal bisexual population, the females are nearly always mated. Unfertilized eggs produce only males; fertilized ones, only females. But a mated female may still produce both sexes, because not every egg receives a spermatozoön.

Many authors report that males molt only twice; others challenge this. According to Osakabe (1967), however, *Tetranychus kanzawai* Kishida males may molt either two or three times.

The rate of development of the immature stages is influenced by temperature, humidity, and quality of the food. Specimens in the different stages may vary considerably in their susceptibility to hazards of the environment.

## Biology of Some Important Species

### *Panonychus ulmi* (Koch)

Many publications concerning the biology and ecology of *Panonychus ulmi* have appeared (e.g., Gilliatt, 1935; Geijskes, 1938; Wiesmann, 1940; Kuenen, 1943, 1946*a*, *b*, 1949; Günthart, 1945, 1957; Cagle, 1946; Andersen, 1947; Wybou, 1949, 1951; Blair and Groves, 1952; Fjelddalen, 1952; Hueck, 1953; Mori, 1955, 1957, 1961*a*, *b*; Parent and Beaulieu, 1957; Günthart and Günthart, 1959; Ehara, 1960; Rota, 1961-1962; Cutright, 1963; Bondarenko, 1964; Collyer, 1964*a*; Livsic, 1964; Saba, 1964; Balevsky, 1965; Böhm, 1966; Musa and Dosse, 1966; Musa, Dosse, and Tebcherany, 1968). The sources of the literature indicate the widespread dis-

tribution of this species; it occurs in almost all commercial fruit-growing regions. Only the most important data concerning its biology and ecology are mentioned here.

Hibernation takes place in the egg stage on the branches and twigs of many host plants, the most important being apple, pear, plum, walnut, and grape. Beament (1951) described the structure and formation of the summer egg and the diapausing egg. Both types have a common basic shell structure, consisting of an outer, thick wax layer and a cement layer of oil and protein which attaches the wax layer to the underlying "shell" layer enclosing the living material.

The diapausing eggs hatch in spring and give rise to several generations of mites. The hatching period varies according to the climatic zone, being later in colder zones. In Canada, hatching began about mid-May (Gilliatt, 1935; Parent and Beaulieu, 1957), whereas in Virginia hatching started the last week of April (Cagle, 1946). Tsugawa, Yamada, and Shirasaki (1961) attempted to determine both the total effective and the lower limit temperatures for the development of winter eggs. They found that a total effective temperature of 195.4 day-degrees was required to complete development, and that at 7° C no development took place. Examination of the relation between climatic conditions and the initial date of hatch revealed a high inverse correlation with the temperature during April. Three formulas based on average, minimum, and maximum temperatures are provided to aid in forecasting the first day of hatch.

Dicker (1963) found differences in the hatching period of winter eggs in English orchards. In 1960 and 1961, 50 per cent hatch occurred nine and 17 days earlier, respectively, in an orchard that had been regularly sprayed with acaricides than in one nearby, where acaricides never had been used. Observations in other regularly sprayed orchards showed that the date of hatch of 50 per cent of the winter eggs could vary as much as 31 days in the same district. Variation in the time of hatching, between individual sampling units, was greatest for mites in unsprayed orchards. These results suggest that acaricides may eliminate certain components of the original mite population, thereby altering the hatching period.

During a five-year study, Light *et al.* (1968) observed variations of two to three weeks in the date at which 50 per cent hatch was reached, while all gradations, from early to late hatching, were represented in the orchards studied. The differences in hatching were not constant from year to year. However, the same populations retained the order in which they reached 50 per cent hatch. Therefore, an approach to predicting the date of hatch of 50 per cent of the winter eggs such as that suggested by Tsugawa, Yamada, and Shirasaki (1961) in Japan and by Lienk (1963) in New York state seems to be of little value in England.

Lienk (1967) reported a remarkable change in seasonal abundance of *Panonychus ulmi* on apple in New York. As recently as 10 years ago this species was considered to be an early-season pest; recently, it has shown a constant tendency to peak later in the season. The early pattern being still much the same, the period of maximum activity no longer declines abruptly by early August, but instead occurs later in the season. Lienk provides no explanation for this phenomenon.

In Virginia, Cagle (1946) found an average oviposition period of 12.4 days, averaging 18.8 eggs per female and 1.5 eggs per day. Andersen (1947) found average egg production of 27, 16, 14 eggs per female in the first, second, and third summer generations, respectively. In laboratory experiments in Lebanon, Musa, Dosse, and Tebcherany (1968) found a very high reproduction in the first four generations. In 1966, mean egg

production ranged from 85.1 to 105.5 per female; in 1967, it ranged from 81.3 to 92.8 per female. Parent and Beaulieu (1957) obtained 10 to 35 eggs per female for the first three generations, but as many as 90 for some individuals of the fourth generation; Kuenen (1946*a*, 1949) reported a maximum of 35 eggs per female; Andersen (1947), 45 eggs; and Blair and Groves (1952), 46 eggs. Post (1962) obtained a mean egg production per female of 10.7 to 16.2. Although considerable variation is evident, the literature indicates that the reproductive potential of this mite is lower than that of many *Tetranychus* species.

This mite causes damage by puncturing the cells of the leaves. Bronzing and premature leaf drop often follow. Consequently, photosynthesis and respiration are impaired (Blair, 1951; Avery, 1964), resulting also in a decrease in the numbers of flower buds on apple, for example, the following season (van de Vrie, 1956). In autumn, the winter eggs are deposited, the deposition being determined by photoperiod and temperature (Lees, 1950, 1953*a*, *b*) and to some extent by the condition of the host plant (Wiesmann, 1940; Kuenen, 1946*b*, 1949; Blair and Groves, 1952). This species is commonly the most important spider mite on fruit trees in temperate zones of the world. It is a "ballooning" species, and its movements by this means can be significant (Marlé, 1951).

Hueck (1953) studied the population dynamics of this species in the Netherlands. He discusses the curves of births and survival, and proposes a probabilistic mathematical population model.

## *Panonychus citri* (McGregor)

The citrus red mite has been reported from many parts of the world, including North and South America (Boyce, 1936; Ebeling, 1959; Munger, 1963); India (Rao and Rao, 1964); China (Huang *et al.*, 1963); Taiwan (Cheng, 1966); Japan (Shinkaji, 1961*a*, *b*; Tanaka and Inoue, 1962; Ehara, 1964); Russia (Siharulidze, 1962; Ignatova, 1968) and South Africa (A. J. Smith, 1953; van Rooyen, 1966). It is presumed to be native to the Orient, where citrus also originated (Fleschner, 1952; Ebeling, 1959). It is currently considered the most important pest of citrus in California (Ebeling, 1959; Munger, 1963).

*Panonychus citri* feeds on both leaves and fruits, causing a bronzing or silvering of the surface. Severe infestations may cause defoliation, which may be accentuated under certain conditions, such as hot, dry winds (Boyce, 1936; Ebeling, 1959).

A generation of the citrus red mite can be completed in three weeks during warm weather in southern California, and there may be as many as 12 to 15 generations per year (Quayle, 1912; Ebeling, 1959); 18 generations per year were reported by Huang *et al.* (1963) from Kwantung. Relationships between temperature and developmental period were shown by English and Turnipseed (1941), Fukuda and Shinkaji (1954), Shinkaji (1959), and Munger (1963). The influence of humidity on development was studied by Fukuda and Shinkaji (1954) and Shinkaji (1959).

Fecundity has been studied by several workers. Munger (1963) obtained an average of 96 eggs per female and an average longevity of 23 days at 24° C in laboratory experiments. English and Turnipseed (1941) and Ebeling (1959) reported a maximum of about 50 eggs per female. They showed that the life span and period of oviposition are considerably longer during cool months than during warm months. *Panonychus citri* commonly has two peaks of abundance—one in spring or early summer and one in fall or early winter (Henderson and Holloway, 1942; Shinkaji, 1959; Muma, 1961*b*). During those periods, the temperature may be most favorable (English and Turnipseed, 1941), but the age of the foliage may also be an important factor (Henderson and Holloway, 1942; Jeppson *et al.*, 1957; Cheng, 1966).

However, high populations can occur in some places at almost any time of the year (Jeppson, *et al.*, 1957; Muma, 1961*b*). All stages can be found in midwinter in California and Florida, although Shinkaji (1961*a*, *b*) and Ehara (1964) report that where the species occurs in the colder areas of Japan, the winter is passed in diapause in the egg stage.

Citrus seems to be the only important host plant, but *Panonychus citri* has also been found on other host plants, such as pear and mulberry (Quayle, 1912; Shinkaji, 1961*a*; Ehara, 1964).

Adult females spin down on silken threads, apparently when foliage becomes unfavorable through excess feeding or from other causes. They are then carried by air currents—an important means of dispersal (Fleschner *et al.*, 1956). A unique method of studying movement was employed by Cressman (1963) and Tashiro (1966), who made field releases of an albino strain discovered by Wilkes (1963). Fleschner (1958*b*) discussed some of the major factors affecting the abundance of the citrus red mite, including predation, pesticides, soil, water, direct and indirect effects of climate, and host-plant genetics.

## *Tetranychus urticae* (Koch)

The taxonomic status of this species is very confused. Its great variability, the long range of host plants on which it has been found, and the diversity of opinion among taxonomists have led to a long list of synonyms (e.g., Geijskes, 1939; Gasser, 1951; Pritchard and Baker, 1955; Dosse, 1964*b*).

There is no doubt that this is one of the most polyphagous species of the family Tetranychidae, with a long list of host plants (e.g., Zacher, 1949; Linke, 1953; Baker and Pritchard, 1953; Fritzsche, 1959; Avidov and Harpaz, 1969). It is a major pest on cultivated plants, such as vegetables (Ehara, 1962; Bognar, 1963; Bravenboer, 1963; Saba, 1964; Basu and Pramanik, 1965); ornamentals (van Marle, 1951; Dosse, 1953*b*; Boczek and Kropczynska, 1964); fruit trees (Gasser, 1951; Collyer, 1953; Ryke and Meyer, 1958; Bravenboer, 1959; Nucifora, 1960; Mathys, 1963; Alfaro, 1964; Ehara, 1964; Saba, 1964); hops (Linke, 1953; Kac, 1963); cotton (Mohamed, 1963); and strawberry (Wilcox and Howland, 1956; W. W. Allen, 1959; Oatman and McMurtry, 1966). It also occurs on many weeds.

The mites overwinter as diapausing adult females (van de Bund and Helle, 1960), which are tolerant of low temperatures (Stenseth, 1965). During summer, many generations may develop, the number of eggs deposited depending largely on the temperature (Bravenboer, 1959; van de Bund and Helle, 1960) and the quality of the host plant (Fritzsche, 1957, 1961; Fritzsche, Wolfgang, and Opel, 1957; Nielsen, 1958; T. F. Watson, 1964; Cannon and Connel, 1965; Stoner and Stringfellow, 1967; Storms, 1969). Bondarenko (1950, 1958) found that only adult females can enter diapause; that photoperiod is of great importance in the inception of diapause; and that, to a lesser extent, temperature and nutrition exert an influence.

According to Nuber (1961), termination of diapause depends primarily on temperature and the presence of suitable food. Light seemed to exert little influence, provided the diapausing mites had been exposed to sufficiently low temperatures. Mites that had not been exposed to low temperatures needed a long period before egg production was initiated. Certain ecological aspects of diapause are treated later (p. 359).

Reproduction may occur throughout the winter in lower latitudes (Baker and Pritchard, 1953; Dosse, 1967). This species has been found to lay eggs at an average of five or more per female per day at warm temperatures (Lamiman, 1931; Cagle, 1949; Williams, 1954; Watson, 1964). Williams (1954) observed an unusual production of 16 eggs per female

per day. The total number of eggs per female may commonly exceed 100 (Cagle, 1949; Linke, 1953; Bravenboer, 1959; van de Bund and Helle, 1960), but the mean is closer to 40 to 80. More details on egg production and various conditions influencing reproduction and population increase are treated on pages 354-374.

Dispersal of *Tetranychus urticae* on the host plant was studied by Helle (1962) and Hussey and Parr (1963*b*). Helle reports that during the short preoviposition period (24 hours at 25° to 30° C), the females migrate to fresh leaves higher up on the plant. He draws attention to a significant resulting fact: the females have already been fertilized when they arrive on the fresh leaves; both male and female offspring develop from the haploid and diploid eggs dedeposited; and brother/sister matings must be very common. Such sibling matings result in the rapid local increase in frequency of rare genes, and lead to development of homozygous populations, as is the case with resistance to acaricides.

Hussey and Parr (1963*b*) postulate that *Tetranychus urticae* spreads by three different methods: migration of the teneral females to oviposition sites; migration from heavily infested plants by dropping off; and migration over the soil surface in accordance with the plane of polarized light. The effect of these dispersal mechanisms is to restrict mite populations to one portion of a glasshouse from season to season, with relatively slow lateral spread from these centers during each growing season. This restricted area of occurrence can be important for the introduction and effectiveness of predators (Bravenboer, 1959, 1963) and for genetic aspects arising from sibling matings (Helle, 1962).

Foott (1965*a*) studied the geotactic responses of diapause and nondiapause females of *Tetranychus urticae* on peach seedlings in Quebec. His findings demonstrate that most of the diapause females were positively geotactic, while the nondiapause females were negatively geotactic. This explains why this species commonly occupies three different habitats during the year. In orchards, in spring and early summer, it lives on groundcover plants; it moves to the trees in summer; and it hibernates, during winter, under the bark, in crevices, or on the ground.

To the methods of spread in the field must be added the movements arising to some degree from strong winds (Boyle, 1957) and accidental phoresy. *Tetranychus urticae* has not been observed to suspend itself on silken threads, by which some tetranychids are readily transported by less forceful air currents (Marlé, 1951; Fleschner *et al.*, 1956; Boyle, 1957; Hussey and Parr, 1963*b*).

Kac (1963) studied the influence of temperature on the population dynamics of *Tetranychus urticae* on hops in Yugoslavia. She found that the effects of high February temperatures on overwintering females established the potentials for high-density outbreak during summer. On the basis of the mean temperatures during the month of February, a method for predicting outbreak and determining the necessity for chemical control was suggested.

### *Tetranychus cinnabarinus* (Boisduval)

Until recently, this species was often treated as *Tetranychus urticae*, but recent studies have shown it to be distinct (Boudreaux, 1956; Parr and Hussey, 1960; van de Bund and Helle, 1960). It occurs on ornamentals (Carmona, 1960; van de Bund and Helle, 1960; Ehara, 1964; Boczek and Kropczynska, 1966), vegetables (Carmona, 1960; Ehara, 1962), fruit trees (Kriegler and Meyer, 1963; Damiano, 1964; Dosse, 1964*a*; Kriegler, 1964; Plaut and Cohen, 1967), tobacco (Milne, 1962), cotton (Baker and Pritchard, 1953; Hassan, Hahel, and El Badry, 1959*a*) and weeds (Dosse,

1964*a*, 1966; Saba, 1964). The biology closely resembles that of *T. urticae*, but according to van de Bund and Helle (1960), *T. cinnabarinus* does not enter diapause under glasshouse conditions in the Netherlands, as does *T. urticae*. It may reach high numbers even in midwinter on *Ricinus communis* L. in coastal areas of southern California (McMurtry, unpublished observations).

Dosse (1964*b*, 1966) studied the occurrence of diapausing mites of the *Tetranychus urticae-cinnabarinus*-complex in Lebanon. He found different types of mites, depending on the altitude. In the mountains at an altitude of approximately 4,500 ft *T. urticae* on apple has a real diapause; in the coastal areas, *T. cinnabarinus* reproduces the year around. At altitudes of approximately 3,000 ft, females of the *T. urticae-cinnabarinus*-complex on *Viola* sp. did not migrate for overwintering. Some overwintered on the leaves, but changed color to orange; others maintained the dark-reddish color, but lost the lobes on their striae; still others remained as normal summer females and continued reproducing.

Although it does not produce "ballooning threads," this species may be carried by wind (Boyle, 1957).

## *Tetranychus atlanticus* (McGregor)

This species is widespread in the United States and is considered a serious pest of cotton (Baker and Pritchard, 1953; Leigh, 1963*a*), strawberries (Cagle, 1956), and soybeans (Baker and Connell, 1963). It is also reported to be an important pest of alfalfa, melons, clover, parsley, and eggplant (Pritchard and Baker, 1955). The mites cause a reddish coloration of cotton leaves, and relatively small numbers can cause defoliation (Baker and Pritchard, 1953; Leigh, 1963*a*).

The biology of *Tetranychus atlanticus* was studied in detail by Cagle (1956). Hibernation occurs in the adult stage, with females that are bright orange in color. Although these females may lay eggs before turning orange, little or no feeding and no egg laying were observed after the color change had taken place. Cagle found that 15 to 16 generations per year occurred in Virginia. The average incubation period in the insectary was as short as four days, and the combined immature stages as short as five days, depending on the time of year. Reproduction averaged well over 100 eggs per female, and in some cases over seven per female per day.

Baker and Connell (1963) studied the morphology and the functioning of the mouthparts of *Tetranychus atlanticus* and examined injured leaf tissue microscopically. Their results are discussed on page 378.

## *Tetranychus pacificus* (McGregor)

The Pacific spider mite, *Tetranychus pacificus*, occurs in the western United States and Canada, being especially common in the interior valleys of California. It is considered one of the most serious pests of fruits, grapes, and cotton, and is also a pest on such crops as walnuts, alfalfa, clover, vetch, beans, and melons (Lamiman, 1935; Pritchard and Baker, 1952; Smith and Stafford, 1955).

The biology of this species has been discussed by Lamiman (1931) and L. M. Smith and Stafford (1955), and certain special features, by Flaherty (1967). The mites hibernate beneath the bark or in crevices, as light-orange females. In the spring, these females change to the typical greenish color with black spots, after which egg-laying starts. Early feeding on weeds has been observed, before the mites appear on foliage of woody, deciduous hosts. The duration of incubation and immature development combined is 10 to 14 days in warm weather. Fifty to 100 eggs are laid during an oviposition period of two to four weeks, with the rate being as high as five eggs per day. High temperatures induce rapid reproduction

and development, and the highest densities usually occur in midsummer. High populations, especially during times of high temperatures and low humidities, cause severe injury and defoliation.

## *Tetranychus mcdanieli* (McGregor)

This species was recognized as an agricultural pest about 1950, when it suddenly replaced another species, *Tetranychus pacificus*, as the most damaging mite species on apple in the northwestern United States (Newcomer, 1954). In detailed experiments, Newcomer demonstrated that *T. pacificus* and *T. mcdanieli* are biologically distinct species. No explanation was offered for the rather rapid substitution of *T. mcdanieli* for *T. pacificus* in the Pacific Northwest. Within a decade it had reached pest levels from British Columbia to New Mexico, and was developing strong resistance to acaricides in some areas (O'Neill and Hantsbarger, 1952; Hoyt and Harries, 1961; Hoyt and Kinney, 1964; Hoyt, 1966). It has been found on apple, plum, prune, and raspberry in the United States (Pritchard and Baker, 1955). Robinson (1952) found it on more than 20 different cultivated trees, shrubs, and flowering herbs; he rated it the predominant phytophagous mite species in Manitoba. Nielsen (1958) studied the biology of this species in Utah. Of interest is Dondale's (1967) report that the situation in Ontario differs from that in adjacent parts of the United States. Outbreaks of *T. mcdanieli* are unknown in Ontario, and the only recorded host plant is raspberry, the one on which it was originally collected and described (McGregor, 1931). Dondale's work suggests that a diversity of predators normally maintains *T. mcdanieli* in nonoutbreak conditions in eastern Ontario. Comparison of predator populations in eastern and western regions may reveal an explanation for the striking differences.

The adult females overwinter; they hibernate on the trunks and in shelter around the stems of the trees in orchards in the Pacific Northwest. During summer many generations may develop and thus reach relatively high levels immediately before or during harvest. These high levels result in reduced fruit size and in poor fruit color, and possibly affect maturity (Hoyt, 1967). Overwintering females may frequently be found in the calyx end of apples, and are difficult to remove. This species develops its greatest populations in the higher sections of the trees, and produces profuse webbing (Hoyt, 1967). Hoyt demonstrated that the naturally-occurring predatory mite *Typhlodromus occidentalis* is capable of keeping *Tetranychus mcdanieli* at low levels in commercial orchards in Washington.

## *Tetranychus viennensis* (Zacher)

This species has been reported to be of economic importance in *Austria* (Böhm, 1966), *Bulgaria* (Balevsky, 1967), *England* (Hirst, 1920), *France* (Chaboussou and Bessard, 1954; Rambier, 1954, 1964), *Germany* (Zacher, 1949; Dosse, 1953*a*; G. F. W. Müller, 1957), *Hungary* (Bognar, 1963), *Lebanon* (Dosse, 1967), *Portugal* (Carmona, 1964), *Spain* (Alfaro, 1964), *Switzerland* (Gasser, 1956, 1963; Mathys, 1960), *Turkey* (Göksu, 1968), and the *U.S.S.R.* (Ugarov and Nikloski, 1937; Beglarov, 1959; Bondarenko, 1964). The biology of this species closely resembles that of *Tetranychus urticae*. Only adult females overwinter. During summer many generations may develop. G. F. W. Müller studied the morphology, biology, and ecology of this species in Germany. He found it to occur almost entirely on *Rosaceae*, with four to five generations developing annually. Highest natural mortality was in the egg stage, followed by that in the immature stages, in decreasing order. Gasser (1963) found that adverse weather conditions drastically reduced the density on cherry in Switzerland. Beglarov

(1957) reported an extremely high winter mortality. Consequently this species is scarce in spring, but increases rapidly during summer.

### *Tetranychus kanzawai* (Kishida)

The tea red spider mite, *Tetranychus kanzawai*, is a common pest of tea in Japan, where it causes much damage to young leaves (Osakabe, 1959, 1967). It feeds especially on various *Fabaceae* and *Rosaceae*. Tea, soybeans, mulberry, hops, and grapes are among the preferred hosts.

The population density in tea plantations fluctuates with the season; high densities were found from March to June and from September to December, but differences were observed according to the district. *Tetranychus kanzawai* passed the winter as diapausing females at Kanaya, while in the southern districts, all stages could be found in winter, including both diapausing and nondiapausing females.

Dispersion is effected by crawling, air currents, and plantation laborers. Fertilization of the tea bushes influenced the population development (Osakabe, 1963*b*). A positive correlation was found between the levels of nitrogen and phosphorus and mite density, but a negative correlation was found with potassium and manganese (Osakabe, 1963*b*, 1967). (For further details see p. 382.)

### *Oligonychus coffeae* (Nietner)

This species is considered to be a serious pest on tea in India and Ceylon (Cranham, Ranaweera, and Rajapaksa, 1962; Cranham, 1966). Its bionomics has been studied by Ananthakrishnan (1963), Das (1959, 1960), and Das and Das (1967). According to Das (1959), *Oligonychus coffeae* has been recorded on a wide variety of other host plants in India and other countries. It normally feeds on the upper surfaces of the leaves; in cases of severe infestations, particularly under dry weather conditions, the lower surfaces and the young leaves are also infested. The mites live under a cover of webbing, where they are protected against inclement weather. This species is found on tea throughout the year, but it attains highly injurious densities only from March to June. With the monsoon rains, it practically disappears. A second light attack may develop in September or October. Dispersion mostly takes place by crawling from bush to bush. Other agencies, however, such as wind, cattle, and plantation laborers, can effect dispersion.

### *Oligonychus punicae* (Hirst)

The avocado brown mite, *Oligonychus punicae*, is a pest of certain varieties of avocado in southern California. It was apparently first noticed in the Carlsbad region of San Diego County in the late 1920's (McGregor, 1941; Ebeling, 1959). It can now be found in nearly all avocado-growing areas of southern California, but reaches high densities only in the coastal and intermediate climatic areas. In interior areas, it has been observed only in small numbers, severe summer weather possibly being the limiting factor.

Pritchard and Baker (1955) recorded *Oligonychus punicae* from tropical Asia and Central America, and suggest that it may have been introduced into California from the latter area. These authors list collection records from pomegranate as well as from avocado.

According to McMurtry and Johnson (1966), feeding by *Oligonychus punicae* on avocado leaves is confined to the upper surfaces, except during severe infestations, and causes a brownish discoloration or "bronzing." In extremely heavy infestations, the entire upper leaf surface and part of the lower surface become bronzed, and defoliation may even occur. Seasonal increase usually begins in early summer with a peak in late summer, followed by an abrupt decline. The time of increase varies considerably; it is sometimes delayed until late summer, with the peak density

occurring in fall or early winter. Causes of these variations are not known.

Abrupt declines are commonly associated with biotic factors: predation, intraspecific competition, or both. If not controlled by other factors, *Oligonychus punicae* ultimately becomes self-limiting by intraspecific competition. The leaf bronzing caused by the feeding mites renders the leaf unsuitable for feeding and reproduction, as has long been known in other mite species (Henderson and Holloway, 1942; Kuenen, 1949; Fleschner, Hall, and Ricker, 1955). McMurtry and Johnson (1966) found the population curves where intraspecific competition was considered to be the main limiting factor to be remarkably different from those where natural enemies were considered to be the main limiting factor. In the first case, the populations remained at high levels for several weeks, while in the latter, the trends showed a single peak followed almost immediately by a rapid decline, rather than a prolonged leveling-off period. McMurtry (1970) showed that a self-limiting process in *O. punicae* on avocado can be operating according to the following principles: As the population density becomes high, feeding damage becomes extensive on the upper surfaces of the leaves. Some of the females balloon from the leaves; the conditions for the remaining population become progressively less satisfactory as virtually all of the upper surfaces become bronzed. Reproduction and development are adversely affected on these leaves, and feeding is further hindered by the accumulation of webbing, cast skins, and waste products. Ballooning of females increases along with migration to the under surfaces of leaves and to immature leaves where the potential for increase is low. As little favorable food substrate remains, larvae die soon after hatching. Males seem to survive the longest. There are, however, sufficient survivors for an eventual resurgence in the population, even on small seedlings (McMurtry and Scriven, 1966). Although other factors, especially predation, usually intercede, under field conditions, before this process becomes general (Fleschner, Hall, and Ricker, 1955; Fleschner, 1958*a*; McMurtry and Johnson, 1966), intraspecific competition nevertheless may operate in small areas of a tree or orchard, and this phenomenon can be important in the population dynamics of *O. punicae*. McMurtry and Scriven (1966) studied some prey-predator interactions under greenhouse conditions; Fleschner, Hall, and Ricker (1955) studied the development of this species on predator-free and predator-infested parts of avocado trees. Fleschner (1958*a*) listed 21 predator species.

## *Bryobia rubrioculus* (Scheuten)

To the extent of our information, *Bryobia rubrioculus* is conspecific with *B. arborea* Morgan and Anderson and with *B. redikorzevi* Reck. Morphological and ecological data provided by Reck (1947), van Eyndhoven (1955, 1956*a*, *b*, 1958), Morgan and Anderson (1957), and Anderson and Morgan (1958) support this view. Much of the literature on this species is under the name of *B. praetiosa* Koch. However, it can be distinguished morphologically and ecologically from *B. praetiosa*, which lives on herbaceous plants (van Eyndhoven, 1955; Morgan and Anderson, 1957; Morgan, 1960). *B. rubrioculus* is widespread in deciduous fruit orchards in the United States, Canada, Europe, and South Africa. Information on the injury it causes was reviewed by Anderson and Morgan (1958). In Europe, this species was studied by Wybou (1949, 1951), Mathys (1954, 1955, 1957), Kremer (1956), Beglarov (1957), Gäbele (1959), Alfaro (1964), Bondarenko (1964), and Iacob (1963*a*, *b*, 1964). It was studied in South Africa by Georgala (1955, 1958) and Kriegler (1964); in Canada by Morgan and Anderson (1957), Anderson

and Morgan (1958), and Herbert (1962, 1965); and in the United States by Summers (1950).

Winter is passed in the egg stage on the twigs of fruit trees. The eggs usually hatch somewhat earlier than do those of *P. ulmi*. There is a maximum of four generations in British Columbia and three in northern California and Nova Scotia, although portions of the populations may have only one generation (Summers, 1950; Anderson and Morgan, 1958; Herbert, 1962, 1965). In Europe, three to four generations may develop; but portions of the populations may have fewer generations per year. Kremer (1956) found that females of the second generation oviposited some winter eggs, and females of the third generation produced only winter eggs. In insectary studies in South Africa, Georgala (1958) found six generations during the 1951-1952 and 1952-1953 seasons.

In general, the developmental period is long in contrast to that of other tetranychids (Kremer, 1956). Herbert (1962) found that over 77 per cent of the postembryonic development time is spent in quiescence. This slow development has been suggested as the reason that this species is not a more destructive pest (Summers, 1950; Herne and Putman, 1960; Herbert, 1962). Another reason could be its relatively high susceptibility to pesticides (Croft and Jorgensen, 1969).

Ecological factors, such as voltinism, egg hatching, rates of development, and intratree distribution, have been studied in detail by Georgala (1955, 1958), Kremer (1956), Iacob (1963*a*, *b*, 1964), and Herbert (1962, 1965).

*Bryobia rubrioculus* is apparently entirely parthenogenetic (Pritchard and Baker, 1955; van Eyndhoven, 1955; Kremer, 1956; Georgala, 1958), which may explain why resistance to acaricides in this species is unknown, since the phenomena associated with inbreeding in sexual reproduction that are related to development of resistance (Helle, 1965) would be lacking.

## The Potential for Increase

### Rate and Duration of Egg Laying

As with many arthropods, the pattern of oviposition in tetranychids generally consists of a short preoviposition period, a rapid increase to a peak a few days later, followed by either a slow or a rapid decline. In unmated females the peak may be delayed until after mating. A diurnal rhythm has been demonstrated for *Tetranychus urticae* by Polcik, Nowosielski, and Naegele (1965) and for *Eotetranychus suginamensis* (Yokoyama) by Yokoyama (1932). Increased temperatures result in higher peaks of oviposition, but an abrupt decline often occurs after the peak (Nielsen, 1958; Bravenboer, 1959; Nickel, 1960; Davis, 1961; Watson, 1964). Shinkaji (1959) found that oviposition declined at temperatures of about 30° C for *Panonychus citri*. Bravenboer (1959) found the optimum temperature for *T. urticae* to be 28 to 32° C. With *Oligonychus coffeae*, Das and Das (1967) found an inverse correlation with temperatures, varying from 12 eggs at 32° C to 107.3 eggs at 20° C. A female may produce from two to three, up to 15 to 20 eggs in a single day, depending on the nutrition, temperature, species, humidity, and perhaps on photoperiod. Records on egg production are numerous; five to six per day is probably near average for many species. Data for various species from various parts of the world are provided in table 1.

Table 1 shows that the total egg production is quite variable, probably for many different reasons. Boudreaux (1958) stressed the influence of relative humidity on egg production in *Tetranychus telarius* (L.) (= *T. urticae*); twice

TABLE 1

REPRODUCTIVE CAPACITY OF VARIOUS SPIDER MITE SPECIES AS RECORDED IN THE LITERATURE

| Mite species and host plant | Number of eggs per female | | References |
|---|---|---|---|
| | Average | Maximum | |
| *T. cinnabarinus:* | | | |
| bean | 107.4 | 158 | Van de Bund and Helle (1960) |
| carnation | 89.5 | 128 | Van de Bund and Helle (1960) |
| *T. kanzawai:* | | | |
| tea | 40.6–52.4 | — | Osakabe (1967) |
| *T. urticae:* | | | |
| bean | 111 | 202 | Bravenboer (1959) |
| bean | 67.7 | 117 | Gasser (1951) |
| bean | 123.3 | 178 | Van de Bund and Helle (1960) |
| clover | 39.8–100.1 | 194 | Cagle (1949) |
| carnation | 15.8 | 42 | Van de Bund and Helle (1960) |
| carnation | 93 | 128 | Dosse (1953*b*) |
| raspberry | 90 | 204 | Garlick (1928) |
| hops | 94 | 128 | Linke (1953) |
| cotton | ... | 110 | McGregor and McDonough (1917) |
| | 18.8–79.5 | 149 | Paradis (1955) |
| *asparagus plumosus* | 70 | 123 | Wilson (1931) |
| *P. ulmi* (1st gen.): | | | |
| apple (2.1 eggs/day) | 27 | 45 | Andersen (1947) |
| *P. ulmi* (2nd gen.): | | | |
| apple (1.3 eggs/day) | 16 | 32 | Andersen (1947) |
| *P. ulmi* (3d gen.): | | | |
| apple (1 egg/day) | 14 | 32 | Andersen (1947) |
| apple | 29 | 52 | Balevsky (1967) |
| apple | 11.2 | 46 | Blair and Groves (1952) |
| apple | 18.8 | 69 | Cagle (1946) |
| apple | 6.6–34.9 | 69 | Gilliatt (1935) |
| apple | .. | 37 | Kuenen (1946*a*) |
| plum | 25–48 | 75 | Leski and Predki (1964) |
| *P. ulmi* (3d gen.): | | | |
| apple | 71.8 | .. | Musa and Dosse (1966) |
| *P. ulmi* (4th gen.): | | | |
| apple | 44.2 | .. | Musa and Dosse (1966) |
| *P. ulmi* (5th gen.): | | | |
| apple | 36.5 | .. | Musa and Dosse (1966) |
| *P. ulmi* (6th gen.): | | | |
| apple | 27 | .. | Musa and Dosse (1966) |
| *P. ulmi* (7th gen.): | | | |
| apple | 7.4 | .. | Musa and Dosse (1966) |
| *P. ulmi* (1st gen.): | | | |
| apple (2.6 eggs/day) | .. | 83 | Newcomer and Yothers (1929) |
| *P. ulmi* (2nd gen.): | | | |
| apple (2.4 eggs/day) | .. | 91 | Newcomber and Yothers (1929) |
| *P. ulmi* (3d gen.): | | | |
| apple (2.5 eggs/day) | .. | 59 | Newcomer and Yothers (1929) |
| apple | 10–35 | 90 | Parent and Beaulieu (1957) |
| apple | 10.7–16.2 | .. | Post (1962) |
| apple | 15–16 | .. | Ross and Robinson (1922) |
| *P. citri:* | | | |
| citrus | .. | 50 | Ebeling (1959) |
| citrus | .. | 50 | English and Turnipseed (1941) |
| citrus | 96 | .. | Munger (1963) |
| *B. rubrioculus:* | | | |
| apple | 16 | 32 | Balevsky (1967) |
| apple | .. | 25–30 | Gäbele (1959) |
| apple | .. | 6–47 | Georgala (1958) |
| apple (1st gen.) | 20.8–21.9 | 31–33 | Kremer (1956) |
| apple (2nd gen.) | 15.7–17.3 | 23–25 | Kremer (1956) |
| apple | 9.1–13.8 | .. | Post (1962) |

TABLE 1—*Continued*

| Mite species and host plant | Number of eggs per female | | References |
|---|---|---|---|
| | Average | Maximum | |
| *T. mcdanieli:* | | | |
| apple | 69.0 | 78 | Nielsen (1958) |
| pear | 50.6 | 87 | Nielsen (1958) |
| peach | 54.6 | 87 | Nielsen (1958) |
| apricot | 55.3 | 102 | Nielsen (1958) |
| sour cherry | 85.0 | 119 | Nielsen (1958) |
| sweet cherry | 119.1 | 176 | Nielsen (1958) |
| prune | 72.1 | 134 | Nielsen (1958) |
| *T. viennensis:* | | | |
| apple | 39.2–44.5 | .. | Balevsky (1967) |
| *T. evansi:* | | | |
| *Solanum douglasii* | 163.7 | .. | Qureshi, Oatman, and Fleschner (1969) |
| bean | 124.5 | .. | Moutia (1958) |
| *O. coffeae:* | | | |
| tea | 36.1–91.0 | 137 | Das (1959) |
| tea | 12.0–107.3 | 2–159 | Das and Das (1967) |

as many eggs were produced under dry conditions as under moist ones. The impact of host-plant quality is discussed on page 382.

The record indicates that certain of the other genera may average considerably lower in total fecundity than does *Tetranychus*. A high rate of oviposition contributes to a high intrinsic rate of increase, and this may explain why some species frequently increase violently and are common pests while others rarely reach pest status in spite of their continuous presence. Of course, other reasons may also be involved.

## Embryonic Development and Respiratory Mechanism of Eggs

Few studies have been made on the embryonic development of spider mite eggs. In 1868, Claparède published on the egg development of *Tetranychus urticae;* Gasser (1951) reports on his own and on Wiesmann's studies. Fukuda and Shinkaji (1954) published observations on the development of *Panonychus citri* eggs. Dittrich (1965, 1968) published in detail on his work with *T. urticae.*

The respiratory mechanism of eggs of *Tetranychus urticae, Panonychus ulmi,* and *Eotetranychus tiliarum* (Hermann) was studied by Dittrich and Streibert (1969), who showed that the eggs have a unique respiratory system. The authors state: "Two embryonic stigmata of a complicated structure pierce the shell during the contractive phase of the germ band. The stigmata are connected to a highly specialized part of the intermediate membrane which covers the embryo, characterized by a large number of perforations interspersed and fringed with ridges which are formed by the intermediate membrane. The perforated portions of the intermediate membrane allow an air plastron 0.2 to 0.3 $\mu$ thick to be present between the shell and the embryo. The air filled space has the appearance of two lateral and one frontal band connecting these two lateral parts when viewed under shallow light incidence. The perforations are the probable sites of gas-diffusion out of, and into, the embryo."

## Rate of Development

Development from egg to adult may vary from as few as six days to 10 or more, depending on the species, the host plant, temperature, and other factors; development from egg to egg is about two days longer since the preoviposition period usually amounts to approxi-

mately two days. Representative species concerned in these results are *Tetranychus urticae* ((Gasser, 1951; Linke, 1953; Bravenboer, 1959); *T. mcdanieli* (Nielsen, 1958); *Panonychus citri* (English and Turnipseed, 1941; Shinkaji, 1959; Munger, 1963); *T. desertorum* (Nickel, 1960); *Eotetranychus uncatus* Garman (Ubertalli, 1955); *E. sexmaculatus* (Riley) (McGregor, 1950); *Oligonychus platani* (McGregor) (Butler and Abid, 1965); *Panonychus ulmi* (Andersen, 1947; Doreste, 1964).

Rate of development, an important feature in analysis of field populations, poses many problems for the population analyst. The influences of varying temperatures on development of the egg and of the immature stages are difficult to estimate. This is discussed on page 362.

## Preoviposition Period

The preoviposition period may be completed in 24 hours or less (Cagle, 1949; Nielsen, 1958; Nickel, 1960; Davis, 1961; Musa, Dosse, and Tebcherany, 1968). Bravenboer (1959) gives the following data for *Tetranychus urticae*: 27° to 33° C (0.5 day); 22° to 27° C (1 day); 18° to 22° C (2 days); 13.5° C (5 days). For the same species, Klein (1936) found the following values: 24° to 26° C (1 day); 20° to 23° C (2 days); 13° to 19° C (3 days). Less detailed but comparable values for the preoviposition period of this species have been reported (Garlick, 1928; Wilson, 1931; Cagle, 1949; Gasser, 1951; Linke, 1953; and Marneffe and Delhaye, 1953). Davis (1961), for *T. multisetis* (=*T. cinnabarinus* ?) gives the following data: 35° C (0.5 day); 26.7° C (1.25 days); 22.2° C (2 days). Das and Das (1967) reported preoviposition in *Oligonychus coffeae* at 32° C (0.8 day); 30° C (0.9 day); 27° C (0.9 day); 25° C (1.2 days), and 20° C (2.3 days).

In field experiments with *B. rubrioculus*, Kremer (1956) found the following preoviposition periods: at 10.8° C (5.7 days); 13.7° C (4.6 days); 15.2° C (3.8 days); 18.3° C (2.5 days). In laboratory experiments for this species, Kremer found at 15° C (4.2 days); 20° C (2.4 days); 25° C (1.5 days) and 30° C (1 day). The variation from these mean values is indicated by Kremer. For *Panonychus ulmi*, Andersen (1947) found a preoviposition period of 2.5 to 3.5 days under field conditions.

## Sex Ratios and Sex Determination

In tetranychids, virgin females produce only male progeny; mated females produce both sexes, but usually a high percentage of females. Schrader (1923) distinguished two types of eggs and larvae in *Tetranychus urticae*: with three and six chromosomes, respectively. Schrader concluded that males develop from unfertilized eggs and are haploid, whereas females develop from fertilized eggs and are diploid. Arrhenotoky is also found in other tetranychids (McGregor and Newcomer, 1928; Klein, 1936). Cytological studies on sex determination in bisexual species of tetranychids were carried out by Helle and Bolland (1967). They state:

"It appeared that in 13 of the 14 examined species the tested eggs always had two numbers of chromosomes. The number per egg and per species was constant; per species, the ratio of the number of chromosomes was always 2:1. Moreover, virgin females of several examined species (viz. five *Tetranychus* species, *Eotetranychus carpini* (Ouds.), *Eurytetranychus buxi* (Garman)) only produced eggs with the lowest (haploid) number of chromosomes, these eggs developing into males only. These facts all accord with an arrhenotokous type of reproduction. Moreover, they suggest that all bisexual forms of the Tetranychidae are arrhenotokous. . . . The number of chromosomes in the 14 examined species are very low, the haploid number ranging from 2 to 7. The number 3 occurs very frequently in the subfamily Tetranychinae."

Only females of *Tetranycopsis horridus*

(Can. et Fanz.) have been found; this species is not bisexual. The eggs always showed four chromosomes. This species apparently has a thelytokous parthenogenetic reproduction, according to Helle and Bolland (1967).

For more detailed information regarding sex determination in various Acari the reader is referred to Oliver (1964, 1965*a*, *b*).

Davis (1961) reported that 32.4 per cent of the progeny from mated females of *Tetranychus multisetus* McGregor were males. Cagle (1962) reported 27.8 and 32.2 per cent males, respectively, for two different seasons, from females of *Panonychus ulmi* exposed to males. In a long-term, predator-prey interaction study, Laing (1969) found 2.9 females to 1 male in populations of *T. urticae*, in which males appeared to be usually available. Others have obtained generally similar results (English and Snetsinger, 1957; Nielsen, 1958). Boudreaux (1963) stated that a normal sex ratio does not exist, and that the ratio of sexes depends on the amount of spermatozoa introduced during the mating act.

The mating process in *Tetranychus urticae*, which takes place usually immediately after the last molting of the female, is described by Helle (1962), Boudreaux (1963), and Overmeer (1967). While copulation often takes place several times, studies of Boudreaux (1963) and Helle (1967), on successive matings with genotypically different males, showed that the first mating generally is the effective one. In general, a single impregnation will suffice to provide a female with diploid eggs for the rest of her life, to be used in combination with unfertilized, haploid eggs (Helle, 1967).

Blauvelt (1945) described the reproductive system of *Tetranychus bimaculatus* Harvey (= *T. urticae*) as consisting of one pair of ovaries, a single oviduct, vagina, and a receptaculum seminis. The descriptions given by Anwarrulah (1962) and Dosse and Langenscheidt (1964) agree with Blauvelt's, especially regarding the presence of a receptaculum. According to these authors, the receptaculum is connected to the vagina by a curved duct. It has been supposed that the aedeagus is brought into the vagina and the receptaculum seminalis is filled with sperm. Such a system suggests that the eggs receive the spermatozoon just before deposition. Van Eyndhoven (1967) gave a detailed description of the aedeagus with a separate ductus ejaculatorius, in *T. lintearius* Dufour. He also mentioned the copulation orifice of the female, which is situated just before the anal slit in the plain triangular area between the folds of the vagina. It is closer to the beginning of the vagina than indicated by the above-mentioned authors. Neither Blauvelt (1945) nor Anwarrullah (1962) nor Dosse and Langenscheidt (1964) mentioned the tiny orifice, and even Ewing (1914, page 12, fig. 4), who gave a detailed description and drawing of the female genital area, had not observed this orifice.

Van Eyndhoven (personal communication, 1967) found that this genital system is basically the same for all tetranychids. In the Tetranychini it is extremely fine, and difficult to detect; the ductus to the receptaculum seminis is rather short, very narrow, and more or less straight. In contrast, in the Bryobini this ductus is wider, very long, and winding. Van Eyndhoven believes that the spermatozoa probably return along this ductus to the vaginal aperture and then penetrate it, to fertilize the eggs at some stage in their development at which they are susceptible to fertilization. He thinks that the great differences between the ductus in the females of the Bryobini and that in the Tetranychini might have something to do with the distribution or rationing of the spermatozoa. Fertilization of the

immature oöcytes can also be deduced from arguments provided by Boudreaux (1963) and Helle (1967).

Gasser (1951) reported successful mating of males with deutonymphs of *Tetranychus urticae*, and Helle (1962) observed that males of *T. urticae* attempted to copulate with deutonymphs or even teleiochrysalids. These attempts, however, were not successful. Overmeer (1967) never observed matings between female deutonymphs and males.

Beament (1951) described the reproductive system of *Panonychus ulmi* in some detail. The egg receives its shell layer in a sac-like ovary, and then passes into a glandular ovipositing pouch which is evaginated through the genital aperture at oviposition. The pouch secretes the cement over the shell layer after this has made contact with the substrate; the outer wax layer is then secreted over the cement.

Males are unknown in some species of the Bryobini (Fenton, 1951; Baker and Pritchard, 1953; van Eyndhoven, 1955; Kremer, 1956; Georgala, 1958; Anderson and Morgan, 1958; Balevsky, 1967).

## Seasonal History and Dormant Stages

Tetranychids inhabiting cold regions commonly pass the winter in a dormant stage. Except for this period of reproductive inactivity, reproduction continues. Since development is fast, several to many overlapping and nearly indistinguishable generations may be produced each year. This fact poses problems for the population analyst, as discussed on page 364.

The dormant stage commonly is the diapausing, adult female, which presumably has been impregnated in the fall and does not feed until the following spring. They often possess a characteristic orange or yellowish color, apparently resulting from fat-body development (Boudreaux, 1963). McEnroe (1961*a*, 1963) states that the epithelium of the midgut is responsible for the accumulation of an orange lipid material that forms the characteristic color in the overwintering form. Helle (1968) is of the opinion that the color change is not caused by fats, but by the synthesis of an unknown caretenoid (probably astaxanthine) in the haemolymph, the function of which (if any) is unknown. Helle states that in albino spider mites, also, the photoperiodic induction leads to diapausing females which are clear white. Reiff (1949) attributed this change in color to the leaf metabolism in the host plant.

Pritchard and Baker (1952) and Dosse (1964*b*) demonstrated morphological differences between summer and diapause forms in the structure of the integumentary striae on the dorsal body surface. The former authors concluded that all mites belonging to the genera *Tetranychus* and *Eotetranychus* in northern climates exhibit this difference. Van de Bund and Helle (1960) and Parr and Hussey (1966) found intermediate forms and variations in these striae; thus, care is necessary in using this character for specific identification (Boudreaux and Dosse, 1963; Dosse, 1964*b*).

Three factors induce diapause: Photoperiod (Bondarenko, 1959; Linke, 1953; Bondarenko and Kuan, 1958; Helle, 1962, 1968; Parr and Hussey, 1966, for *T. urticae*; Osakabe, 1962, for *T. kanzawai*; Miller, 1950; Lees, 1950, 1953*a*, *b*, for *Panonychus ulmi*); temperature (Bondarenko, 1950; Lees, 1953*a*; Linke, 1953; Bondarenko and Kuan, 1958; van de Bund and Helle, 1960; Helle, 1962; Parr and Hussey, 1966; Osakabe, 1962); and nutrition (Reiff, 1949; Gasser, 1951; Pritchard and Baker, 1952; Lees, 1953*a*; Linke, 1953; Bondarenko, 1958; Parr and Hussey, 1966). Of the three, photoperiod and temperature are dominant; nutrition has a minor role. When food

is adequate, it exerts no influence, but when inadequate, it directs development toward diapause even when photoperiod and temperature conditions would not normally induce it (Wiesmann, 1940; Kuenen, 1949; Blair and Groves, 1952, for *P. ulmi*; Geispitz, 1960; Parr and Hussey, 1966, for *T. urticae*).

Populations of *Tetranychus urticae* inhabiting different latitudes demonstrate differences in response to photoperiod (Bondarenko and Kuan, 1958), the critical photoperiod decreasing one hour for each 3 degrees less in latitude. Rambier (1965) also reported from France that tendency toward diapause can vary considerably according to the geographical origin of the population. Bondarenko and Asatur (1960) found the critical daylength for induction of diapause in *Panonychus ulmi* to be 16 to 18 hours at 15° C; Razumova (1967) found it to be 17 hours at 15° C for this species. Both studies were on populations from the Leningrad region in the U.S.S.R. Bengston (1965) reported for Queensland (Australia) 13 hours at 15° C; Miller (1950), in Tasmania, found 12 hours at 15° C—both studies for *P. ulmi*. In England it was shown to be 14 hours at 15° C (Lees, 1953*a*, *b*). These data indicate a genetic flexibility for adaptation by *P. ulmi*, in photoperiodic response.

Geispitz (1960) provided evidence for variability in the response of *Tetranychus urticae* to photoperiod. He showed that changes in the critical daylength were achieved when mites of different geographical origin were bred, during several months, in continuous light at temperatures differing conversely from those of their natural habitat. Helle (1968) studied the genetic variability in photoperiodic response in *T. urticae*. A number of lines were inbred by sibmating, for seven generations, from a parent stock obtained from *Sambucus nigra* in the Netherlands. Exposure of these inbred lines to different photoperiodic regimes showed a diversity of photoperiodic responses, indicating a great genetic variability in the original colony. Reciprocal mass crosses between one line with a low-level response and lines with a high photoperiodic response demonstrated that high-level response was dominant over low-level response. In backcrosses to low-level response males, the transmission of the character was apparently different in the two types of $F_1$ hybrids; the difference could be explained by assuming a cytoplasmic determinant. Helle also considered the possibility that the difference in inheritance resulted from a peculiar haplo-diploid sex determination.

As a rule, diapause can be terminated by a period of chilling, although wide variations may occur within one species. Lees (1953*a*) found that diapause ended after exposure of *Tetranychus urticae* to temperatures below 10° C for 100 days. Bondarenko (1958) found that in the Leningrad region, exposures of this mite to 3° to 5° C for 55 days was sufficient to end diapause. Parr and Hussey (1966) found that after diapausing mites were exposed to 7° C, the percentage of females terminating diapause when subsequently exposed to 25° C was increased from 80 per cent after 14 days to 100 per cent after 65 days. Helle (1962) reported that after entering diapause at 18° C under a 12-hour photoperiod, some mites reverted to the nondiapause form without previous cold treatment. In this case, the speed of reversal varied widely—between 2 and 14 days. Parr and Hussey (1966) found that 55 per cent of newly diapausing females resumed feeding and egg-laying within seven days, without prechilling, when kept at 25° C and 16 hours daylength. This partial reversibility from winter form to summer form was also reported by Lees (1953*a*) for *Panonychus ulmi*. Bondarenko (1958), however, found no resumption of activity in newly diapausing *T. urticae* females kept in the dark at 18° to 22° C.

The properties of diapausing females

enable them to survive adverse conditions, because they can withstand low temperatures (Lloyd, 1922; Bondarenko, 1958) provided air humidity is high (Bondarenko, 1958; Helle, 1962; Parr and Hussey, 1966). They are also less susceptible to acaricides, as shown by Tibilova (1932) and Parr and Hussey (1966).

Dubynina (1965) studied the effect of short daylength on different generations of progeny of overwintered females of *Tetranychus urticae* in the U.S.S.R. The immature stages were found to be slightly sensitive to short days for a few generations following hibernation, this photoperiod reaction increasing successfully for four to six generations. The ability of the immature stages to react to short days, after passing a certain number of generations, explains why, in spring, when temperatures are favorable for development, but days are still short, diapause in the progeny does not occur. This is contrary to the observations of Parr and Hussey (1966) who found that, although *T. urticae* on cucumber, in heated glasshouses in England, terminated diapause during January, their offspring entered diapause under those conditions. Similar observations on the re-entry into diapause of first-generation females of *T. urticae* were also reported by Lloyd (1922) and Speyer (1924, 1925, 1926). Dubynina (1965) furthermore reported on the existence of two types of termination of diapause—one with a cyclic periodicity and one with a linear reaction. The first one was present when diapause was induced by short-day and low-temperature conditions; the second, when diapause was induced under conditions of long days, changing temperatures, and unfavorable food conditions. The ecological significance, as Dubynina suggests, is that the first type of diapause enables the mites to overwinter; the second type enables them to withstand adverse conditions during the vegetation period.

Razumova (1967) studied the variability of photoperiodic response during successive generations in *Panonychus ulmi* and *Tetranychus viennensis*. The results showed that the photoperiodic response in successive generations is a cyclical phenomenon.

Gasser (1951) claimed that summer females of *Tetranychus urticae* could be transformed to winter females within five to seven days at any time by transferring them to withering leaves, but Parr and Hussey (1966) obtained no diapausing females on such leaves when daylength and temperature were not conducive to diapause. These workers found that under short daylength and medium temperature, however, a marked increase occurred in the incidence of diapause among mites reared on senescent leaves.

Bravenboer (personal communication, 1968) found that *Tetranychus urticae* on cucumber, in glasshouses in the Netherlands, is becoming increasingly damaging during January and February when light conditions are still suitable for inducing diapause. This suggests a change in phototactic response, which has not yet been analyzed.

In several species the egg is the diapausing stage; *Panonychus ulmi*, some species of *Bryobia*, and *Petrobia* overwinter as eggs (Kuenen, 1946*a*, *b*; Andersen, 1947; Blair and Groves, 1952; Baker and Pritchard, 1953; Lees, 1953*a*, *b*; Smith and Weber, 1954; Zein-Eldin, 1956; Anderson and Morgan, 1958; Cox and Lieberman, 1960; Mori, 1961*a*; Tsugawa, Yamada, and Shirasaki, 1961). Lees' (1953*a*) study furnishes insight into the factors that govern diapause in *P. ulmi*.

In some species diapause is either facultative or absent, since in warmer areas reproduction continues throughout the year (Baker and Pritchard, 1953; Malcom, 1955; Boudreaux, 1963; Dosse, 1964*a*, 1966). Such species possess a genetic variability and plasticity relative to different climatic conditions

(Bondarenko and Kuan, 1958; Parr and Hussey, 1966). In northern Japan *Tetranychus kanzawai* overwinters as diapausing females; in the southern districts it is found in both diapause and nondiapause forms (Osakabe, 1962, 1967). *Panonychus citri* on pear in the lower latitudes in Japan has no diapause, whereas in the higher latitudes it overwinters in the egg stage (Shinkaji, 1961*a*, *b*). Some species exhibit no diapause, although their numbers may be markedly reduced during adverse seasons, as with *Oligonychus coffeae* on tea during the monsoons in India (Das, 1959; Ananthakrishnan, 1963; Cranham, 1966), and *P. citri* on citrus in Taiwan (Cheng, 1966). Lees (1953*a*) demonstrated that *Metatetranychus bioculatus*, a species inhabiting some regions in India, is without diapause and that photoperiod has no influence on its development.

Boudreaux (1963) summarized the evidence concerning the factors operating in diapause in the tetranychids; De Wilde (1962) reviewed photoperiodism in insects and mites.

Helle (1961), in the Netherlands, and Saba (1961*b*), in Germany, both claimed that the proportion of diapausing mites in populations resistant to organophosphorus compounds was significantly lower than in susceptible populations.

## Meteorological Factors

Spider mites, like other arthropods, are greatly affected by meteorological conditions. The species have adapted in various ways to meet this challenge and the seasonal challenges to life, often through response to stimuli or "clues" to impending adversity presented by meteorological factors. Thus, photoperiod, a more reliable index of the advance of the season than is temperature, is a key factor, particularly in the inducement of diapause.

Temperature, humidity, rain, light, and wind are also important in the life of spider mites. The physiological ecology of insects as discussed by Andrewartha and Birch (1954) and Messenger (1959) provides a general orientation to these relations. Limited specific data relative to certain species of spider mites are given below, although information on the role of meteorological factors in the field ecology of tetranychids is rather limited. Much of it is based on general observations, some on specific studies showing the influence of one or more factors on development or survival or the inception of diapause at the physiological level. Some deal with phenological aspects of the life cycle and the possibilities of predicting outbreaks by use of meteorological data. Very little precise information is available showing the quantitative impact of meteorological factors in relation to the total factors involved in the natural control or population dynamics of tetranychids—that is, in the form of their contributions to the total generation mortality or their influence on natality and movements. (For further discussion see p. 365.)

**Temperature.** A number of workers have treated temperature as related to tetranychid development, survival, or reproduction: for *Panonychus ulmi* (Newcomer and Yothers, 1929; Andersen, 1947; Blair and Groves, 1952; Miller, 1952; Mori, 1961*b*; Tsugawa, Yamada, and Shirasaki, 1961; Parent, 1965); for *Bryobia rubrioculus* (Kremer, 1956; Anderson and Morgan, 1958; Georgala, 1958); for *Tetranychus urticae*-complex (Cagle, 1949; Gasser, 1951; Linke, 1953; Iglinsky and Rainwater, 1954; Bravenboer, 1959; Laing, 1969); for *P. citri* (English and Turnipseed, 1941; Fukuda and Shinkaji, 1954).

Low winter temperatures cause mortality in overwintering stages, and represent a prime challenge which has been met in many species by development of cold-tolerant or diapausing stages, commonly eggs or adult females, as previously discussed. Temperature has a role in inception and/or termination or diapause. McGregor (1914), Klein (1936), Lienk and Chapman (1958), MacPhee

(1961) and Stenseth (1965) report tolerance of tetranychids to either or both cold and heat. Dierick (1948) found that sprays used against the winter eggs of *Panonychus ulmi* in the Netherlands retarded hatching of eggs that were not killed. Thus, use of such materials may result in a spurious impression of the inherent time-temperature-development relations.

Elmer (1965) reports that *Eotetranychus yumensis* (McGregor) may have an estivating stage, as it is a desert species and is inactive in summer. During an observation period of 11 years in Yugoslavia, Kac (1963) found that a relation existed between the population levels attained by *Tetranychus urticae* and the conditions to which the overwintering females were exposed. Mean temperatures during February were of much importance; relatively high temperatures during that month almost invariably were followed by rapid increases of this species. Relatively low temperatures in a mild environment may favor *E. sexmaculatus* on citrus in Florida (Pratt and Thompson, 1953; Muma, 1958), but may reduce *Panonychus citri* and *E. banksi* for a considerable period (Simanton, 1965).

Cold weather in spring apparently causes mortality of hatching larvae of *Panonychus ulmi* (Cutright, 1963; Oatman, 1965). At certain stages of development, *Bryobia rubrioculus* appears to be more favored by cool than by hot weather. In Germany, Kremer (1956) found that the maximum hatch of winter eggs of this species occurred between 20° and 25° C; temperatures higher or lower had adverse effects on hatching. In British Columbia, Canada, Anderson and Morgan (1958) found that both *B. rubrioculus* (= *B. arborea*) and *B. praetiosa* were more abundant during cool, wet years than in warm, dry ones.

There is evidence of selection for cold-tolerant strains; Bengston (1965) reported high mortality of winter eggs of *Panonychus ulmi* exposed to −12° C in Queensland, Australia; Lienk and Chapman (1958) found high mortality when winter eggs of the same species were exposed to −33° to −36° C in New York. MacPhee (1961) found that winter eggs of *P. ulmi* from New Brunswick were killed at −31° C, while eggs from Quebec were killed at −37° C. MacPhee showed experimentally that hybrids of parents from the different localities produced eggs typical of the less cold-hardy strain, suggesting that cold-hardiness is recessive. In Norway, Somme (1966) found a correlation between low temperatures and mortality of winter eggs of *P. ulmi* following the extremely cold winter of 1965-1966; −41° C caused a decrease in hatching to 0.7 per cent while at −14.5° C, 73.3 per cent hatched. Observations by Lienk and Chapman (1958) in New York indicated a similar situation. Some species, e.g., tropical and subtropical ones, have no cold-tolerant or diapausing stage. Their distributions may be limited by mean minimal temperatures. Nickel (1960) considered *Tetranychus desertorum* to be limited in the western United States by mean monthly winter temperatures of approximately 4.4° C; in laboratory trials, he found that 10° C had some lethal effect. Mori (1961*b*) reported the following data for the limits of female activity: *Panonychus ulmi*, 4.8° to 9.8° C; *T. viennensis*, 9.2° to 18.5° C; *T. telarius* (= *T. urticae*) 6.7° to 13° C; and *Bryobia praetiosa*, 6° to 14° C. Shinkaji (1962) found the corresponding values to be 8° to 9° C for *P. citri*. Osakabe (1967) found that the theoretical zero points for development of eggs, larvae, protonymphs, and deutonymphs of *T. kanzawai* were 8.7°, 14.6°, 13.4°, and 13.2° C, respectively.

Mean incubation periods for *Tetranychus telarius* (= *T. urticae*-complex) ranged from 2.4 days at 32.5° C to 33.2 days at 11.5° C (Harrison and Smith, 1961). According to Cagle (1949), Gasser (1951), van Marle (1951), Linke (1953), and Bravenboer (1959), these values varied between 2.5 days at 34° to 38° C and 19 to 20.5 days at 12° to 15° C. The

time required for development from hatching to adult varied from three days at 32.5° to 38° C to 21 days at 12° to 15° C. According to Das and Das (1967), the time required for development from hatching to adult for *Oligonychus coffeae* varied from 4.9 days at 30° C to 8.7 days at 20° C.

In Japan, Tsugawa, Yamada, and Shirasaki (1961) found that no development of winter eggs occurred at 7° C or below. They also found a high correlation, useful in forecasting, between the temperatures in April and the first hatching of the winter eggs.

Hatching of diapause eggs and renewed activity of overwintering adults are generally synchronized with development of host-plant foliage, and both are associated with the advance of suitable spring temperatures. In Canada, hatching of winter eggs of *Panonychus ulmi* began about mid-May (Gilliatt, 1935; Parent and Beaulieu, 1957), whereas in Virginia, hatching commenced the last week of April (Cagle, 1946). Parent and Beaulieu (1957) found that over-all hatching was highest when the hatching period was short and early, that is, delayed hatching resulted in greater egg mortality. It was not determined whether this was due to increased predation or physiological reasons. Miller (1952) found the duration of winter egg hatching of *P. ulmi* in Tasmania to be longer than that reported for Europe or the U.S.A.—that is, extending over 50 to 64 days. Position on the tree did not appear to affect hatching time. In the Netherlands, Geijskes (1938) reported five, and Kuenen (1949) four generations per year for *P. ulmi*. Collyer depicts three, and partially four, generations for this species in England (1964*a*), and five generations of the same species in New Zealand (1964*b*). Miller (1952) studied the effect of temperature on the development of *P. ulmi*, and found a slightly faster rate of development under fluctuating temperatures in contrast to constant ones of approximately the same values. Parent (1965) studied the influence of temperature on the embryonic and postembryonic development of *P. ulmi* in Quebec. He found that embryonic development begins at 8.9° C, increases between 11.5° and 24.5° C, and decreases at over 24.5° C. Similarly, the development of postembryonic stages begins at 8.4° C, increases between 11.5° and 22.5° C, and decreases beyond that point.

André (1942) stated that damage by tetranychids in France is often worse after a severe winter than a mild one because their predators have less opportunity to feed.

The number of generations in tetranychid species and their seasonal activity are correlated with temperature, modified by other factors, such as nutritional condition of the host plant. Examples are *Oligonychus punicae* (Hirst) (McMurtry and Johnson, 1966), *Tetranychus desertorum* (Nickel, 1960), *Panonychus citri* (Jeppson *et al.*, 1957) and *T. urticae* (Gasser, 1951; Linke, 1953; Hussey, Parr, and Crocker, 1957; Bravenboer, 1959). Jeppson *et al.* (1957) found that high populations of *P. citri* may occur even in winter in southern California, and Hussey, Parr, and Crocker (1957) found that, in greenhouses, the duration of the egg stage for females of *T. urticae* decreased from 5.9 days at 21.1° C to 2.3 days at 35° C, and the duration for larvae, protonymph, and deutonymphs combined, decreased from 7.4 days at 21.1° C to 3.4 days at 32.2° C, and rose to 4.1 days at 36.7° C. The retardation perhaps partly resulted from the necessity for frequent transfer to fresh leaf disks because leaves deteriorated rapidly at 36.7° C.

Mori (1961*b*) reported the temperature (°C) preferences of four species of tetranychids: *Panonychus ulmi*, 25 to 28; *Bryobia praetiosa*, 21 to 24; *Tetranychus viennensis*, 25 to 30; and *T. urticae*, 13 to 35.

Relatively little is known about the upper limits of temperature tolerance in tetranychids. Mori (1961*b*) reported the following temperatures (°C) at which

death by heat occurred for adult females: *Panonychus ulmi*, 44 to 47; *Tetranychus viennensis*, 43.5 to 45; *T. telarius*, 45 to 46.5; *Bryobia praetiosa*, 45 to 46.5. Values are also given for males. Shinkaji (1962) found that adult females of *P. citri* are killed at 46 to 47° C. Roesler (1953) observed that in the Pfalz, German Federal Republic, densities of *P. ulmi* on fruit trees declined drastically after temperatures reached values of 40° C for several days. Kremer (1956) studied this relation in detail in *B. rubrioculus* in the laboratory. He found that 100 per cent mortality occurred after exposure for 36 hours to 39° to 40° C or 43° to 44° C, but only after 60 hours at 35° to 36° C. For *P. ulmi* the periods of exposure resulting in 100 per cent mortality at the abovementioned temperatures were 24, 8, and 36 hours, respectively. This shows that *B. rubrioculus* can stand higher temperatures than *P. ulmi*. Such results explain why, in areas of high temperatures, *B. rubrioculus* on fruit trees can be a more important species than *P. ulmi*. However, differences in predator action, and other factors, could also be involved.

**Humidity and temperature.** Humidity, and humidity in combination with temperature, are important factors in spider mite ecology. Loss or gain of water from the atmosphere by small organisms like mites is fundamental to their existence (Lees, 1946; Winston, 1963*a*, *b*, 1964). The amount of feeding they do and thus the injury they cause, may be related to their water balance (Wharton and Cross, 1957; Wharton, 1963). Tetranychid mites feed on moisture-laden plant tissue, and thus make up for loss of water to the atmosphere. The egg stage, however, may become rapidly desiccated in dry air. Huffaker (1958) and Huffaker, Shea, and Herman (1963) found that *Eotetranychus sexmaculatus* eggs on oranges in a laboratory ecosystem study dehydrated and failed to hatch if humidity fell to 40 per cent for very long at temperatures of about 27° C.

Nickel (1960) showed that a West Coast stock of *Tetranychus telarius (= T. urticae)* developed faster, with higher egg production, under low humidity (25 to 30 per cent) as contrasted with high (85 to 90 per cent). He found the reverse to be true for *T. desertorum*, however. Boudreaux (1958) observed reduced egg production and oviposition period and increased mortality of newly-hatched larvae under high humidity, in contrast to low humidity, for four species of tetranychids, and postulated that water loss by evaporation determines the amount that the mite can take in by feeding. Thus, under low humidities, both intake of nutrients and reproduction will be greater. Boudreaux's conception agrees with Nickel's results for *T. urticae* and with his own for the four species, but not for Nickel's results on *T. desertorum* (McEnroe, 1963). Moreover, McEnroe's results for the Blauvelt strain of *T. urticae* were contrary to Nickel's findings. McEnroe concluded that although considerable water can be lost through the tracheal system at low humidity, fluid excretion by this route is not an absolute requirement. Boudreaux (1963) further summarizes the findings:

"The problem of water conservation in such small animals as spider mites is met through a combination of adaptations. The stylophore (fused bases of the chelicerae) can be retracted in such a way that the peritremes and spiracular openings can be completely closed (Blauvelt, 1945), thus restricting evaporation when necessary. The cuticle is relatively waterproof (Gibbs and Morrison, 1959; McEnroe, 1961*a*) and the diet is liquid. Further water conservation is effected through the production of guanine, an insoluble purine typical of arachnoids, as the chief nitrogenous excretion (McEnroe, 1961*b*). Water sufficient for maintaining life is obtained probably through oxidation of diapause fat in overwintering females (McEnroe, personal communication) and the eggs are covered with an extremely waterproof wax

(Beament, 1951; Lees, 1961). Oxygen consumption in diapausing *T. telarius* is very low compared to that of active forms, and the stylophore generally restricts water loss by closing the tracheae (McEnroe, 1961*a*)."

McEnroe (1963) further stated: "Large volumes of water can be passed rapidly through the digestive system and excreted without requiring energy for selective absorption and transport to the tracheal system for excretion. . . . The excretion of excess water as a fluid rather than as a vapor allows the mite to feed at high relative humidity."

Mori and Chant (1966) studied the influence of air humidity on the hygrotaxis and hygrokinesis of *Tetranychus urticae* under laboratory conditions at 23.3° C. In combinations of high versus low humidities, sharp reactions to avoid the high humidities were observed. In less extreme combinations, the responses of the mites were less obvious. *T. urticae* showed quite different kinetic responses to different levels of humidity. It almost stopped moving after being exposed to high humidities for four hours, but when exposed to lower humidities (76 and 33 per cent) it continued to move for 24 and 12 hours, respectively. No differences were noted in the reactions of males and females. Winston (1963*a*, *b*) found that *Bryobia praetiosa* also avoided high air humidities. When the mites were given a choice of two humidities, the majority always chose the lower.

Numerous reports indicate that hot, dry weather is conducive to outbreaks of tetranychids (Ewing, 1914; Garman, 1923; Frost, 1924; Hamilton, 1926; Andersen, 1947). These early observations, and later ones, have at times been based on abundance of mites, at other times on levels of injury. However, relatively greater injury for a given level of mite damage may occur during hot, dry periods (p. 377).

Recent data shed light on the very significant differences among various species and situations. Rodriguez (1964) suggested that changes in the physiology of the plant under drought conditions may make the plant more suitable for reproduction of the mites. Bondarenko (1949) reported an osmotic pressure increase from high rates of fertilizers and this was correlated with increased densities of *Tetranychus urticae*. Andres (1957) studied the relation of temperature and humidity to reproduction and survival of three tetranychids in California. High temperatures and low humidities were more favorable to *T. pacificus* than to *T. urticae* and *T. atlanticus*. The latter was best suited to low temperatures and higher humidities, with *T. urticae* being intermediate. Leigh (1963*a*) considered that these relative standings, presumably operating in conjunction with their interspecific competition, seemed to explain the occurrence of these three species on cotton in the San Joaquin Valley of California; i.e., *T. pacificus* dominates on the drier, hotter west side; *T. urticae* on the more humid, cooler east side; and *T. atlanticus* in the central area, or overlapping the other two. Nickel (1960) felt that the dry summers may explain why *T. desertorum* is not a major pest in central California. Butler's (1955) observation that *T. urticae* in Arizona was less abundant in dry alfalfa plots than in irrigated ones is compatible with the above view, although Butler considered that the difference may have been due to improved nutrition afforded by the irrigated plants. Frogatt (1921) considered the unusually long, dry spring of 1920 responsible for serious damage by *T. telarius* to ornamentals in Sydney, Australia. Griffith and Wene (1954) found that *Oligonychus pratensis* (Banks) was more injurious in a dry field than in an irrigated one in Texas.

Crashes in populations of *Panonychus citri* in southern California have often been associated with periods of high temperature and low humidity. Apparently, these conditions not only cause direct mortality but also change the condition of the leaves so that they are no

longer so favorable for reproduction, and may cause a shift to a migrant phase (p. 347). Both high temperatures and low humidities were considered important by Jeppson *et al.* (1957) and Jeppson, Complin, and Jesser (1961), but on the basis of laboratory studies, Munger (1963) concluded that high temperature alone is the limiting factor. His data indicated that mites were more adversely affected by high temperatures at high humidities than at low humidities. Jeppson (personal communication) suggested that during periods of strong east winds, mites may be exposed to lower humidities than those Munger tested.

*Panonychus citri* originally was a pest in California only in the coastal and subcoastal areas having relatively cool, semi-humid conditions (Boyce, 1936; Quayle, 1938). However, it has now become a serious pest in warm, dry, interior areas as well (Lewis and Schilling, 1950; Munger, 1963). It has been suggested that *P. citri* has become adapted to the interior areas or that changes in the pest-control practices have released it from control by natural enemies. Jeppson and Carman (1960) suggest that a combination of such factors may be responsible for the increase.

In California, the cooler, more humid coastal areas are favorable for development of *Eotetranychus sexmaculatus* (Jeppson, 1952). This species has a statewide distribution in Florida, where high humidities predominate (Muma, 1961*b*). Huffaker's observation of the desiccation of eggs of this species at low humidities, cited above, may help to explain these distributions.

Muma (1961*a*) observed differences in spider mite populations between clean-cultivated and minimum-cultivated citrus groves. Although the cause could not be determined, differences in microclimate would seem to be a possibility.

Beament (1951) reported that the summer eggs of *Panonychus ulmi* are very vulnerable to desiccation up to six hours after laying, and will not survive that period in relative humidities (R.H.) lower than 75 per cent. After that period, however, they can survive at 30 per cent R.H. or lower. Experiments with this type of egg showed that about six hours after being laid, they become suddenly much more waterproof, suggesting that a wax layer is produced by the developing organism. Winter eggs, transferred immediately after oviposition to an atmosphere of even 20 per cent R.H., do not desiccate. Experiments showed that the winter eggs have already received their inner wax layer at the time of oviposition; according to Beament, this difference obviously is an adaptation to the site of oviposition.

Mori (1957) presents an excellent account of the interrelations of temperature and air humidity to the separate phases, embryonic development, and hatching of *Panonychus ulmi* eggs. Results are presented in hygrothermograms. For embryonic development, the best condition lies between 15° C, or lower, and 32° C, and between 43 and 100 per cent R.H. For hatching, the best conditions lie between 15° C, or lower, and 31° C, and 65 to 100 per cent R.H. Becker (1952), in experiments on the influence of constant temperatures and relative air humidities on the development of *P. ulmi* found an optimum in hatch at 24° C and 90 per cent R.H. Lower humidities increased mortality of the eggs.

Fukuda and Shinkaji (1954), for *Panonychus citri*, and Bodenheimer (1951), for *Eutetranychus banksi* (McGregor) (=*Anychus orientalis* Zacher) and *Eotetranychus altheae*, also give data on the importance of relative humidity and temperature. Osakabe (1959, 1962, 1967) found the ranges of temperature and humidity for successful hatching of *Tetranychus kanzawai* to be 15° to 30° C and 46 to 93 per cent R.H. Relative humidities of 20 and 100 per cent had adverse effects on the hatching of eggs, and inhibited development of the immature stages. In the field, however, the popula-

tion development was not correlated with these atmospheric conditions. Das and Das (1967) studied the interrelations of temperature and air humidity on eggs of *Oligonychus coffeae* in northern India. They found that no eggs hatched at 34° C, irrespective of air humidity, or at 17 per cent air humidity, irrespective of temperature. The optimum conditions for over 90 per cent hatch were provided by a combination of temperatures within ranges of 20° to 30° C, and 49 to 94 per cent R.H.

Helle (1962) and Bondarenko (1958) showed the need for high relative humidity if diapausing females of *Tetranychus urticae* are to survive the winter. Parr and Hussey (1966), in their studies on the optimum conditions necessary for winter survival, found also that *T. urticae* required low temperatures and high humidities to survive the winter successfully; at 6° C many mites held at 75 and 93 per cent R.H. survived for more than eight months. At 40 per cent R.H. and 6° C the rate of survival was much lower. Higher temperatures (16° and 25° C) increased mortality, although here again, the mites showed a marked response to a moist atmosphere. Discussing these findings, Parr and Hussey state: "No records of winter temperature and humidity are available for hibernating sites within unheated glasshouses, but whereas in temperate climates winter temperatures in general are suitable for successful hibernation, it is doubtful whether the humidity in the hibernating sites is ever favorable. This factor, together with the considerable temperature rises which occur under glass during winter sunshine, is probably responsible for high mortality amongst hibernating populations."

Kuenen (1946*b*) found that winter eggs of *Panonychus ulmi* are sensitive to very high humidities; when the eggs were kept at 100 per cent R.H., only a few hatched. The highest percentage of hatch was found to take place between 60 and 80 per cent R.H. On the other hand, the eggs seem to have a good protection against the loss of water; Kuenen found that even at zero R.H. a few larvae hatched.

Kremer (1956), in Germany, found that the percentage of hatching in winter eggs of *Bryobia rubrioculus* was higher at low humidity than at high; he found 90.8 and 75.4 per cent hatch at 5 and 96 per cent R.H., respectively. This finding could also partly explain why this species is of more economic importance in the continental areas in Europe than in the coastal climates.

**Rain and wind.** Early workers credited rain and wind with reducing populations of mites by washing them from the foliage (Frost, 1919; Ross and Robinson, 1922; C. C. Hamilton, 1926; Franklin, 1929). After rainy periods, Kremer (1956) found large numbers of dead *Bryobia rubrioculus* (=*B. praetiosa*) on the leaves. In laboratory experiments he found that exposing this species to wet conditions for 4, 8, and 16 hours caused 30, 70 and 95 per cent mortality, respectively. Corresponding figures for *Panonychus ulmi* were 5, 10, and 40 per cent mortality, respectively. The quiescent stages were not affected. Tanaka and Inoue (1959) and Cheng (1966) present data showing reductions in *P. citri* after heavy rains; *Oligonychus coffeae*, as stated elsewhere, is greatly reduced during the monsoons (Das, 1959).

Heavy rains might be expected to cause severe losses, particularly in species that inhabit the upper surfaces of leaves and are not heavy webbers, and the effect may be intensified if heavy rains are accompanied by turbulent wind, which would also tend to expose the lower surface of the foliage. Tanaka (1963) reported that in Japan not only the active stages but also the eggs of *Panonychus citri* are swept off by typhoons. Osakabe (1967) found that the multiplication of *Tetranychus kanzawai* on tea in Japan was remarkably inhibited by rain and, especially, by a combination of rain and wind, which re-

sulted in great reduction. The observed reductions may also be intensified following the rainy season, because the food quality of the leaves has also become impaired.

Blair and Groves (1952) found that *Panonychus ulmi* was not swept off by rain, because all the mites were to be found on the under surface of the leaves, huddled along the midribs and veins. This is in contrast to Kuenen's (1946*a*) findings, showing reduction in the numbers of mites after heavy rains.

Wind as related to movements from area to area is discussed on page 371.

**Light.** The importance of light in photosynthesis and production of food for mites is obvious. Responses to light, of migration or no migration, may be quite important in the dynamics of mite populations. Suski and Naegele (1963*b*), in studying the reaction of *Tetranychus urticae* to light, reported that this species exhibits "sedentary" and "dispersal" phases. On a fresh leaf of favorable food, the mites showed little or no response to light. The authors state: "But as soon as the leaves are destroyed by mite feeding, a shortage of food supply and a decrease in relative humidity on the leaf surface (Boulanger, 1958), occur, with consequent desiccation. Food deficiency and desiccation produce an increase in activity in the mite population, or in other words, cause a change to the "migratory" phase, and in interaction with some still unknown factor (or complex of factors) cause a taxis-type light response. Both increased activity and positive light reaction with other stimulus response sequences, enable the animal to search more effectively for new food resources."

The morphology of the eyes of *Tetranychus urticae* was studied by McEnroe (1969*a*). After describing the morphology and anatomy of the eyes, McEnroe states:

"The morphology of the anterior eye shows that this eye can act as a scanning-point detector. The movable lens shifts the optical axis dorsoventrally, while the retinal cells remain stationary at the base of the vitreous body. The dense mass of red oil droplets shields the retinal cells, and the change from a lower refractive index of the vitreous body to the higher refractive index of the surrounding red-oil guard prevents internal reflections. This elimination of internal reflections insures only light entering along the central axis of the vitreous body can stimulate the retinal cells.

"The structure of the posterior eye with its lack of guard oil, coupled with the transparent cuticle of the mite, would indicate that light, although collected more efficiently by the convex lens, need not enter through the lens to stimulate the retinal cells. Indeed, examination of live mites under the microscope shows that light from below can pass through the body of the mites and exit through the posterior eye. The greater number of cells in the anterior eye suggests that receptors for both green and U.V. are present in the posterior eye. The posterior eye, in contrast to the anterior eye, would appear to be almost an omnidirectional receptor with its maximum efficiency in the dorsal quadrant. These eyes obviously do not resolve an image but serve as point detectors. The few sensory cells present would restrict the dynamic range of the eyes. The optic mass at the root of the optic nerve, by its appearance and analogy to other arthropods, would appear to be a prime candidate for a neurosecretory role."

A number of other workers have recently expanded our knowledge of the photoreceptors and light orientation of certain mite species (Camin, 1953; Mori, 1955, 1962*a*, *b*; Hughes, 1959; George, 1963; Suski and Naegele, 1963*a*, *b*; Suski, 1965; Naegele, McEnroe, and Soana, 1966; McEnroe, 1969*a*, *b*; McEnroe and Dronka, 1969). Mori (1955) showed that the susceptibility to light in *Panonychus ulmi* is related to the developmental stage and to levels of hunger; adults of *P. ulmi*, *Tetranychus viennensis* and *T. urticae* (= *T. telarius*) showed

positive phototaxis irrespective of sex, nutritional state, and the season during which they were collected (Mori, 1962*a*).

Suski (1965) reported that starvation in *Tetranychus urticae* produces a "state of capability" to develop a light response and that this state of capability is apparently so related to the degree of starvation as to facilitate responses of different sign, and possibly of different kind, in a fixed order. These behavioral patterns are apparently evolutionary adaptations enabling the mite to use light as a token stimulus in the search for food.

McEnroe and Dronka (1969) analyzed the reaction of adult females of *Tetranychus urticae* to light of different wavelengths; they showed color vision for the near ultraviolet (U.V.) and green spectral regions (McEnroe and Dronka, 1966). In addition, green light made possible the separation of photonegative (green−) and photopositive (green+) behavioral classes from a population. The photoresponse of these two classes showed that although the green and U.V. receptors were independent, they could also act in the green+ class. McEnroe and Dronka (1969) postulated:

". . . that independent U.V. and green receptors are situated in the anterior eye. The anterior eye with its movable lens, shielded retinal cells, nonreflective vitreous body, and more numerous retinal cells is morphologically suitable for a directional U.V. and green photoreceptor. The congruence of the 380-m$\mu$ and 530-m$\mu$ response lobes in the green− and the green+ classes shows a common morphological location for these receptors in the anterior eye. The symmetry of these lobes around 0° indicates a shift in optical axis of the anterior eye by movement of the lens. The independence of horizontal 380-m$\mu$ response in the green− class and 530-m$\mu$ response in the green+ class to vertical illumination shows that these receptors are in the shielded anterior eye. The influence of vertical illumination at 380 m$\mu$, but not 530 m$\mu$, on the behavior of the green+ class shows the presence of an U.V. receptor in the unshielded posterior eye."

A schematic diagram of the logic associated with the photoreceptors is presented (McEnroe and Dronka, 1969).

Hussey and Parr (1963*b*) postulate that, among other factors, light can be important in the spreading of *Tetranychus urticae*.

Hueck (1951, 1953) found that winter eggs of *Panonychus ulmi* in the Netherlands hatched less successfully when kept continuously in darkness, in contrast to daylight, at 25° C and 75 per cent R.H. Inspection of unhatched eggs kept in the dark showed that a great proportion contained what seemed to be fully developed larvae, whereas this was rarely encountered in eggs kept under daylight. These observations suggest that the development of eggs in the dark is arrested primarily at about the moment of hatching.

This suggestion is supported by the fact that the greatest proportion of eggs hatched during the daylight, and observation of the strong positive phototaxis of the larvae. Hueck (1953) suggested that rupture of the egg shell is performed by the larvae. In view of these facts, it seems likely that light provides a stimulus to the fully developed embryo to break the egg shell.

Hueck (1951) reported that winter eggs of *Panonychus ulmi* hatched primarily during daytime. He suggested that the short wavelengths in some way were physiologically related to the red pigment of the winter eggs, and that they influenced embryonic development. Becker's (1952) results partly supported Hueck's findings; a higher percentage hatch was obtained under light conditions as compared to darkness. However, he found that there were no indications of physiological relations between red light and the red yolk pigment, since the embryonic development progressed in the absence at the same rate as in the presence of red light.

Yet Kirby and Gambrill (1954) studied the hatching of summer eggs of *Panonychus ulmi* under artificial conditions and found that light was not essential for hatching, at least beyond the diffuse daylight reaching the eggs during the short period required for the counting. According to Cranham (1966), the reduction of shade-tree cover can markedly increase the incidence of red spider, *Oligonychus coffeae*, on tea, but other cultural trends, notably higher rates of manuring and changes in pruning practices, have received little attention.

Das (1963) studied the effect of density of shade and manuring rate on this species in northern India. Infestation developed much less under medium and heavy shade than under light shade or none. High dosages of nitrogenous fertilizer (ammonium sulfate) greatly reduced the mite attack in unshaded and lightly shaded plots, but had virtually no effect under heavier shade. Phosphate and potash applied separately or in combination had no significant effect. These results are in contrast with those of Osakabe (1963*b*, 1967) in Japan, who found, in pot trials, that *Tetranychus kanzawai* was increased by high levels of nitrogen and potash and reduced by high levels of phosphate and manganese.

Light as related to diapause development is discussed on pages 359-361.

## Mobility and Other Features

Of the three avenues to change in population numbers in a given population area, natality and mortality have received substantial study, albeit not too critical, while movements into or out of the area have generally been neglected. With species like tetranychids this factor may be most important. Some species form "ballooning threads" by which they lower themselves from a leaf, and are picked up by air currents and carried for some distance. Fleschner *et al.* (1956) intercepted such drifting mites on sticky-coated boards placed 20 feet in the air. Fleschner (1958*a*) considered that population decreases resulting from mass emigration may be as striking as those from predation. Among species known to balloon away in this manner are *Panonychus ulmi*, *P. citri*, *Oligonychus punicae*, and *Eotetranychus sexmaculatus* (Ewing, 1914); Ebeling, 1934; Steer, 1940; Kuenen, 1946*a*; Andersen, 1947; Marlé, 1951; Fleschner *et al.*, 1956; Coghill and Ingram, 1962; Post, 1962; Cutright, 1963), and *Tetranychus pacificus* (Newell, 1941).

Andersen (1947) collected all stages of *Panonychus ulmi* on sticky traps after short periods of relatively strong winds in Germany; Marlé (1951) studied air dispersal of this species in England. She used a wind funnel, suction air traps, and greased plate traps. Most of the migrating mites were found to be adult females, the greatest number being found at periods of peak populations in each generation. The mites descended by spinning gossamer threads on which they let themselves down. These threads were formed in still air, following upon relatively calm periods when temperatures were above 21.1° C and relative humidity was low. Post (1962) was of the opinion, however, that wind-borne dispersal of *P. ulmi* was of minor importance under her experimental conditions.

Osakabe (1967) found that large numbers of *Tetranychus kanzawai* were carried by wind and were collected at 0.5 to 1.0 meter from the plants. On occasion, the mites were lifted as much as 10 meters into the air. He also found that the number of air-borne mites was correlated with the seasonal population fluctuation on the tea bushes.

Boyle (1957) demonstrated that *Tetranychus cinnabarinus* was carried by wind but that, in the absence of a ballooning thread, stronger winds were needed than with other tetranychids. Ewing (1914) reported that *T. urticae* was blown from trees for a considerable distance, but Coghill and Ingram (1962) could find little evidence of wind dispersal for *T. urticae* in England. Huffaker and Spitzer (1950) found that strong

air currents inhibited build-up of *Tetranychus urticae* (= *T. bimaculatus* Harvey) on young pear trees in a controlled experiment, probably through blowing the mites off or impairing their reproduction.

Hussey and Parr (1963*b*) showed experimentally that, although *Tetranychus urticae* was more active in sunlight than in darkness, the presence of light had no effect on the rate of migration from infested leaves. The influence of air humidity, however, was very marked; it inhibited movement, thus supporting the evidence reported by Suski and Naegele (1963*a*, *b*).

Gharib (1967) reported that *Paratetranychus afrasiaticus* (McG.), a species damaging date palms in Iran, is transported by birds and insects, especially by *Polistes olivaceus* (Deg.).

The effects of tetranychids drifting into the population area may be just as important as those of movements away. Perhaps this process serves to constantly replenish endemic populations that are at or near the point of annihilation by predation or other causes. Almost no information is available on this.

## Competition and Miscellaneous Factors in the Potential for Increase

Competition is obviously a factor in the actual increase potential. Although the term "competition" can be misleading, and some ecologists reject a number of the ways in which it has hitherto been used, we think it can be applied to those cases in which a limited amount of food is available.

Populations of a given tetranychid species obviously become self-limiting if not controlled by other factors. As the density becomes high and extensive feeding causes discoloration and leaf damage, the food supply becomes less suitable, and competition presumably becomes severe (see p. 382). Overcrowding may lead to premature deposition of winter eggs by *Panonychus ulmi* which, under these conditions, is usually reduced in numbers (Wiesmann, 1940; Kuenen, 1946*a*; Blair, 1951). Under these conditions, *Tetranychus urticae* begins to abandon the host when leaves become chlorotic (Hussey and Parr, 1963*b*). Fleschner *et al.* (1956) and Fleschner (1958*a*) found that, as citrus leaves become injured, large numbers of females of some species, e.g., *Eotetranychus sexmaculatus*, lower themselves on silken threads and are carried away by air currents. Henderson and Holloway (1942) found that *P. citri* confined on leaves previously damaged by feeding had a reduced reproduction and a slightly higher mortality in comparison with mites confined on undamaged leaves. McMurtry and Johnson (1966) and McMurtry (1970) found similar responses of *Oligonychus punicae* on damaged vs. undamaged avocado leaves. Fleschner *et al.* (1956) observed declines in densities of this species on damaged leaves in the field while the populations were increasing on new, undamaged leaves on the same tree.

Davis (1952*a*) noted various, apparently competitive changes during a population cycle of *Tetranychus* sp. on banana squash: (1) a reduction in the number of eggs per female, even while the total population was still increasing; (2) increases in the percentage of nonviable eggs following the population peak; and (3) mortality of the immature stages. These observations certainly indicate the sometimes obvious fact that extensive feeding causes a physiological change in the foliage, resulting in less favorable food supply. Large numbers of some mites, however, seem to cause little damage. Also, leaves may recover sufficiently to support a later increase in a mite population even though their appearance does not markedly change. McMurtry and Scriven (1966) observed three subsequent population fluctuations on heavily damaged leaves of *Persea* seedlings in a greenhouse experiment.

Huffaker, Shea, and Herman (1963) found that, as the physical complexity of the ecosystem was increased, the regulating role of food depletion on the mite population came into play at lower densities because of the greater hazards involved in movement from a depleted to an undepleted area.

The effect of host-plant condition in some situations may take place before the absolute density of the mites becomes high (Huffaker and Kennett, 1956; McMurtry and Johnson, 1966). In Huffaker and Kennett's case, the intensity of cyclical prior injury to strawberry plants by the cyclamen mite (not a tetranychid) determined whether a subsequent population increase would reach a high, intermediate, or only a low maximum. Cutright (1963) considered that foliage fed on by even a few mites of certain species may be less suitable for a future generation.

Bravenboer (1959) counted the dead and living mites on bean leaves in an undisturbed population, and concluded that a relationship exists between population density and natural mortality in *Tetranychus urticae*; high numbers of mites per leaf coincided with a higher percentage of dead mites, in contrast to that associated with lower numbers of mites per leaf. Yet the leaves examined appeared to be injured equally, and conclusion on this relationship between food and mortality is therefore not well founded. Moreover, the time elapsed between infesting of the leaves and observation was unknown, and the time elapsed may affect the number of dead mites present, because they may remain on the leaf, in the webbing, for quite a long time under greenhouse conditions.

Regarding interspecific competition, Kuenen and Post (1958) showed that the presence of *Bryobia rubrioculus* hampered development of *Panonychus ulmi*, and the latter's presence reduced the numbers of *B. rubrioculus* developing on fruit trees in the Netherlands. When either species occurred alone, it attained higher numbers than when both were present. The influence of *B. rubrioculus* on *P. ulmi* appears to be less pronounced than vice versa. Chapman and Lienk (1950) and Lienk and Chapman (1951) suggested that competition from *P. ulmi* could be an important factor in the characteristic late seasonal build-up of *Tetranychus urticae* on apple in New York. Their data indicate that in plots where *P. ulmi* was virtually eliminated, there was an earlier infestation by *T. urticae* (= *T. telarius*) than in those plots in which *P. ulmi* infestation persisted. They also observed that even in the absence of *P. ulmi*, *T. urticae* increased relatively slowly and did not attain peak density until mid-August. Rodriguez (1958) investigated the comparative nitrogen-phosphorus-potassium nutrition of *P. ulmi* and *T. urticae*; he found that the latter developed more rapidly than did *P. ulmi* under the same conditions. Grob (1951) and Rota (1967) reported that the females of *T. urticae*, which infested apple trees early in the season in Switzerland and in northern Italy, respectively, do not reproduce so fast as do those on weeds. During the season, however, composition of the leaves changes in favor of *T. urticae*, and as it has a faster rate of development than *P. ulmi*, it can then displace the latter species.

Newcomer and Yothers (1929) reported that either species—*Panonychus ulmi* or *Tetranychus urticae*—may be dominant, depending on which one infests the trees first. Roesler (1953) observed, in Germany, that *T. urticae* migrated from the weeds into the trees after *P. ulmi* had died out as a result of very high temperatures. Oatman (1965) thought that the late build-up of *T. urticae* populations on fruit trees was most likely due to a seasonal movement of this species into the fruit trees from the drying or depleted groundcover coincidental with the time that *P. ulmi* was naturally decreasing. Foott (1962, 1963) found that populations of *T. urticae* were able to suppress *P. ulmi*

because of their production of webbing, greater fecundity, faster rate of development, and greater ability to thrive on foliage injured by previous feeding. There was no evidence, however, that this occurred in the orchard. Webster (1948) indicated that *P. ulmi* and *T. pacificus* were rarely found on the same leaves, suggesting the possibility of competition between them. It has also been stated that in western Europe, fruit trees infested by *T. urticae* seemed to be avoided by *P. ulmi*.

Ability to produce webbing may be involved in interspecific competition, as suggested by Foott (1962, 1963). Georgala (1955) found that *Bryobia rubrioculus* on fruit trees was restricted to web-free areas on leaves where *Tetranychus urticae* (= *T. telarius*) was present. Also, Rota (1967) is of the opinion that the webbing of *T. urticae* on fruit trees in northern Italy is an advantage for this species in its competition with *Panonychus ulmi*.

Van de Vrie (1962) showed that the selective action of pesticides can preclude development of several susceptible species, thus decreasing the pressure of interspecific competition and favoring the possibilities for high densities of unaffected species. (For further discussion see page 402.)

The control of insect pests and fungus diseases by pesticides, apart from directly influencing the mites present on the plants, may drastically influence the amount of food, its quality, and the period of its availability. Apple leaves severely attacked by apple scab (*Venturia inaequalis* (Cke.)) drop prematurely, thus reducing the amount of available food (Gilliatt, 1935). Leaves of plum trees damaged by the fungus *Stereum purpureum* were shown to be less favorable for *Panonychus ulmi* than healthy leaves (Kuenen, 1946*a*, 1949). The impact of pesticides on the reproductive potentials of tetranychids is discussed on page 398.

A number of other factors related to the host-plant and agricultural practices may influence rather directly the actual increase of tetranychids. Among such factors are differences in species, variety or biotype of the host-plant, sources of alternate hosts, soil-mineral-water relations, biochemical composition of the leaves, dispersal pressure and impact of pesticides, and other management features.

Movements either into the population or out of it may also greatly affect the rate of change in the population, and movements are affected in a number of ways, including competition and the nutrition afforded by the plant (p. 382), light (p. 368), and wind (p. 371).

## ECONOMIC INJURY AND LEVELS OF SPIDER MITE ABUNDANCE

As stated previously, spider mites often cause severe crop losses. When they reach outbreak status, no one doubts their potential for damage. As is true for many or most arthropod pests of crops, however, little is known about the maximum levels that can be tolerated without economic loss. Injury is related to many variables, with their influences extremely difficult to estimate.

In the United States, for the period 1951–1960, the following average annual crop losses (per cent) were attributed to mites: hops, 6; mint, 7; citrus, 2.5; strawberries, 10; lima and snap beans, 3; and apples, 7; mites led all other "insect" losses for these crops except for Mexican bean beetle on beans (Le Clerg, 1965). Losses attributed to spider mites for the previous decade (Fracker, 1954) were apparently much less, for their contributions to crop losses were not tabulated specifically except for losses caused to floriculture crops in greenhouses (5

per cent). These records agree with opinions of a great body of entomologists throughout the world, reviewed by Huffaker, van de Vrie, and McMurtry (1969), that spider mites were much less troublesome prior to introduction of the new insecticides following World War II.

Vergani (1953) gives an account of the damage caused to various crops by tetranychids in Argentina, including *Bryobia rubrioculus* on apple and pear, *Tetranychus urticae*-complex on many crops, *Eutetranychus schultzi* (Blanchard) (=*Anychus schultzi*) on castor bean, *E. banksi* (McGregor) on citrus, and *Panonychus ulmi* on various plants, including peach. Anyone who has seen the devastation that can be wrought by *T. urticae* on strawberries or on certain vegetable crops will never doubt this specie's destructive potential (e.g., Oatman, 1970).

Yet E. H. Smith (1966), referring to economic losses due to insects and mites, stated: "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. Both Smith and Chant emphasized that treatments are often made that are not justified in terms of the potential direct gain, even disregarding additional undesirable consequences that often ensue.

It is noteworthy, here, that in the United States, a panel of the President's Science Advisory Committee (1965), reporting on the cotton insects, stated: "Damage from the bollworm, spider mites and aphids (on cotton) would be relatively insignificant in boll-weevil-infested areas except for the current procedures (intensive use of pesticides) used to control the boll weevil."

Injury by mites is related to many unpredictable variables, including the intensity of attack, weather conditions, either concurrent or immediately following, the species of mite, the crop species and even the variety, and, among other relationships, specific tolerance or susceptibility features related to nutrient elements in the leaves and the chemicals applied to the crop (DeOng, 1919; Frost, 1919; Garman, 1923; Geijskes, 1938; Listo, Listo, and Kanervo, 1939; Rahman and Sapra, 1940; Steer, 1940; Kuenen, 1943; Andersen, 1947; Austin and Massee, 1947; van de Vrie, 1956; Canerday and Arant, 1964*a*, *b*; Westigard, Lombard, and Grim, 1966). Certain indications of the scope of these relations are now apparent.

The effect on the yield of cucumbers from different degrees of damage caused by different population densities of *Tetranychus urticae* was experimentally studied by Parr and Hussey (1962) and Hussey and Parr (1963*a*) in England. These authors used a damage index, the definitions of which are given in the 1963*a* paper. At intervals of approximately three weeks, about one-third of the foliage was rated for damage. The significance of the critical level has been confirmed in experiments under several growing conditions for cucumbers. Surprisingly, it was found that yield was unaffected until leaf damage rose to a level corresponding to about 30 per cent of the total leaf area. Hussey and Parr (1963*a*) demonstrated that when a spray program kept the leaf injury below that level, the crop was unaffected. Parr and Hussey (1962) showed that an interval of five weeks elapses between severe leaf damage and resulting decrease in yield. This estimate was confirmed by plotting the weekly crop losses for each experimental plot against the plot damage index five weeks earlier. They stated: "Assuming a 30-week growing season and the five weeks interval between leaf damage and yield reduction, it is necessary for the mites to be controlled for 25 weeks." They say that this could be achieved by as few as four sprays if they were properly applied and timed in relation to leaf damage, but even if spraying were poorly done and control were not achieved, no more than eight sprays

should be needed, although use of 12 was a common practice.

From leaf-damage assessments, Hussey and Parr (1965) postulated a theoretical pattern for the control of *Tetranychus urticae* by the predatory mite *Phytoseiulus persimilis* Athias-Henriot (=*P. riegeli* Dosse), the strategy being based on keeping leaf damage from approaching the critical level.

Kuenen (1946*a*) and Andersen (1947) reported reduction of chlorophyll and assimilation products in leaves damaged by *Panonychus ulmi*. Chapman, Lienk, and Curtis (1952) found an increase of 23.1 per cent in numbers of apples on trees on which spider mites were controlled. Contrary to earlier reports (Lathrop, 1951), Kuenen found that fruit from injured trees were better colored than were those from mite-free trees. In further studies, Lienk, Chapman, and Curtis (1956) found that uncontrolled mite feeding for one season caused a reduction in bloom the following year of 75 per cent in the Cortland variety and 34 per cent in Red Delicious. At harvest, the yield reductions amounted to 64.8 and 35.8 per cent, respectively. In the U.S.S.R., Bondarenko and Asatur (1960) found a reduction of 34 per cent in leaf area on young apple trees on which a density of 75 to 85 individuals of *P. ulmi* per leaf was found. Growth of branches and trunks was also reduced. Late apple varieties were the most susceptible.

In field experiments on apple in the German Federal Republic, Unterstenhöfer (1954) found a 20 to 51 per cent reduction in yield in the year of attack. Van de Vrie (1956) showed that early injury reduced the mean weight per apple, but continuing attack had no further influence. Kolbe (1968) reported a reduction in yield of apple trees during the year of attack of 39 to 51 per cent; the carry-over effect resulted in yield reductions of 32 to 38 per cent in Germany. Gould (1965) found that heavy infestations of *Panonychus ulmi* reduced yield significantly on apple trees during two successive years in England; the yield loss was in total number of apples produced. No obvious differences were recorded in fruit size or quality.

Blair (1951) provided a detailed description of external symptoms and internal damage on apple leaves, caused by *Panonychus ulmi*, as did Trägardh (1915), Geijskes (1938), Kuenen (1946*a*) and van de Vrie (1956). These authors present illustrations of cross-sections of leaves to illustrate the cell injury caused by this mite. McGregor (1913) illustrated comparable cross-sections, with reference to damage on cotton by *Tetranychus urticae* (=*T. bimaculatus*). Chapman, Lienk, and Curtis (1952) reported that mites reduced the chlorophyll content of leaves by 15 to 35 per cent. Cory (1922) and Cottier (1934) reported reduction in quality and quantity of apples due to an attack by *P. ulmi*, while Hammer (1943) found a premature drop of young fruits.

Avery and Briggs (1968*a*, *b*), in a series of elegant experiments, studied the damage caused by *Panonychus ulmi* to leaves of plum and apple. Histological studies of leaves artificially inoculated with mites revealed that mites on the lower leaf surface did not damage the uppermost layer of palisade mesophyll cells. These workers also showed that mites on both leaf surfaces at first feed on tissues close to the veinlets, damaging mesophyll and bundle-sheet cells. The "bronzing" developed by the latter is associated with damage to interveinal tissues and not with any qualitative biochemical difference from speckling. Avery and Briggs (1968*a*) did not find damage to epidermis cell walls, indicating a path of the mites' stylets, and suggested that the stylets do not penetrate epidermis cells, but pass between them.

The growth of fruit trees can be much reduced by *Panonychus ulmi*, as shown by Massee (1927), Andersen (1947), Chapman, Lienk, and Curtis (1952), Lienk, Chapman, and Curtis (1956), van

de Vrie (1956), Avery (1962), Avery and Briggs (1968*b*), and Briggs and Avery (1968); and the number of flower buds may be strongly reduced the year following the attack (Cory, 1922; Herrick, 1929; van de Vrie, 1956). In a series of experiments, Avery (1962), Briggs and Avery (1968), and Avery and Briggs (1968*b*) showed that the damage caused by *P. ulmi* on plum rootstocks occurs in two phases; in the first, shoot and root growth is affected; in the second, the photosynthetic capacity is impaired. These workers further showed that high mite densities decreased growth, but low densities increased shoot extension. They postulated that damage results from an imbalance in the growth-regulator complex (discussed on p. 379).

Discussing the effect on fruit buds, DeOng (1919) suggests that there is some reduction of sugar in attacked leaves, which makes the trees more liable to frost injury. Collyer (1964*b*) pointed out that very high overwintering populations of *Panonychus ulmi* may result in severe injury to the opening leaf buds and subsequently to the blossoms of apple in New Zealand; numbers of up to 10 per leaf are tolerable, but above that level, leaf damage may soon occur.

Kuenen (1946*a*, 1949) reported that *Panonychus ulmi* in the Netherlands causes greater damage in hot, dry spells, although some workers report particular damage in cool, wet weather (Jary and Austin, 1937). More serious damage to citrus leaves through mesophyll collapse results from *P. citri* feeding during hot, dry weather than during cool periods (Quayle, 1938; W. R. Thompson, 1944). As a result of work with *P. ulmi* and *Tetranychus urticae* on Bartlett pear, Huffaker and Spitzer (1950) suggested that a given level of mite-days of feeding within a brief period will cause more severe leaf scorch than an equal total feeding spread over a longer period. Hot, dry weather concurrent at such a period of intense feeding seemed to intensify the damage, possibly through desiccation. Some repair of tissue, retarding water loss when attack is less intense, but prolonged, is suggested.

Westigard, Lombard, and Grim (1966) studied the influence of four population levels of *Tetranychus urticae* on mature Anjou pear trees in Oregon during a three-year period. Fruit size, fruit finish, preharvest fruit drop, fruit set, and terminal growth were unfavorably influenced by mite feeding. These workers found that fruit set appeared to have been highly responsive to mite damage occurring during the preceding year. Preharvest fruit drop was associated with high mite populations in the same year, however, with strong indications that a carry-over effect may be present. Improved fruit finish was generally associated with low mite populations. There was some evidence that mite-induced fruit injury may occur late in the season. This is particularly important for biological or integrated control attempts, because the economic effect may be influenced by the period in which peak populations are present.

Boulanger (1958) and Avery (1964) compared carbon dioxide assimilation of mite-damaged leaves with that of healthy leaves of plum and apple. They concluded that the assimilation of carbon dioxide by the damaged leaves is reduced very little until the leaves become visibly, severely damaged.

Dustan and Stevenson (1961) found that severe leaf scorch of several pear varieties may result from relatively low densities of *Panonychus ulmi*. Spider mite damage has sometimes been credited with outright death of the host plant: potato (Landis and Davis, 1947); young cotton plants (Leigh, 1963*a*); strawberry (Huffaker, unpublished observations); apple seedlings (van de Vrie, unpublished observations). Flaherty (1967) stated that *Eotetranychus willamettei* (McGregor) rarely causes economic damage on grapes in the San Joaquin Valley of California, even though it attains high numbers. *Tetranychus pacificus*, how-

ever, which co-infests some commercially treated vineyards with *E. willamettei*, causes severe damage at relatively low densities. Growers have for years treated early indications of mites without regard to which species is concerned.

McGregor and McDonough (1917) reported that in 1912, in South Carolina, 20,000 acres of cotton were damaged by spider mites and that yield was reduced. Leigh (1963*a*) stated that five species of *Tetranychus* are pests of cotton in California, and that general injury by any of them results in loss of vigor, reduced yields, and inferior quality, and in the case of *T. atlanticus*, even moderately low infestations are severe, as this species causes leaf abcission. Light to moderate infestations of the other species may be of little significance. Roussel *et al.* (1951) reported a reduction in seed cotton yield of 45 per cent resulting from attack by *Allonychus braziliensis* (McGregor). Canerday and Arant (1964*a*, *b*) reported that the yield of cotton was reduced to 14 to 44 per cent by *T. cinnabarinus* and 13 to 22 per cent by *T. atlanticus*. Furr and Pfrimmer (1968), in studies on the influence of early-, mid-, and late-season infestations of *T. urticae*, found that early- and mid-season infestations reduced the yield of cotton considerably; late-season infestations had no effect. Reynolds *et al.* (1967), in California, found that sugar content in sugar beet was increased by 0.3 per cent and yield by 2.6 tons per acre when *T. urticae* was controlled properly.

Boudreaux (1958) suggested that because of the heavier water demand at periods of high atmospheric evaporation, mites may take in greater quantities of nutrients in meeting their water demand, thus resulting in increased reproduction and eventual damage. Thus, feeding by the individual, and the number of individuals, may be increased.

Harries (1966) reported that N- and P-deficient fruit seedlings were more susceptible to injury by *Tetranychus urticae* than were ones having adequate levels. Hammer (1943) remarked that mite-injured foliage is more susceptible to spray damage, and this is in accord with Cory's (1929) data. In view of the suggested hormonal-like roles of DDT and certain other materials (R. K. Chapman and Allen, 1948; Huffaker and Spitzer, 1950; Hueck, 1953), certain chemical applications might be expected to increase the likelihood of abscission or burning from mite feeding.

Very little is known about repair (if any) of mite-damaged tissues and the consequent tolerance that may develop through repair, associated with less intense, albeit prolonged injury. Chapman, Lienk, and Curtis (1952) reported recovery of apple leaves from early-season mite feeding, but no recovery from mid-season injury, indicating that young leaves may repair tissues sufficiently to reduce water loss if not to replace chlorophyll. The observation of McMurtry and Scriven (1966) and McMurtry (1970) of two subsequent population fluctuations on heavily damaged leaves of *Persea* seedlings also suggests some kind of repair in the leaf tissue. Boulanger (1958) did not find evidence of leaf "recovery" in apple leaves injured by *Panonychus ulmi*. Rather, the longer the leaves experienced reduced chlorophyll, the less thrifty were the trees on entering dormancy. Even light damage in May was considered to be important. Boulanger found that loss in color occurs, however, before any significant damage to the chlorophyll.

Injury to plants by tetranychids is related to their method of feeding. They damage protective leaf surfaces and they may affect the stomatal guard cells, thereby increasing water loss (Boulanger, 1958); damage the palisade and spongy parenchyma cells (McGregor and McDonough, 1917; Kuenen, 1946*a*; Blair, 1951; Baker and Connell, 1963; Avery and Briggs, 1968*a*); and inject toxic substances into the plant (Leigh, 1963*a*). The latter author reported that

*Tetranychus atlanticus* ". . . appears to induce a toxic reaction in the cotton plant which brings about rapid abcission of leaves, even death of plants, whereas other species on cotton do not cause this reaction"—a suggestion that has some support in the work of Storms (1968, personal communication; and 1969), and Liesering (1958, 1960). The latter reports that *T. urticae* not only exhausts 18 to 22 cells per minute, but also injects certain substances into the plant. Feeding mites were shown to inject substances that were translocated to other regions of the plants (Avery and Briggs, 1968*b*). These authors used a radioactive tracer ($^{14}CO_2$) to investigate whether *Panonychus ulmi* on young plum trees injects materials into the leaves when feeding. They state: "The autoradiographs of all eleven plants showed shadows of parts of the plant from which the mites were excluded. Some were very faint, but others were clearly defined and included shadows of axillary shoots, extending internodes, roots, and the bark of stem sections, demonstrating that radioactive material was injected by the mites and translocated from the feeding region to both the roots and young shoots." Wiesmann (1968) also demonstrated that *T. urticae* injects some substance during the feeding act that dissolves the contents of the cells, allowing the mite to suck them. This process is repeated several times during the feeding act.

Liesering (1958) and Zukova (1963) studied the biochemical activities associated with *Tetranychus urticae* feeding on bean and cotton, respectively. Liesering found that assimilation decreased by 10 to 15 per cent and leaf pigments were altered, chlorophyll being changed to pharophytine. Zukova found reduced amylase and proteolytic enzyme activity, reduction of total protein, nonproteinic nitrogen, and crude protein, and accumulation of nitrogenous substances in the stem and reduction of them in the roots. Since she found no foreign enzymes in the plant tissues, Zukova assumed that mites, unlike sucking insects, ingest the contents of the cells, and that digestion is entirely intraintestinal. This conclusion is at least questionable, because spider mites have well-developed salivary glands.

Avery and Lacey (1968) obtained evidence of an imbalance of growth-regulatory substances associated with mite infestation. They showed that greater quantities of gibberellin-like promoters were present in the tissues of mite-infested plum plants than in those of the controls. Indications were for greater quantities of auxin-like promoters, however, with the exception of indoleacetic acid, in the tissues of the mite-free plants. Storms (1971) found a growth-stimulating effect, especially on the axillary buds, caused by *Tetranychus urticae* on bean plants. He showed, by using a radioactive tracer ($^{32}P$), that injected substances are transported primarily to the growing parts of the plants. These substances seem to have a temporarily inhibiting effect on the egg production of *T. urticae*.

Generally speaking, however, critical experiments at the physiological level provide little evidence to support the various statements on the injurious influences of tetranychids on their host plants. Furthermore, the relations between density and duration of associated densities, weather, and so forth, and economic importance are, in many cases, obscure. This last point is an important consideration in planning a program for biological or integrated control of plant-inhabiting mites.

## HOST PLANT–TETRANYCHID RELATIONS

Beyond the basic life history of a particular phytophagous mite, a primary consideration is the basic interaction between mites and their host plants. The

nutrition derived, and the favorability of the micro-habitat afforded by the host plant are basic, whether or not overpopulation or other factors come into play.

## Plant Species: Varietal and Structural Features

General observations and some detailed records reveal that different plant species or varieties present different increase potentials for tetranychids. These differences may be associated with the nutriment afforded by the plant, the ease with which it can be obtained, or the favorability of the micro-environment. Differences in population increases of mites on different biotypes or varieties have been demonstrated in various studies. Examples include cotton and related plants, with some biotypes showing a high degree of resistance (Abul-Nasr, 1960; Leigh and Hyer, 1963)—citrus (Fleschner, 1958*b*), orange fruits (Huffaker, 1958; Huffaker, Shea, and Herman, 1963), geranium (Snetsinger, Balderston, and Craig, 1966), grape (Flaherty, 1967), bean (Fritzsche, 1957, 1961, 1962*a*; Fritsche, Wolfgang, and Opel, 1957; Watson, 1964), deciduous fruit trees (Garman and Townsend, 1938; Kuenen, 1949; Nielsen, 1958; Downing and Moilliet, 1967), tea (Osakabe, 1963*a*, *b*, 1967), and tomato (Gilbert, Chinn, and Tanaka, 1966; Stoner and Stringfellow, 1967; Stoner, Frank, and Gentile, 1968; Gentile, Webb, and Stoner, 1969).

The chemical constitution of the host plant may influence fecundity, egg viability, and the mortality and rate of development of the immature stages. Breukel and Post (1959) demonstrated this for *Panonychus ulmi*, while Post (1962), working with *Bryobia rubrioculus*, concluded from laboratory evidence that such food quality exerted no distinct influence although deposition of winter eggs was found to occur earlier when food quality was deficient.

Leigh and Hyer (1963) and Abul-Nasr (1960) found marked differences in development of mite populations of different biotypes of cotton and related species, with certain biotypes showing a high degree of resistance. Fleschner (1958*b*) found that *Panonychus citri* developed more rapidly on lemon trees than on orange trees. Fritzsche (1957, 1962*a*, *b*) and Fritzsche, Wolfgang, and Opel (1957) showed that the most severe mite damage to bean by *Tetranychus urticae* occurred on the variety having the highest nitrogen content.

Differences in reproduction and population development of mites on different species of host plants are common and even more striking since the plants vary from being almost totally resistant to being highly favored by the mites. Certain studies on varietal differences mentioned above also involved different host-plant species. To these may be added, for example, results with *Tetranychus urticae*-complex on bean, beet, tomato, and cyclamen (Fritzsche, 1961), cotton, mulberry, peach, morning glory, alfalfa, and many other host plants (Hodosevic, 1963); *Panonychus ulmi* on pear, plum, and walnut (Doreste, 1964); *Eotetranychus sexmaculatus* on grapefruit and orange (Pratt and Thompson, 1953). Gilbert, Chinn, and Tanaka (1966) reported on tolerance of certain tomato varities to *T. telarius* in Hawaii; Stoner and Stringfellow (1967) found resistance of certain tomato varieties to be associated with reduction in the fecundity of *T. urticae* in Maryland. Stoner, Frank, and Gentile (1968) demonstrated that the resistance of certain tomato varieties to *T. cinnabarinus*, as measured by oviposition tests, was associated with the number of glandular hairs on the leaves; resistant varieties had more than did susceptible ones. The difference in susceptibility continued, however, when the glandular hairs were broken and the exudate removed, indicating that this is not the sole mechanism of resistance.

Leaf structure has been shown to be related to mite damage or to symptoms

commonly associated with damage. Kuenen (1946*a*, 1949) found severe damage from *Panonychus ulmi* on pear and plum varieties that had a thin cuticle. The thickness of the palisade mesophyll was not determined. Post (1962) showed that the highest density of *P. ulmi* occurred on leaves which, in addition to having a higher total nitrogen content, had a thicker palisade mesophyll. Baldini (1960) showed that fertilization of apple leaves by means of foliar urea sprays both increased the chlorophyll and nitrogen content and thickened the mesophyll, especially the spongy mesophyll. Pickett and Birkeland (1941, 1942) also reported effects of chemical sprays on leaf structure. Normal development of the palisade tissue was prevented because the cells remained smaller, and this difference between sprayed and unsprayed leaves increased during the season.

Blair (1951), in England, reported an association between visible damage in different varieties of apple and the number of layers of mesophyll. Such injury occurred earlier in varieties with only one layer than in varieties with several layers. In this connection, size of the leaf is also important. According to Blair, in varieties having large leaves and a thick layer of palisade mesophyll, the nutrients in the lower layers are exhausted less rapidly, and the leaf is therefore slower to show discoloration.

Kuenen (1949) suggested that when the thicker upper cuticle of apple leaves is softened by higher temperatures it may be pierced more easily by *Panonychus ulmi*. Only feeding on the upper surface of the leaves causes discoloration; cells of the spongy parenchyma do not show bronzing when punctured. Consequently, a large population of mites may be present for a considerable time without doing any visible damage. Then, during a few hot days, the mites may move to the upper sides of the leaves and cause sudden, extensive bronzing.

It is noteworthy, in passing, that Putman (1958) reported that nectary secretions of peach leaves cause some mortality of *Panonychus ulmi*. Related factors may explain why some plants are not suitable hosts for certain species.

Before leaving the matter of host plants, it is worth noting that presence or absence of alternative host plants may influence the rate of infestation of cultured plants, in turn influencing the potential of certain species to become pests. Several species have a large number of hosts, and since many of them are weeds, populations may survive and cause reinfestation following a clean-up. Examples are: *Tetranychus urticae* moving from weeds or covercrops to fruit trees or grapes, in northern Italy (Rota, 1967) and in Switzerland (Grob, 1951), and *Tetranychus pacificus* populations which continued to feed and reproduce on vetch during the winter of 1950 and 1951; thus, destructive populations were present in the spring to move into newly planted crops, such as cotton (Pritchard and Baker, 1952) in California.

## Physical Surface Features

That leaf surface texture, vestiture, and contours (ridges, depressions) are important in the reproductive potential of a resident tetranychid has long been recognized. Such features may serve as tough impediments to feeding, as substrates for attachment of webbing or as direct protection from disturbing or harmful microweather on the leaf surfaces. The degree to which vestiture may be an advantage, or even a disadvantage, varies with the species, particularly with the amount of webbing it forms.

Strong webbers, like *Tetranychus urticae*, *T. pacificus*, and *Eotetranychus sexmaculatus*, will develop more uniformly heavy populations, and more quickly, on smooth plant surfaces if the latter are covered with a lint or floc than if left untreated. On untreated surfaces, initial development is slow and more restricted to depressions and rough places, where suitable anchorage for webbing is avail-

able (Finney, 1953; Huffaker, 1958; Scriven and Fleschner, 1960). Weak webbers, like *Panonychus ulmi*, *P. citri*, and *E. willamettei*, under harsh situations tend to colonize along, and remain close to the midribs and veins, which furnish protection. As populations develop, cast skins, dead bodies, and debris or dust particles favor a spreading habitation, even if the nutriment is being progressively altered. Some species commonly have their earliest and most pronounced development in situations where road dust or industrial dust accumulates on the foliage (Holloway, Henderson, and McBurnie, 1942; Fleschner, 1958*b*). Fleschner (1952) obtained increases in *P. citri* on dust-treated citrus terminals from which predators were removed by hand.

## Aging and "Conditioning"

The "conditioning" of foliage to a point at which it is unsuitable for food is not always due simply to depletion of the nutriment supply. Changes associated with aging, unfavorable surface hardening, drying, wax deposition, or inherent changes in the nutritive composition may be involved. Henderson and Holloway (1942) found that *Panonychus citri* laid more eggs on new leaves than on old ones, and that marked population increases were often correlated with spring and fall periods of flush, tender growth—a point confirmed by Jeppson *et al.* (1957). *Tetranychus urticae* also reproduced more rapidly on young leaves of bean (Henneberry, 1962*b*; T. F. Watson, 1964), as did *T. atlanticus* on soybean (Cannon and Connell, 1965). On the other hand, *Oligonychus punicae* reproduced more rapidly on mature, dark-green leaves of avocado than on young, light-green ones, and no significant population increases were observed in the spring, when the trees contained mostly young leaves (McMurtry and Johnson, 1966).

## Plant Nutrition

Since drought alters plant chemistry, Rodriguez (1964) suggested that it may increase favorability for mites. On the other hand, Specht (1965) obtained retarded development of *Panonychus ulmi* populations on small apple trees under water stress, which he attributed to the chemical change in the leaves. Bondarenko (1949) reported that high rates of fertilizers on cucumbers increased the osmotic pressure of the plant sap two to three times over that of untreated plants, and this increase was correlated with population increases of *Tetranychus urticae*. Rodriguez and Neiswander (1949) also found a positive correlation between soluble salts in greenhouse soils and *T. urticae* on tomatoes.

Fleschner (1958*b*) observed that lemon trees at Oxnard, California, consistently had higher mite populations than did comparable ones at Fillmore. Rooted cuttings from a single parent tree were planted in drums containing soil from the two orchards, and grown at a third location. The plants in soil from the Oxnard location developed markedly higher *Panonychus citri* populations, suggesting a difference in soil chemistry.

Van Emden (1966) presented extensive data showing the varying effects of different rates of nitrogen and potassium on two species of aphids, in terms of reproduction. The variability suggests what we also find in tetranychids (table 2).

**Nitrogen.** Increases in mite population have commonly been associated with nitrogen fertilization or cultural conditions indicating such treatment (Kuenen, 1946*a*, 1949; Garman and Kennedy, 1949; Post, 1962). Some such references, however, cannot be taken to mean a relationship to nitrogen. Kuenen showed that reproduction of *Panonychus ulmi* on leaves of trees under good cultivation management was higher than that on ones in neglected orchards; in the

TABLE 2

INFLUENCE OF THE ELEMENTS N, P, K, AND Ca ON THE REPRODUCTION OF VARIOUS MITE SPECIES AS REPORTED IN THE LITERATURE

| Mite species and host plant | Levels of elements* | | | | | | | | References | Laboratory or field exp. |
|---|---|---|---|---|---|---|---|---|---|---|
| | High N | Low N | High P | Low P | High K | Low K | High Ca | Low Ca | | |
| *T. atlanticus:* | | | | | | | | | | |
| soy bean | + | | + | | ○ | | | | Cannon and Connell (1965) | L |
| *T. urticae:* | | | | | | | | | | |
| *Phaseolus vulgaris* | | + | | + | | + | | | Fritzsche (1957) | L |
| *Phaseolus vulgaris* | + | | | | | | | | Fritzsche (1961) | L |
| *Phaseolus persicae* | + | | | | | | | | Garman and Kennedy (1949) | L |
| *Pyrus malus* | + | | ○ | | ○ | | ○ | | Hamstead and Gould (1957) | F |
| *Pyrus malus* | | − | | − | | − | | | Harries (1966) | L |
| *Phaseolus lunatus* | + | | | | | | | | Henneberry (1962*b*) | L |
| *Phaseolus lunatus* | + | | + | | + | | | | Henneberry (1962*a*) | L |
| *Phaseolus lunatus* | + | | + | | | | | | Henneberry (1963) | L |
| *Phaseolus lunatus* | + | | | | | | | | Henneberry (1964) | L |
| *Pyrus malus* | | + | | | | | | | Hukusima (1958) | L |
| *Cucumis* sp. | + | | | | + | | | | LeRoux (1954) | L |
| *Cucumis* sp. | | | | | | | ○ | + | LeRoux (1959) | L |
| *Solanum lycopersicum* | + | + | + | | + | | ○ | + | Rodriguez (1951) | L |
| *Solanum lycopersicum* | + | | + | + | | | | | Rodriguez (1958) | L |
| *Pyrus malus* | + | | | | ○ | | | | Storms (1969) | L |
| *Phaseolus lunatus* | | − | | − | | − | | | T. F. Watson (1964) | L |
| *T. kanzawai:* | | | | | | | | | | |
| tea | | | | | | + | | | Osakabe (1963*b*) | F |
| tea | + | | + | | | | | | Osakabe (1967) | F |
| *P. ulmi:* | | | | | | | | | | |
| *Pyrus malus* | + | | | | | | | | Breukel and Post (1959) | F |
| *Persica vulgaris* | + | + | | | | | | | Chaboussou (1960) | L |
| *Pyrus malus* | ○ | ○ | | | | | | | Lord and Stewart (1961) | F |
| *Pyrus malus* | + | | | | | | | | Post (1958) | F |
| *Pyrus malus* | + | | | | | | | | Post (1962) | L, F |
| *Persica vulgaris* | ○ | | | | | | | | Putman (1964) | F |
| *Pyrus malus* | ○ | | ○ | | | | | | Rodriguez (1958) | L |
| *Pyrus malus* | − | | − | | ○ | | | | Mathys, Baggiolini and Stahl (1968) | F |
| *B. praetiosa:* | | | | | | | | | | |
| Trifolium sp. | + | + | + | | + | | | | Morris (1961) | L |

NOTE: Fritzsche (1957, 1961) reported the positive influence of leaf sugar content on the reproduction of *T. urticae* feeding on *Phaseolus vulgaris* and artificial substrates, respectively; Henneberry (1962*a*) did so for *T. urticae* feeding on *Phaseolus lunatus*.

* Artificially increased (High) or decreased (Low) levels of corresponding elements in nutritive solution or leaf tissues, as reported by the authors. + = increased reproduction observed; − = decreased reproduction observed; ○ = no influence on reproduction observed.

well-kept orchards the leaves had a higher nitrogen content. Huffaker and Spitzer (1950) found that populations of *P. ulmi* on pears in the Sierra foothills in California declined in late July or early August, in contrast to similar declines in September in the Santa Clara Valley, and that these declines were independent of either mite density or predator action. Thus, either or both seasonal changes and nutritional physiology were suggested as causes. H. A. Dean (1959) felt that *Eutetranychus banksi* (McGregor) is affected by seasonal changes in leaf chemistry.

Kuenen and Post (1958) reported a field increase in *Panonychus ulmi* associated with pruning and nitrogen fertilization of a formerly neglected apple orchard, and with the observed higher nitrogen content of the leaves. Breukel and Post (1959) found that *P. ulmi* on apple leaves with a higher nitrogen content, under laboratory and semi-field conditions, had a higher egg production per female, and a faster rate of development.

Post (1961, 1962) also studied the changes that resulted when a young, well-managed (cultivated, pruned, and fertilized) orchard was converted into a neglected one by suspension of cultural practices. Both sprayed and unsprayed blocks reacted in the same way; in both situations the mite population declined in conformity with the reduction in

nitrogen content of the leaves. There was no difference in mite densities in spite of the fact that in the sprayed block, enemies may be supposed to have been inhibited, while in the unsprayed blocks, they were not.

Many additional results indicate a positive correlation between nitrogen level and mite increase, mainly through fecundity. The following studies are representative: *Tetranychus urticae* (= *T. bimaculatus*) on apple—the seasonal mite peaks closely followed the seasonal nitrogen level (Hamstead and Gould, 1957); *Panonychus ulmi* and *T. urticae* on apple rootstock in gravel cultures (Storms, 1967, 1969); *T. urticae* on beans, associated with total nitrogen and reducing sugars resulting from the use of fertilizers (Fritzsche, 1957, 1962*a*; Fritzsche, Wolfgang, and Opel, 1957); *T. urticae* on beans (Henneberry, 1962*a*, *b*, 1963; T. F. Watson, 1964), and on cucumber (LeRoux, 1954) and apple (Rodriguez, 1958); *T. atlanticus* on detached leaf discs of soybean (Cannon and Connell, 1965); *T. kanzawai* on tea, in pot trials (Osakabe, 1963*b*, 1967); *Bryobia praetiosa* on beans (Morris, 1961).

Fritzsche (1957, 1962*a*) and Fritzsche, Wolfgang, and Opel (1957) considered that, of the total nitrogen content of the host plant, the insoluble nitrogen compounds and glutamine and glutamic acid are particularly conducive to reproductive response. The level of soil nitrogen may not necessarily mean a corresponding level of plant nitrogen; phosphorus may affect nitrogen absorption (Henneberry, 1962*a*; Rodriguez, 1958).

Harries (1966) found that although nitrogen-deficient plants were less favorable for reproduction of *Tetranychus urticae*, they were more susceptible to injury from the feeding. This suggests an optimum nitrogen level—even though it favors some increase, it may result in less damage.

In contrast to these results, Rodriguez (1951) found lower populations of *Tetranychus urticae* associated with high nitrogen level in tomato plants. He pointed out that the absorbed nitrogen in the plants was generally twice the level of that in apple foliage reported above (Rodriguez, 1958). Leigh (1963*a*) reported that cotton frequently suffers more severe mite injury in nitrogen-deficient soil than in soil of adequate or high nitrogen levels. He seems to infer a higher population level, not just a greater susceptibility of the plant to injury. He adds that the shorter, more open growth under nitrogen-deficient conditions may have increased mite favorability by increasing the temperature and lowering the humidity (Andres, 1957; Nickel, 1960; Davis, 1961). Hukusima (1958) reported that *Panonychus ulmi* on apple in Japan produced more offspring with an increase in nitrogen levels in nutrient solutions, whereas *T. urticae* was more reproductive on nitrogen-deficient trees. Lord and Stewart (1961) and Putman (1964) found nitrogen level not to be associated with mite increase.

Many conflicting results of studies on the influence of nitrogen on reproduction in phytophagous mites have appeared in the literature. For example, Breukel and Post (1959), in the Netherlands, found *Panonychus ulmi* on apple to be stimulated at a difference of only 0.35 per cent nitrogen, while Putman (1964) did not find any difference in the reproductive capacity of the same species on peach with differences in nitrogen content of at least 1.25 per cent. These conflicting findings are difficult to explain; they probably can be attributed in part to the period in which the leaf samples for nitrogen determination were collected. Storms (1969) correctly states: "If the experiment extends over a long period of time, for example some months, it is not sufficient in most cases to carry out one or two leaf analyses. The seasonal variability could be greater in itself than the induced differences in the N content of the leaf." The seasonal variability of the nitrogen content of the leaf is, among

other factors, determined by the age of the leaf, nutritional status of the plant, and by different factors involved in nitrogen uptake, such as moisture content of the soil, fertilization, mineralization, leaching, and competition among plants.

**Potassium.** Apparently contrasting results have been obtained with regard to the effect of potassium on mite response. Osakabe (1963*b*) obtained an increase in *Tetranychus kanzawai* on tea, with lower potassium levels. T. F. Watson (1964) obtained a reduction of *T. urticae* on potassium-deficient beans; LeRoux (1954) obtained increased fertility of this species at high potassium levels. Cannon and Connell (1965) found no significant differences in results with different potassium levels. Storms (1967) reported some evidence of a decrease in egg production in *Panonychus ulmi* on rootstocks in gravel cultures provided with high potassium levels; in the experiments with *T. urticae*, however, varying the ratio of potassium and manganese did not alter the mean daily egg production on high or low nitrogen levels in the nutrient solution (Storms, 1969). Morris (1961) found a greater fecundity in *Bryobia praetiosa* on clover at medium levels of potassium than at higher or lower levels. Chaboussou (1960, 1966*a*, *b*) and Chaboussou, Delmas, and Dureau (1961) indicated an important relation between the potassium level and the ratio of potassium to nitrogen in the leaves, and mite abundance.

**Phosphorus.** As with nitrogen, a number of workers have found phosphorus levels to have significant effects on mite reproduction. T. F. Watson (1964) found that a phosphorus deficiency reduced fecundity of *Tetranychus urticae* even more than did a deficiency of nitrogen or potassium. Rodriguez (1951) reported that absorbed phosphorus was positively correlated with increase in this species, up to a certain level, above which it was negatively correlated, and Morris (1961) obtained a similar trend for *Bryobia praetiosa*. Henneberry (1963), however, found that progeny production in *T. urticae* on bean was correlated with decreases in phosphorus. Osakabe (1963*b*, 1967), working with *T. kanzawai* on tea, in pot trials, found a positive correlation with phosphorus. These apparently conflicting results suggest that complex interactions are involved.

Cannon and Connell (1965) studied *Tetranychus atlanticus* on soybean leaf discs from plants furnished nutrient formulations composed of nitrogen, phosphorus, and potassium in sand cultures. While nitrogen had a striking positive influence, the effects of phosphorus and potassium seemed to depend upon the ion interrelationships of the solutions. Varying phosphorus in one sequence of formulations did not affect fecundity, while use of a much higher level in another formula increased fecundity. Rodriguez, Chen, and Smith (1957) found that nitrogen-phosphorus-potassium balance in the plant was altered by use of DDT, lindane, and BHC, in some cases resulting in increased plant growth and/or mite populations. Chaboussou (e.g., 1960, 1963, 1964, 1966*a*, *b*, 1967) also found that a number of pesticides affect nitrogen and potassium levels in the leaves. (See also p. 399.) As he did with nitrogen, Harries (1966) also observed less production but greater damage by *T. urticae* on phosphorus-deficient trees.

**Other elements and miscellaneous relationships.** LeRoux (1959) found a negative correlation between *Tetranychus urticae* reproduction, on cucumber, and calcium level, but increased reproduction when sulfur was increased from 192 mg/liter to 288 and 384 mg/liter. Osakabe (1963*b*, 1967) obtained negative correlation between reproduction of *T. kanzawai* on tea and magnesium level. Cannon and Terriere (1966) found no response in *T. urticae* on bean from various concentrations of iron, magnesium, zinc, and cobalt. Terriere and Rajadhyaksha (1964) found that metal chelates either applied directly to leaves

or absorbed from the media resulted in reduced fecundity of *T. urticae*. Fritzsche (1961) and Henneberry (1963) observed accelerated reproduction in *T. urticae* with increase in sugars or total water-soluble carbohydrates.

As the data indicate, much conflicting opinion exists as to the influence of the quality of the natural food base on the population development of spider mites. Many attempts have been made to explore this difficult area. The influence of the concentrations and ratios of certain ions in the nutrient solution is extremely difficult to evaluate, as the interactions of ions have an important role in the uptake of ions by the roots. The relation between the chemical composition of leaves and the concentration of minerals in the nutrient solution is not very clear, and may vary with the species of host plant, soil type, and other factors.

It seems obvious that studies on mites grown on artificial substrates may furnish insight into these problems. Fritzsche (1959), Rodriguez (1964), and Storms (1967) have attempted to rear *Tetranychus urticae* on artificial diets, but have not yet succeeded. Campbell (1959), Seay (1963), and Sun (1963) also studied the possibilities of culturing *T. urticae* on chemically-defined diets. They also were apparently unsuccessful, due partly to lack of sufficient knowledge of the essential nutritional requirements and partly to technical limitations of the methods used. Preliminary results obtained by Storms, Harrewijn, and Noordink (1967) with chemical-balance trials, in which the role of the elements can be evaluated quantitatively in a short period of time, show more promise of gaining insight into the feeding physiology of tetranychids.

Carbohydrate metabolism has been studied extensively in insects, but relatively little is known about it in tetranychid mites. The results of Fritzsche (1959), who reported on the importance of reducing sugars for the rate of reproduction in *Tetranychus urticae*, suggest that this species may have special nutritional requirements and that its carbohydrate metabolism may possess some unusual features. Eberhardt and Voss (1961) demonstrated that *T. urticae* possesses several glucosidases that are capable of hydrolyzing various carbohydrates, namely, maltose, sucrose, trehalose, melibiose, lactose, melezitose, and raffinose, to their respective monosaccharides. The presence of glucosidase, cellulase, pectinase, and polygalactaronase, however, could not be demonstrated.

Mehrotra's studies (1960, 1961) suggest that *Tetranychus urticae* possesses all the necessary enzymes, except lactic dehydrogenase, for the utilization of hexose phosphates through the Embden-Meyerhof and the hexose-monophosphate pathways. The occurrence of some of the enzymes of the Krebs cycle in *T. urticae* has also been reported by Mehrotra (1963). He states: "... although the various metabolic pathways in the two-spotted spider mite have been shown, detailed knowledge of the rate-limiting in the Embden-Meyerhof and hexose-monophosphate pathways has not been fully elucidated. Such knowledge is of great significance for the understanding of the physiology and host specificity of this important pest. The availability of various channels for the metabolism of carbohydrates could permit the organism to adapt itself to varied conditions."

Whether or not spider mites may influence directly the physiological condition of the leaf by injecting salivary substances needs close investigation. Storms (1969, and unpublished data) presents some evidence that *Tetranychus urticae* inserts saliva into the leaf, the function of which is unclear. Wiesmann (1968) showed that *T. urticae* injects some substance into the plant tissue; this substance dissolves the content of the cells, which the mites then suck. Leigh's (1963*a*) belief that *T. atlanticus* induces a toxic reaction in cotton is cited

on page 379; the studies of Avery and Lacey (1968) and Briggs and Avery (1968*a*) on the imbalance of growth-regulatory substances are discussed on page 379.

If a better understanding of the food requirements of phytophagous mites is achieved, it will be possible to define more precisely the ecological significance of the altered quality of the host plant frequently observed after application of fertilizers or pesticides. We may also speculate on the possibility of influencing the population development of these mites by changing their food substrate through managing the fertilization of the host plant.

## EFFECTS OF AGRICULTURAL CHEMICALS

Certain chemicals applied to crop plants for pest and disease control, for minor-element deficiencies, for fruit setting or thinning, or for defoliation, may have acute influences on the development of mites. Some kill mites directly, but these substances are not considered here. It may be noteworthy, however, that in field experiments a slight acaricidal effect may sometimes be overlooked, resulting in the spurious impression that the material did not affect the mites. This frequently causes difficulties in analyzing the results of field experiments, for instance on fruit trees, because "untreated" plots often cannot exist because of the damage caused by fungus or by insect attack.

We also omit studies on the resistance of mites to acaricides. We note, however, that susceptibility to acaricides may vary with the nutritional state of the host plant, with a resulting pseudo-resistance or vigor-tolerance. Neiswander, Rodriguez, and Neiswander (1950) found that the susceptibility of *Tetranychus urticae* (= *T. bimaculatus*) to malathion was influenced by the host plant species on which the mites were fed; Fritzsche (1961) found that the susceptibility of this species to methyl-parathion decreased with increasing age of the leaves. Henneberry (1964) also showed that the condition of the host plant affected the malathion susceptibility of two strains of *T. urticae* (= *T. telarius*); Kady (1965) found similar results with this species and parathion susceptibility; the mechanism by which this effect was produced is unknown. Huwald (1965) studied the influence of quality of the host plant on development of resistance to TEPP in *T. urticae*; on beans grown under continuous light, the development of resistance was slower. Although Huwald described the differences in appearance between plants grown under continuous light and those grown under "normal" conditions, he did not study the physiological differences caused by the treatments. Saba (1961*a*) also pointed to the influence of the host plant on development of and decline in resistance to acaricides.

The effects of artificial diets and of starvation on the susceptibility of insects to insecticides were observed by several investigators, and reviewed by Potter (1956) and Gordon (1961). The effect of pesticides on the balance of arthropod populations in field situations was reviewed by Ripper (1956), and similar studies pertaining to mites were made by Boudreaux (1963), Bartlett (1968), and Huffaker, van de Vrie, and McMurtry (1969).

We have discussed the pronounced effects of leaf chemistry on mite response (p. 382). Application of agricultural chemicals to the foliage may conceivably affect certain of the described complex relationships or act in other ways to alter the plant's attractiveness to mites. Whether or not the principal influences arise through alterations in leaf chemistry or through the chemicals' adverse

effects on enemies of the phytophagous mites was discussed by Huffaker, van de Vrie, and McMurtry (1969). What follows is a detailed consideration of chemical influences on leaf chemistry only.

Without references to possible mechanisms, Massee (1929) and Massee and Steer (1929), for tar oil, and Thompson (1939) and Holloway, Henderson, and McBurnie (1942), for applications of foliar sprays for minor-element deficiencies, pioneered in showing the implication of agricultural sprays in mite increases for *Panonychus ulmi* and *P. citri*, respectively. Kuenen (1946*a*) found an increase in *P. ulmi* on cherry after application of lead arsenate, and on apple, in the Netherlands, after application of lime sulfur and Bordeaux mixture, also without reference to possible causative mechanisms. Austin and Massee (1947) obtained a response to the use of tar oils as dormant sprays. Many investigators have since reported increases or outbreaks of tetranychids following the use of various chemicals. Hueck (1953), Ripper (1956), Boudreaux (1963), and Bartlett (1964, 1968) summarized several of these instances. Some observers attributed a great many of the increases to the effect of the materials in destroying the natural enemies of the mites. Others attributed the observed phenomena to nutritional or subtle physiological effects produced in the host plant or in the mites themselves, while a few attributed the increases to the reduction of inter- and intraspecific competition. Many studies were rather uncritical, while others were better documented; in some of the critical studies, the results do not agree, and therefore remain controversial.

Many cases of increases of tetranychids were related to the use of DDT alone or in combination with other materials. Baker (1952) stated: "Never before, however, have so many pests with such a wide range of habits and characteristics increased to injurious levels following application of any one material as has occurred following the use of DDT in apple spray programs." Baker rightly attributed this only in part to the effects of DDT on the complex of enemies.

DDT aroused the big spurt of publications in this area, but other materials, insecticides as well as fungicides, have also been involved. Inert-particle residues were also implicated as a causative factor in the response of *Panonychus citri*, following sprays for minor-element deficiencies (Holloway, Henderson, and McBurnie, 1942; Fleschner, 1952), while field and industrial dust drift or talc used in pesticide treatments were also implicated (DeBach, 1947; Fleschner, 1952, 1958*b*).

Table 3 lists many of the cases of increases in mites under particular situations (with negative effects being obtained in other cases) according to the various spray materials.

For many of the increases listed in table 3, inhibition of natural enemies by spray materials has been considered a primary cause of mite outbreaks; this has been treated earlier by Huffaker, van de Vrie, and McMurtry (1969). Spray materials have also been implicated in other ways. The relations are complex, and results may differ with the concentrations and formulations used (Tew and Groves, 1957; Chiswell, 1962; Chaboussou, 1963, 1966*a*), interaction with the varying chemical composition of the leaves (Bogdanoff, 1964; Chaboussou, 1966*a*, *b*), the species of the host plant, the mite species or particular stock, and whether detached leaves or plants were used in the tests. The method of application, either as sprays or soil treatment, may also have an effect. Several possibilities are indicated by various investigators.

Several miscellaneous materials, as well as the common insecticides, acaricides, and fungicides (table 3) have also been associated with mite abundance.

Gibberellin was shown by Eichmeyer and Guyer (1960) to influence the reproduction of *Tetranychus urticae* (= *T.*

TABLE 3

INFLUENCE OF PESTICIDES ON DEVELOPMENT OF PHYTOPHAGOUS MITES

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| INSECTICIDES | | |
| Aldrin | | |
| *T. bimaculatus:* | | |
| bean | U.S.A. | Klostermeyer and Rasmussen (1953) |
| potato | U.S.A. | Klostermeyer and Rasmussen (1953) |
| *T. tumidus:* | | |
| cotton | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| Azinphos-methyl | | |
| *P. ulmi:* | | |
| apple | England | Chiswell (1962) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| apple | Switzerland | Mathys, Baggiolini, and Stahl (1968) |
| BHC (and Lindane) | | |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| rose | U.S.A. | Henneberry and Taylor (1962) |
| *T. bimaculatus:* | | |
| bean | U.S.A. | Klostermeyer and Rasmussen (1953) |
| potato | U.S.A. | Klostermeyer and Rasmussen (1953) |
| *T. telarius:* | | |
| bean | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| soybean | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| cotton | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| *T. tumidus:* | | |
| cotton | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| *T. urticae:* | | |
| apple | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| *P. ulmi:* | | |
| apple | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| Carbaryl | | |
| *P. ulmi:* | | |
| grape | France | Chaboussou (1966*b*, 1967) |
| apple | England | Chiswell (1962) |
| apple | Poland | Dabrowski (1968) |
| apple | Italy | Dominichini (1963) |
| apple | Switzerland | Günthart and Vogel (1965) |
| apple | U.S.A. | Oatman (1965) |
| apple | U.S.A. | Swift (1968) |
| peach | Canada | Putman and Herne (1960) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| cotton | Egypt | Hassanein (1963) |
| apple | Japan | Hukusima (1960, 1961) |
| bean | Canada | Pielou (1962) |
| apple | Israel | Plaut and Feldman (1966) |
| peach | Canada | Putman and Herne (1960) |
| *T. cinnabarinus:* | | |
| apple | Israel | Plaut and Feldmann (1966) |
| bean | U.S.A. | Attiah and Boudreaux (1964*a*) |
| lima bean | U.S.A. | Attiah and Boudreaux (1964*b*) |
| *T. telarius:* | | |
| grape | France | Chaboussou (1966*a*, *b*) |
| *E. carpini vitis:* | | |
| grape | France | Chaboussou (1966*a*, *b*) |
| *B. rubrioculus:* | | |
| apple | Nerherlands | van de Vrie (1962) |
| *E. willamettei:* | | |
| grape | U.S.A. | Flaherty *et al.* (1966) |
| grape | U.S.A. | Flaherty (1967) |
| grape | U.S.A. | Huffaker and Flaherty (1966) |

TABLE 3—*Continued*

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| *O. coffeae:* | | |
| tea | Ceylon | Cranham (1966) |
| *Tetranychus* sp.: | | |
| apple | Italy | Dominichini (1963) |
| cotton | Egypt | Kady (1964) |
| Chlordane | | |
| *T. bimaculatus:* | | |
| bean | U.S.A. | Klostermeyer and Rasmussen (1953) |
| potato | U.S.A. | Klostermeyer and Rasmussen (1953) |
| *T. telarius:* | | |
| bean | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| soybean | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| Chlorobenzide | | |
| *B. rubrioculus:* | | |
| apple | Netherlands | van de Vrie (1962) |
| DDD | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| apple | Canada | Lord (1962) |
| *B. rubrioculus:* | | |
| apple | Canada | Lord (1962) |
| DDT | | |
| *P. ulmi:* | | |
| apple | U.S.A. | Blackburn (1947) |
| apple | England | Blair and Groves (1952) |
| apple | Australia | Caldwell (1946) |
| apple | U.S.A. | Chambers, Hey, and Smith (1944) |
| apple | U.S.A. | Chandler (1946) |
| apple | U.S.A. | Childs (1947) |
| apple | Canada | Campbell (1945) |
| apple | U.S.A. | Chapman (1947) |
| apple | England | Chiswell (1962) |
| apple | U.S.A. | Clancy and McAlister (1956,*a b, c*) |
| apple | U.S.A. | Clancy and Pollard (1952) |
| apple | England | Collyer (1952) |
| apple | England | Collyer and Kirby (1955, 1957, 1959) |
| apple | U.S.A. | Cutright and Sutton (1947) |
| apple | U.S.A. | Cutright and Vogel (1946) |
| apple | Poland | Dabrowski (1968) |
| apple | U.S.A. | Dean (1946) |
| apple | U.S.A. | Essig (1946) |
| apple | Switzerland | Günthart (1945) |
| apple | Australia | Hogan and Stephens (1946) |
| apple | U.S.A. | Hough (1945, 1946) |
| apple | Netherlands | Hueck (1953) |
| apple | Netherlands | Hueck *et al.* (1952) |
| apple | Japan | Hukusima, Tsugawa, and Taneichi (1958) |
| apple | Netherlands | Kuenen (1946*a*) |
| apple | Germany | Löcher (1958) |
| apple | Canada | Lord (1947, 1949, 1956, 1962) |
| apple | England | Massee (1954, 1956) |
| apple | Switzerland | Mathys, Baggiolini and Stahl (1968) |
| apple | Switzerland | Menzel (1947) |
| apple | England | Muir (1965) |
| apple | Germany | E. W. Müller (1960) |
| apple | U.S.A. | Ortega (1948) |
| apple | Canada | Parent (1967) |
| apple | Australia | Pasfield and Hobeche (1946) |
| apple | U.S.A. | Peterson (1947) |
| apple | Germany | Seifert (1961) |
| apple | U.S.S.R. | Sidljarevic (1965) |
| apple | Canada | Sanford and Herbert (1966) |

TABLE 3—*Continued*

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| apple | U.S.A. | Steiner, Arnold, and Summerland (1944) |
| apple | U.S.A. | Steiner, Summerland, and Fahey (1946) |
| apple | New Zealand | Taylor (1946) |
| apple | England | Tew and Groves (1957) |
| apple | U.S.A. | Whitehead and Bewick (1947) |
| apple | N. Ireland | Willis (1957) |
| grape | France | Chaboussou (1966*a*, *b*, 1967) |
| plum | Poland | Leski (1961) |
| plum | Poland | Burdajewicz (1963) |
| walnut | U.S.A. | Michelbacher (1959) |
| walnut | U.S.A. | Michelbacher and Middlekauff (1949) |
| peach | U.S.A. | Driggers (1946) |
| peach | U.S.A. | Hamilton (1949) |
| peach | Canada | Putman and Herne (1959) |
| pear | U.S.A. | Huffaker and Spitzer (1950) |
| pear | Japan | Hukusima and Kondo (1962) |
| bean | U.S.A. | Klostermeyer and Rasmussen (1953) |
| potato | U.S.A. | Klostermeyer and Rasmussen (1953) |
| potato | U.S.A. | Landis and Davis (1947) |
| potato | U.S.A. | Landis and Gibson (1953) |
| walnut | U.S.A. | Michelbacher and Middlekauff (1949) |
| *P. citri:* | | |
| citrus | U.S.A. | DeBach (1947) |
| citrus | U.S.A. | DeBach, Fleschner, and Dietrick (1950) |
| citrus | U.S.A. | DeBach and Bartlett (1951) |
| citrus | U.S.A. | Ebeling (1945) |
| citrus | U.S.A. | Griffiths and Thompson (1947) |
| citrus | China | Lo and Tao (1964) |
| *B. rubrioculus:* | | |
| apple | Rumania | Balevsky (1960, 1967) |
| apple | U.S.A. | Barnes (1951) |
| apple | Australia | Hogan and Stephens (1946) |
| apple | Rumania | Iacob (1961) |
| apple | Australia | Kemp (1947) |
| apple | Canada | Lord (1949, 1956, 1962) |
| apple | Australia | Pasfield and Bryden (1946) |
| apple | Australia | Pasfield and Hobeche (1946) |
| peach | Canada | Putman and Herne (1959) |
| *T. canadensis:* | | |
| peach | Canada | Putman and Herne (1959) |
| *T. carpini vitis:* | | |
| grape | France | Chaboussou (1966*b*) |
| *T. cinnabarinus:* | | |
| apple | Israel | Plaut and Feldmann (1967) |
| *T. hickoriae:* | | |
| pecan | U.S.A. | King (1954) |
| *T. pacificus:* | | |
| pear | U.S.A. | Barnes (1951) |
| melon | U.S.A. | Michelbacher *et al.* (1952) |
| walnut | U.S.A. | Michelbacher and Middlekauff (1949) |
| *T. telarius:* | | |
| apple | Japan | Hukusima (1963) |
| alfalfa | U.S.A. | Klostermeyer (1959) |
| peach | Canada | Putman and Herne (1959) |
| elm | U.S.A. | English and Tinker (1954) |
| grape | France | Chaboussou (1966*a*, *b*) |
| bean | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| soybean | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| cotton | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| bean | U.S.A. | Rodriguez, Maynard, and Smith (1960*b*) |
| unknown | U.S.A. | Bromley (1948) |

TABLE 3—*Continued*

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| *T. viennensis:* | | |
| apple | Switzerland | Mathys, Baggiolini, and Stahl (1968) |
| *T. tumidus:* | | |
| cotton | U.S.A. | Rodriguez, Chen, and Smith (1957) |
| *O. pratensis:* | | |
| corn | U.S.A. | Walter and Wene (1956) |
| *O. ununguis:* | | |
| oak | U.S.A. | Hoffman and Merkel (1948) |
| *O. coffeae:* | | |
| tea | Ceylon | Cranham (1966) |
| *Tetranychus* sp.: | | |
| cotton | Egypt | Kady (1964) |
| Diazinon | | |
| *P. ulmi:* | | |
| grape | France | Chaboussou (1966*a*, *b*, 1967) |
| *E. carpini vitis:* | | |
| grape | France | Chaboussou (1966*a*) |
| *P. ulmi:* | | |
| apple | England | Chiswell (1962) |
| *T. viennensis:* | | |
| apple | Greece | Soueref and Komblas (1961) |
| Dicofol | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| apple | Japan | Hukusima (1963*a*) |
| apple | U.S.A. | Saini and Cutkomp (1966) |
| Dieldrin | | |
| *T. urticae:* | | |
| cotton | Egypt | A. S. Hassan, Hahel, and El Badry (1959*a*, *b*) |
| cotton | Egypt | A. G. Hassan (1963) |
| apple | U.S.A. | Rodriguez, Maynard, and Smith (1960*a*) |
| *P. ulmi:* | | |
| apple | U.S.A. | Rodriguez, Maynard, and Smith (1960*a*) |
| Dimecron | | |
| *T. atlanticus:* | | |
| apple | Egypt | Abdel-Salam (1966) |
| Dimethoate | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| DNOC | | |
| *P. ulmi:* | | |
| apple | Netherlands | Kuenen (1946*a*) |
| apple | Germany | Redenz-Rüsh (1959) |
| *B. rubrioculus:* | | |
| apple | Germany | Redenz-Rüsh (1959) |
| *E. pomi:* | | |
| apple | Germany | Redenz-Rüsh (1959) |
| *T. urticae:* | | |
| apple | Germany | Redenz-Rüsh (1959) |
| Endrin | | |
| *Tetranychus* sp.: | | |
| cotton | Egypt | Kady (1964) |
| Ethion | | |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| apple | U.S.A. | Swift (1968) |
| Isolan | | |
| *B. rubrioculus:* | | |
| apple | Netherlands | van de Vrie (1962) |

TABLE 3—*Continued*

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| Lead arsenate | | |
| *P. ulmi:* | | |
| apple | England | Chiswell (1962) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| cherry | Netherlands | Kuenen (1946*a*) |
| apple | Canada | Lord (1949) |
| *B. rubrioculus:* | | |
| apple | Canada | Lord (1949) |
| *P. ulmi:* | | |
| apple | Canada | Parent (1967) |
| *T. urticae:* | | |
| apple | Canada | Parent (1967) |
| *P. ulmi:* | | |
| apple | Canada | Sanford and Herbert (1966) |
| *B. rubrioculus:* | | |
| apple | Canada | Sanford and Herbert (1966) |
| Malathion | | |
| *T. urticae:* | | |
| rose | U.S.A. | Henneberry and Taylor (1962) |
| apple | Canada | Parent (1967) |
| *P. ulmi:* | | |
| apple | Canada | Parent (1967) |
| Menazon | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| Methoxychlor | | |
| *T. urticae:* | | |
| rose | U.S.A. | Henneberry and Taylor (1962) |
| Nicotine | | |
| *P. ulmi:* | | |
| apple | Canada | Lord (1949) |
| *B. rubrioculus:* | | |
| apple | Canada | Lord (1949) |
| Parathion | | |
| *T. urticae:* | | |
| peach | France | Chaboussou (1960) |
| *T. telarius:* | | |
| bean | France | Chaboussou (1966*a*) |
| *P. ulmi:* | | |
| grape | France | Chaboussou (1966*a*, *b*, 1967) |
| *E. carpini vitis:* | | |
| grape | France | Chaboussou (1960, 1966*a*, *b*) |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| apple | Switzerland | Mathys, Baggiolini, and Stahl (1968) |
| peach | Canada | Putman and Herne (1959) |
| *T. telarius:* | | |
| peach | Canada | Putman and Herne (1959) |
| *T. canadensis:* | | |
| peach | Canada | Putman and Herne (1959) |
| *P. ulmi:* | | |
| apple | Germany | Rendenz-Rüsh (1959) |
| *E. pomi:* | | |
| apple | Germany | Rendenz-Rüsh (1959) |
| *B. rubrioculus:* | | |
| apple | Germany | Rendenz-Rüsh (1959) |
| apple | Netherlands | van de Vrie (1962) |

TABLE 3—*Continued*

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| *P. ulmi:* | | |
| apple | Netherlands | van de Vrie (1962) |
| *B. rubrioculus:* | | |
| cherry | Rumania | Iacob (1961) |
| Petroleum oil | | |
| *P. ulmi:* | | |
| apple | Canada | Lord (1949) |
| *B. rubrioculus:* | | |
| apple | Canada | Lord (1949) |
| Tar oil | | |
| *P. ulmi:* | | |
| apple | England | Austin and Massee (1947) |
| apple | England | Blair and Groves (1952) |
| apple | Netherlands | Geijskes (1938) |
| apple | England | Massee and Steer (1929) |
| apple | Germany | Redenz-Rüsh (1959) |
| *B. rubrioculus:* | | |
| apple | Germany | Redenz-Rüsh (1959) |
| *E. pomi:* | | |
| apple | Germany | Redenz-Rüsh (1959) |
| *T. urticae:* | | |
| apple | Germany | Redenz-Rüsh (1959) |
| TDE | | |
| *O. coffeae:* | | |
| tea | Ceylon | Cranham (1966) |
| Thiodan | | |
| *B. rubrioculus:* | | |
| tea | Netherlands | van de Vrie (1962) |
| *T. urticae:* | | |
| tea | U.S.A. | Harries (1966) |
| Trithion | | |
| *P. ulmi:* | | |
| grape | France | Chaboussou (1966*a*, *b*) |
| *E. carpini vitis:* | | |
| grape | France | Chaboussou (1966*b*, 1967) |
| Xanthone | | |
| *T. urticae:* | | |
| soybean | U.S.A. | Wingo and Thomas (1948) |
| FUNGICIDES | | |
| Captan | | |
| *P. ulmi:* | | |
| apple | U.S.A. | Boulanger (1963) |
| apple | England | Collyer and Kirby (1955, 1959) |
| apple | Switzerland | Günthart and Vogel (1965) |
| *T. urticae:* | | |
| peach | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| apple | Switzerland | Mathys, Baggiolini, and Stahl (1968) |
| apple | Germany | Müller (1960) |
| apple | Canada | Parent (1967) |
| *T. urticae:* | | |
| apple | Canada | Parent (1967) |
| *P. ulmi:* | | |
| apple | Netherlands | van de Vrie (1962) |
| *B. rubrioculus:* | | |
| apple | Netherlands | van de Vrie (1962) |
| *P. ulmi:* | | |
| apple | N. Ireland | Willis (1957) |
| *T. urticae:* | | |
| bean | U.S.A. | Hunter (1961) |
| peas | U.S.A. | Hunter (1961) |

TABLE 3—*Continued*

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| BORDEAUX MIXTURE AND COPPER PRODUCTS | | |
| *P. ulmi:* | | |
| grape | France | Chaboussou (1966*a*, *b*, 1967) |
| *O. coffeae* | | |
| tea | India | Cranham (1966) |
| *P. ulmi:* | | |
| apple | Netherlands | Kuenen (1946*a*) |
| apple | Canada | Lord (1949) |
| *B. rubrioculus:* | | |
| apple | Canada | Lord (1949) |
| *P. ulmi:* | | |
| apple | Canada | Parent (1967) |
| DNOPC | | |
| *P. ulmi:* | | |
| apple | England | Collyer and Kirby (1959) |
| Dodine | | |
| *P. ulmi:* | | |
| apple | U.S.A. | Boulanger (1963) |
| DRB | | |
| *P. ulmi:* | | |
| apple | Germany | Müller (1960) |
| Ferbam | | |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| apple | Canada | Lord (1949, 1962) |
| *B. rubrioculus:* | | |
| apple | Canada | Lord (1949, 1962) |
| *P. ulmi:* | | |
| apple | Canada | Morgan, Anderson, and Swales (1958) |
| apple | Germany | Müller (1960) |
| apple | Canada | Parent (1967) |
| *T. urticae:* | | |
| apple | Canada | Parent (1967) |
| Folpet | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| Glyodin | | |
| *P. ulmi:* | | |
| apple | U.S.A. | Boulanger (1963) |
| apple | England | Collyer and Kirby (1955, 1959) |
| apple | Canada | Parent (1967) |
| *T. urticae:* | | |
| apple | Canada | Parent (1967) |
| Karathane | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| apple | Canada | Morgan, Anderson, and Swales (1958) |
| apple | Netherlands | van de Vrie (1962) |
| *B. rubrioculus:* | | |
| apple | Netherlands | van de Vrie (1962) |
| Mancozeb | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| Maneb | | |
| *P. ulmi:* | | |
| grape | France | Chaboussou (1966*a*, *b*, 1967) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |

TABLE 3—*Continued*

| Pesticide, mite species, and host plant | Location | References |
|---|---|---|
| *P. ulmi* (?): | | |
| apple | Canada | Morgan, Anderson, and Swales (1958) |
| Phenylmercuriacetate | | |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| Sulfur and sulfur products | | |
| *P. citri:* | | |
| citrus | U.S.A. | McGregor (1942) |
| *P. ulmi:* | | |
| apple | U.S.A. | Clancy and Pollard (1952) |
| apple | England | Collyer and Kirby (1955, 1959) |
| apple | U.S.A. | Cutright (1942, 1944) |
| apple | U.S.A. | Garman (1948) |
| apple | Netherlands | Kuenen (1946*a*) |
| apple | U.S.A. | Lathrop and Hilborn (1950) |
| apple | Canada | Lord (1949) |
| apple | Germany | Müller (1960) |
| apple | Canada | A. D. Pickett (1949) |
| apple | Canada | Pickett, Putman, and Leroux (1958) |
| peach | Canada | Putman and Herne (1959) |
| prune | U.S.A. | Reed (1936) |
| grape | Switzerland | Mathys (1958) |
| *T. telarius:* | | |
| peach | Canada | Putman and Herne (1959) |
| *T. canadensis:* | | |
| peach | Canada | Putman and Herne (1959) |
| TMTD | | |
| *P. ulmi:* | | |
| apple | Switzerland | van de Vrie (1962) |
| apple | Netherlands | Mathys, Baggiolini, and Stahl (1968) |
| Zinc sulphate | | |
| *P. citri:* | | |
| citrus | U.S.A. | DeBach and Bartlett (1951) |
| Zineb | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| apple | Switzerland | Mathys, Baggiolini, and Stahl (1968) |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| Ziram | | |
| *T. urticae:* | | |
| apple | U.S.A. | Harries (1966) |
| *P. ulmi:* | | |
| apple | Switzerland | Mathys, Baggiolini, and Stahl (1968) |
| MISCELLANEOUS | | |
| *Bacillus thuringiensis* | | |
| *P. ulmi:* | | |
| apple | Switzerland | Günthart and Vogel (1965) |
| apple | U.S.A. | Oatman (1966) |
| Gibberellin | | |
| *T. urticae:* | | |
| bean | U.S.A. | Eichmeyer and Guyer (1960) |
| apple | U.S.A. | Harries (1966) |
| bean | U.S.A. | Rodriguez and Campbell (1961) |
| cotton | U.S.A. | Rodriguez and Campbell (1961) |
| *P. ulmi:* | | |
| apple | U.S.A. | Rodriguez and Campbell (1961) |
| Ryania | | |
| *P. ulmi:* | | |
| apple | England | Chiswell (1962) |
| apple | Switzerland | Günthart and Vogel (1965) |

*telarius*) in laboratory experiments on bean plants. These workers found a significant reduction in mite populations; the rate of reproduction was low when mites were confined to treated plants, but rose rapidly when the mites were transferred to untreated ones and vice versa. Rodriguez and Campbell (1961) studied the effects of gibberellin on the population development of *T. urticae* (= *T. telarius*) on bean, cotton, and apple, and of *Panonychus ulmi* on apple. Although growth of the plants was increased, populations of *T. urticae* were reduced on bean and apple; effects on the mites on cotton were variable. *P. ulmi* on apple was increased by application of 10 ppm gibberellin, but reduced by higher rates; positive and significant correlations were found with the percentage of total sugar in the leaves. Populations of both species were generally positively correlated to the percentage content of nitrogen, which was reduced by gibberellin, but were not significantly correlated with reducing sugar. Harries (1966) found no response in mortality or fecundity in *T. urticae* after application of 50 ppm gibberellin on apple seedlings.

Certain chelates and other nutrients have been implicated. Terriere and Rajadhyaksha (1964) found that chelates of iron, manganese, zinc, and magnesium applied to bean leaves in laboratory experiments reduced the fecundity of *T. urticae* (= *T. telarius*) by as much as 90 per cent. The chelates were applied in three ways: by direct spraying of detached leaves; by supplementation of nutrient media in which the beans were grown; and by addition to the media in which the leaves were floated. The last two methods were the most effective. Longer intervals between treatments of the plants or leaves and exposure of female mites produced greater reduction in fecundity, suggesting that some physiological plant process is involved in the chelate effect. Reduced fecundity was also demonstrated on leaves of strawberry, sweet potato, and hops sprayed with the chelates. Terriere and Rajadhyaksha (1964) suggest two possibilities to explain these results: (1) the nutritional suitability of the host plant has been reduced; or (2) some deleterious agent was transmitted to the mites via the plant. The data seem to support the second possibility, although the results were not conclusive.

Foliar applications of different nutrients, boron trioxide, chelates of manganese, zinc, and iron, and urea, to apple, peach, and pear seedlings (Harries, 1966) showed significant effects of some products on egg laying on apple by *Tetranychus urticae*; no effects on mortality were observed. No marked effects on either oviposition or mortality were observed on pear and peach.

Antibiotics have also been associated with mite abundance. Harries (1961) found that egg laying by *Tetranychus urticae* on apple, peach, and rose was strongly reduced by application of cyclohexamine, an antibiotic used against fungus diseases. This effect lasted for two to six weeks. Egg laying and mortality were also influenced by foliar application of several hormones to peach seedlings. Hukusima and Tabata (1968) studied the influence of various concentrations of cyclohexamine on the development of *T. urticae* populations on kidney beans in greenhouse experiments in Japan. A suppression in the reproductive rate was observed correlative with a decrease in total nitrogen concentration after application.

Langenscheidt and Schmutterer (1969) studied the effect of the antibiotic flavomycin on *Tetranychus urticae* in laboratory experiments. At concentrations of 0.01 and 0.1 per cent, mortality was not influenced; concentrations between 0.2 and 0.4 per cent caused mortality in the adult mites, and decreased oviposition considerably; there was also a marked tendency toward delayed postembryonal development. Histological studies showed that the effects on mor-

tality, sterility, and reduction of reproductive capacity were caused by the action of the antibiotic against symbiotic microorganisms in the midgut cells—a statement that finds some support in Harries' (1963) hypothesis.

## POSSIBLE EXPLANATIONS OF MITE INCREASES FROM USE OF CHEMICALS

### Direct Influence on the Mites

Huffaker and Spitzer (1950) were the first to demonstrate a definite increase in population densities of spider mites associated with treatments with DDT under conditions that ruled out predator inhibition as the cause. Thus they suggested physiological stimulation of a nutritional or hormonal nature as one possible cause. Their experiments had been suggested by findings of Chapman and Allen (1948) that DDT can produce an effect on plant growth similar to that of growth hormones. Hueck *et al.* (1952) and Hueck (1953), in field and laboratory trials, then showed that *Panonychus ulmi* on apple leaves treated with DDT produced approximately 50 per cent more eggs per unit of time, in contrast to mites on untreated leaves. Hueck (1953) also suggested the influence of DDT to be hormonal in nature. The experiments by Huffaker and Spitzer (1950), Hueck *et al.* (1952), and Hueck (1953) were not designed, however, to explore whether the stimulatory factor acted as a direct influence on the mites or via the plant, through its nutrition. Löcher (1958), in Germany, found that under DDT treatment the egg production of *P. ulmi* on apple, and *Tetranychus urticae* and *T. urticae* forma *dianthica* Dosse on bean, increased 80, 90, and 70 per cent, respectively. He also found that the DDT did not act through the host plant, but directly on the mites, and that negative or positive results were obtained, depending on whether adults or juvenile stages were treated. Seifert (1961) compared mature ovaries of *P. ulmi* individuals treated with DDT with those of untreated individuals; he found that oögenesis was increased by DDT. In the untreated females, only one egg matured at a time, and it started to develop only after deposition of the previous one. In the mites treated with DDT, however, two eggs developed simultaneously and were ready for oviposition. These histological changes could be observed within the treated generation when protonymphs, deutonymphs, and adult females were treated with DDT. Approximately three weeks elapsed between the treatment and the occurrence of the phenomenon.

There is disagreement on the number of eggs maturing at one time. Beament (1951) reported that one egg matures at a time, presumably because of the final very large size of the egg as compared with the size of the female. Anwarullah (1962), however, always found two developing eggs in *Panonychus ulmi* as well as in *Tetranychus viennensis*, *Bryobia rubrioculus*, and *B. kissophila*. Snieder-Berkenbosch (1955) found two or three eggs developing at a time in *P. ulmi*.

In experiments with *Bryobia rubrioculus* on apple in Bulgaria, Balevsky (1960) found an increase in egg production of 14 to 45 per cent when the mites were bred from egg to adult on leaves treated with DDT. No such increase occurred when adults were treated and kept on sprayed leaves. Also, tests with DDT applied directly to *Tetranychus urticae* and *T. cinnabarinus*, which were then placed on untreated leaves, produced no response in egg production (Attiah and Boudreaux, 1964*a*, *b*; Saini and Cutkomp, 1966).

## Modification of the Plant's Nutritional Quality or Physiology

It has been suggested or shown that DDT at certain concentrations may have an effect on certain plants similar to that of growth hormones (Chapman and Allen, 1948; Huffaker and Spitzer, 1950; T. C. Allen and Casida, 1951; Fleschner, 1952, 1958*b*; Goodman, 1955; Joyce, 1955; Ripper, 1956; Chaboussou, 1966*a*).

Huffaker (1948) translocated DDT from a concentrate supply by means of wicks inserted into holes in the stems and trunks of beans and pears, and in 1948 (unpublished data) he also treated cotyledons of young string beans with DDT. Substantial concentrations of DDT reached the untreated leaves in each case. In some laboratory tests on beans, highly significant increases in fecundity of *Tetranychus urticae* were recorded on treated plants over those on the controls, while in other tests no significant differences were found. These results and related studies on pear (Huffaker and Spitzer, 1950) were conducted in the field and in a greenhouse. In the latter study, a significantly higher initial increase occurred, in the absence of predators, under DDT treatment, but the populations on the controls eventually reached severe densities too. These authors concluded that while DDT may well act as a stimulant, the delicacy of the relationship depends upon concentration, and may lead to contrary results—a view supported by Allen and Casida (1951).

Fleschner (1952) treated basal leaves of citrus terminals with DDT, and *Panonychus citri* introduced onto untreated leaves of those terminals reproduced considerably faster than on the controls, again implying translocation of an effective principle. Further work by Fleschner (1958*b*) supported this finding. Saini and Cutkomp (1966) also used the technique of treating the primary leaves or cotyledons of beans with DDT and using the later trifoliate leaves to test for reproductive response in *Tetranychus urticae* under predator-free conditions. DDT applied in this manner induced an increase. In other experiments, DDT applied directly to the mites produced no response. Negative results with either or both the direct or indirect tests were obtained with *T. urticae* on bean (Attiah and Boudreaux, 1964*a*, *b*; Herne, 1957), on apple seedlings (Harries, 1966), and on alfalfa (Cone, 1963), and with *P. ulmi* on apple (Pielou, 1960*b*).

The controversial and contrary results of Hueck *et al.* (1952) were suggested by Pielou (1960*b*) to be related to the experimental conditions of Hueck's tests. In those tests, as many as 10 females were crowded on a leaf disc with an area of only 3.77 $cm^2$ and such discs decay rapidly. Females had a mean life of 4.5 days only, and an average daily egg production of 0.81, both of which are extremely low.

A number of materials have been shown to be responsible for physiological changes in crop plants: organophosphorus compounds on cotton (El-Rafie and El-Hannaway, 1961; Joyce, 1955); parathion on apple (Aleksidze, 1968); parathion and Ekatin on beans (Bogdanoff, 1964); fungicides (maneb, ferbam, and dinocap) on apple in British Columbia (Morgan, Anderson, and Swales, 1958); various soil insecticides on beans, soybeans, and cotton (Rodriguez, Chen, and Smith, 1957; Rodriguez, Maynard, and Smith, 1960*a*); and on apple trees (Rodriguez, Maynard, and Smith, 1960*b*). Westwood, Batjer, and Billingsley (1960) studied the effects of several organic spray materials on fruit growth and foliage efficiency of apple and pear in Washington state.

As to the effects on mites, Klostermeyer and Rasmussen (1953) observed higher populations of *Tetranychus urticae* on beans and potatoes in soils treated with several chlorinated hydrocarbons, DDT, benzene hexachloride, lindane, and chlordane, and suggested that this

effect was the result of change in the composition of the host plants. Chen (1957), Rodriguez, Chen, and Smith (1957), and Rodriguez, Maynard, and Smith (1960*a*, *b*) studied the relation of insecticides, DDT, dieldrin, and benzenehexachloride in the soil to the nutritional quality of the food plants for *T. urticae* on apple, beans, soybeans, and cotton. Collectively, they found, for example, that nitrogen level and total sugars can be increased with DDT concentration; this promoted reproduction of the plant-inhabiting mite species. They found, however, that potassium and phosphorus content and dry weight of foliage were reduced. Thus, mite reproduction in such a case was negatively correlated with phosphorus, potassium, and dry weight of foliage, but this may be only a spurious correlation. Harries (1966), however, did not obtain marked effects from residues of DDT in the soil on *T. urticae* bred on peach seedlings.

Absorption of chlorinated hydrocarbons by the roots and translocation to the aerial part of the plants was studied by various workers (Casida and Allen, 1952; Lichtenstein and Schulz, 1960; Harris and Sans, 1967). Collectively, they found that DDT may be absorbed or translocated only in trace amounts under normal field conditions. Ware (1968) provided evidence that no DDT-$C^{14}$ or its metabolites were translocated to aboveground parts of alfalfa when the level in the soil was similar to that commonly found in the irrigated agricultural soils of Arizona.

Leaf chemistry has been found to be affected by foliar applications of DDT. Kamal and Woodbridge (1960) found that DDT applications definitely increased the total nitrogen and protein in pear leaves, while malathion, parathion, and systox increased these fractions only to a limited degree. Chaboussou, Delmas, and Dureau (1961) found that after application of DDT on grape in France, the concentration of total nitrogen and protein nitrogen in the leaves increased; this increase was correlated with increases in density of *Panonychus ulmi* on these leaves. The application of DDT, especially early in the season, also resulted in a higher content of potassium; this increase was also correlated with increased densities of *P. ulmi* on grape growing on nutrient solutions with different levels of potassium. After the application of DDT, *Tetranychus telarius* on grape also increased (Chaboussou, 1966*a*, *b*); this increase was observed always to occur at the end of the summer. Since the reasons for this delayed reaction were unclear, Chaboussou suggested a relationship to the content of reducing sugars in the leaves, such as was found by Fritzsche, Wolfgang, and Opel (1957) for *T. urticae* on beans.

Increased densities of phytophagous mites following the application of carbaryl (=Sevin) are common occurrences. Plaut and Feldmann (1966, 1967) found that this insecticide increased the intrinsic power of increase of *Tetranychus urticae* and *T. cinnabarinus* on apple in Israel. From extensive observations, Flaherty (1967) considered that carbaryl caused an increased population response, physiologically, in *T. pacificus* on grape in California. Chaboussou (1966*a*, *b*) demonstrated that on grape in France, *T. urticae* (=*T. telarius*) responded to carbaryl treatment with a marked increase in egg production, the increase being even more pronounced than after DDT treatment under comparable conditions. According to Chaboussou (1966*a*), carbaryl—and also parathion—have a marked influence on the potassium: calcium ratio, the effects being influenced by the period of application (Chaboussou, 1964). Application early in the season lowered this ratio while applications later in the season had the opposite effect. Reduction of the potassium: calcium ratio is correlated with an increase in amino acids and reducing sugars. Rodriguez (1964) and Fritzsche, Wolfgang, and Opel (1957) demonstrated that reducing sugars are

important in the reproduction of tetranychid mites. Chaboussou (1966*a*) suggests that the primary reason for the increase of *Eotetranychus carpini* (Ouds.) is the increase of reducing sugars brought about by the application of carbaryl.

Pielou (1962) found that *Tetranychus urticae* treated with carbaryl, either in the immature or adult stage, on bean leaves, did not respond with increased egg production; he concluded, without providing experimental evidence, that increases of this species under field conditions in Canada are caused solely by the elimination of predators. Harries (1966) also did not find any appreciable effect of carbaryl on *T. urticae* on peach seedlings, but did find this insecticide to be extremely toxic to the photoseiid predators. Likewise, van de Vrie (1964) did not find an increase in population density of *Panonychus ulmi* on apple in response to this insecticide, in the Netherlands. Working with *T. urticae* on alfalfa in the U.S.A., Cone (1963) also found that egg production was not influenced by the application of several insecticides, including DDT.

According to Chaboussou (1966*a*), application of DDT and parathion increases the phosphorus content of the leaves. He showed that phosphorus in nutrient solutions applied to peach increased *Tetranychus urticae* (= *T. telarius*), a finding in accord with results reported by Rodriguez (1964) on the influence of this element on reproduction of this species. In related manner these materials also influence aphids and scale insects (Chaboussou, 1967).

## Effect on Mite Behavior

DDT-treated plants or surfaces appear to cause mites to disperse because of irritation or repellency. Davis (1952*b*) reported that *Tetranychus urticae*-complex (= *T. multisetis*) on a DDT-treated surface exhibited disturbed behavior, indicated by excessive locomotion and poor egg production for the first four days following treatment. After that period, the mites became adjusted and began to feed and lay eggs at a normal rate. In experiments in Canada, Herne (1957) also showed that DDT has a repellent, or irritating effect on *Panonychus ulmi* on peach, while in experiments with DDT-treated and untreated halves of apple leaves, Pielou (1960*b*) demonstrated that *P. ulmi* prefers the unsprayed halves, again indicating the repellent or irritating influence of DDT. Attiah and Boudreaux (1964*b*) also found an increased "restlessness" in *T. urticae* and *T. cinnabarinus* (= *T. telarius*) on bean leaves after DDT treatment.

The exact way in which increased mobility, or migration tendency can lead to an increase in reproduction is still conjectural. *Panonychus ulmi* is known to have a contagious distribution on apple (Kuenen, 1946*a*; Hueck, 1953; Pielou, 1960*a*; Stollwerck, 1962), which changes according to the season (van de Vrie, 1966). Increased mobility could lead to a more uniform distribution; this would lead to an increased reproduction only if density-dependent factors inhibited increase in the original contagious distribution. At high densities, these reducing factors are definitely present (p. 372), but whether they are present at low or moderate densities is questionable. Apparently, DDT treatments exert their influence independent of the density of phytophagous mites. Increased mobility could stimulate the mites to move to leaves formerly inhabited by natural enemies; if these are annihilated by DDT, the phytophagous species is likely to increase. It must be remembered that mite outbreaks are frequently caused by DDT in the absence of predators.

Attiah and Boudreaux (1964*b*) showed that only at relatively high dosages of DDT was any appreciable dispersion evident in *Tetranychus urticae* and *T. cinnabarinus* (= *T. telarius*) on lima beans. The advantages gained by this increased dispersal were more than offset by the toxic effects of DDT on the im-

mature stages. These authors postulated: ". . . that DDT-induced spider mite increases are primarily the result of DDT causing dispersion indirectly, after the all-important removal of natural enemies, all of which are susceptible to DDT. Thus, the removal of natural enemies causes dense localized populations to develop, which then disperse to predator-free surfaces, producing more colonies. . . ."

## Inert Residues Increasing Leaf Suitability

Results reported by Holloway, Henderson, and McBurnie (1957), Griffiths and Fisher (1950), and Fleschner (1952), indicate that either the "inert" particles used in many recommended spray materials or environmental dust produces increases in *Panonychus citri* in California citrus groves above those in the controls. Fleschner's (1952) results were obtained when all predators were kept removed; he interpreted the results to mean that the host plant's resistance had been lowered by the materials used. But the results could also be interpreted to mean that the materials increased the biotic potential of the mites, or that presumably the microweather and/or the microhabitat were made more suitable (see p. 399). *P. citri* was reported to increase after the use of copper and zinc sprays (Thompson, 1942). Griffiths (1951) reported an increase in this species after application of sulfur on citrus in Florida. The differential in mite populations could not be explained by differences in numbers of predators although DeBach and Bartlett (1951) reported that such "inert" materials as zinc sulfate and cryolite reduced populations of red mite predators on citrus. Kuenen (1946*a*) reported an increase in *P. ulmi* on cherry after application of lead-arsenate, and on apple after the use of Bordeaux mixture and lime sulfur. Lathrop (1951) reported that sulfur dust with lead-arsenate, concentrated in a mist spray and applied throughout the postblossom period, promoted severe infestations of *P. ulmi* on apple in Maine, without suggesting an explanation.

The effect of dusts or "inert" materials on natural enemies of insect pests has been extensively studied by Bartlett (1951). Twenty-seven "inert" dusts were examined; materials of mineral origin exerted a rapid killing effect; dusts of botanical origin were much less toxic.

## Release from Competition

Interspecific and intraspecific competition was discussed on page 372. It is evident that if susceptible species in a mixed population of various phytophagous mite species coinfesting the same host plant are annihilated by chemicals, and assuming that those chemicals exert no influence on the remaining species, the latter have access to a larger amount of food, which may allow them to increase. Some support for this phenomenon is provided by van de Vrie (1962). This explanation of mite increase may be valid only if a mixed population was present during the time of application; in the majority of the reported outbreaks, this was not the case.

Control of fungus diseases and insect pests may also result in a larger food supply for the phytophagous mites and may prolong the period of availability of the food apart from the possibility of altering the chemical composition of the leaves (E. W. Müller, 1959, 1960).

## Effect on Sex Ratio and Copulation Frequency

Mathys, Baggiolini, and Stahl (1968) observed a shift in the ratio of females to males after application of fungicides favoring the females, as compared with the untreated population. This was particularly true after treatment with sulfur and tap water, which increased the build-up of populations of *Panonychus ulmi* on apple seedlings grown on Hoagland's solution. These authors offer the

hypothesis that microelements in the tap water may influence sex determination—a new aspect not previously reported in the literature.

Leski (1966), without presenting experimental evidence, suggests that among other effects, the applied pesticides may result in a higher copulation frequency and thus a greater number of diploid eggs. This does not seem to be an important cause of increase in phytophagous mites; Helle (1967) proved experimentally that one copulation is sufficient to provide a female with an appropriate amount of sperm for producing female eggs during the whole oviposition period.

## CONCLUSION

The literature reviewed indicates that the bionomics of the most important tetranychid mite species have been studied in detail, thus providing an insight into the seasonal fluctuations in population density. Much of the existing knowledge was collected primarily to serve as a better basis for chemical control measures. An understanding of the ecology of a pest species is fundamental to the intelligent use of pesticides and the integrated, biological, or pest-management concept of control. For this reason, basic knowledge of the bionomics of tetranychid mites is of great importance in considering the use of biological agents in integrated or biological control.

Although many studies were directed toward providing a basis for chemical control, relatively few data are available regarding the pest status of several species. This is a complicated area for study, because so many variables are involved—host-plant species and quality, mite species, climate, market value of the crop, and so forth. Some of the data refer to extreme conditions, e.g., comparison of fruit trees on which mites were not controlled with those on which excellent control was achieved. Such studies indicate the potential of a pest species, but do not provide an insight into what mite densities can be tolerated. The few available data suggest that, in some instances, unexpectedly higher densities could be left uncontrolled without causing a measurable decrease in crop production, thus lessening the need for chemical applications (Parr and Hussey, 1962; Hussey and Parr, 1965). It seems highly desirable to collect more information on the economic importance and pest potential of several mite species under various conditions of host plant and climate.

Several authors made excellent studies on the relation between the host-plant quality and the tetranychids' capacities for increases. However, several studies are contradictory in their results. Generally speaking, apparently the better the care given the crop plants, the better the facilities offered to the mites, although in some instances the reverse was true (Griffith and Wene, 1954). A primary need is for more thorough knowledge of the nutritional requirements of tetranychids. Such studies are being performed in several places, so that in the future a better understanding of these needs will be realized.

Alterations in the host-plant condition as induced by cultural practices—fertilization as well as application of pesticides—have been demonstrated by several authors. So much solid information is available on these two sources of alterations in host-plant quality that it seems worthwhile to pay attention to both—a consideration sometimes overlooked. The influence of pesticides in improving the host plant's favorability to tetranychids—called "trophobiosis" (Chaboussou, 1966*b*)—certainly deserves detailed study on various crops, under various conditions. Application of materials that do not produce undesirable side effects

may lessen the pressure of mite development on some crops (Günthart and Vogel, 1963, 1965).

The direct effect of pesticides on the pest's intrinsic power of increase in some tetranychid species was studied by various authors, again yielding contrasting results (e.g., Hueck, 1953; Löcher, 1958; Attiah and Boudreaux, 1964*a*, *b*; Herne, 1957). Increased population density after treatment of plants with pesticides is also reported to occur in some insect species, in the absence of predators or parasites, thus demonstrating a physiological background for this phenomenon. Kuenen (1958) reported that *Sitophilus granarius* L. (Coleoptera: Curculionidae) produced 20 per cent more offspring when exposed to 0.10 and 0.125 mg DDT per 100 gm wheat, as compared with beetles in DDT-free wheat. Kuenen suggests that the less susceptible an arthropod species is to DDT, the greater the possibility that reproduction will be stimulated. Van der Laan (1961) reported an increase in density of *Bemisia tabaci* Genn. (Aleurodidae) on cotton in the Sudan Gezira after treatment with DDT. He suggests that changes in the composition of the food are inducing some change in the viability of the eggs, but adds that, in the absence of any proof, this explanation must remain purely conjectural, pending further studies.

Stimulation is not restricted to DDT. Luckey (1968) studied the influence of 14 pesticides on the rate of development of house crickets (*Acheta domesticus* L.). He found that most of the materials increased growth when applied in about 1/84 (range, 1/10 to 1/1,000) of the lethal dose. He refers to this process as "hormoligosis," and discusses the possible mechanism involved in this and related processes.

The references cited indicate that "stimulation" caused by pesticides is a generally occurring phenomenon. Its possible influence on tetranychid outbreaks should also be studied.

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