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Biological Control of Pacific Mites and Willamette Mites in San Joaquin Valley Vineyards

I. Role of *Metaseiulus occidentalis*

II. Influence of Dispersion Patterns of *Metaseiulus occidentalis*

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I. Role of *Metaseiulus occidentalis*

Population studies in southern San Joaquin Valley vineyards showed that the distributional patterns of Willamette mite, *Eotetranychus willamettei* Ewing, and Pacific mite, *Tetranychus pacificus,* differ in the Valley, in the vineyard, and on the vine itself. Pacific mite generally does best under hot and dry conditions while Willamette mite prefers cooler and more humid conditions, although there is considerable overlapping of the two species.

Detailed populations studies showed that untreated vineyards with no histories of pesticide treatment often exhibit more efficient levels of predation than do vineyards which have been treated. Also, contrary to the views of some investigators, these studies indicate that *Metaseiulus occidentalis* (Nesbitt) has no self-limiting aspects in its response to low or high prey densities.

In undisturbed vineyards, a mild predator-prey interaction appears to help perpetuate effective control of low prey densities by *M. occidentalis.* In disturbed vineyards, widely fluctuating predator and prey populations may lead to population crashes and continuation of imbalance. Moreover, when regulating low, but potentially serious, Pacific mite densities in undisturbed vineyards, *M. occidentalis* appears to benefit from the presence of the less seasonally restricted Willamette mite.

Tonnage and fruit-quality data showed that Willamette mite is often not a significant pest. Little differentiation has been made in the past between Pacific mite and Willamette mite, and treatments have been applied as if both were serious pests.

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I. Role of *Metaseiulus occidentalis*[1,2]

INTRODUCTION

SPIDER MITES are becoming a worldwide problem. As interest in their control increases, attention is focused on their predators — particularly among certain species of mites in the family Phytoseiidae.

Thus far, however, many workers have disagreed on the efficacy of these predatory mites (see pp. 279–80 and Huffaker *et al.*, 1969) in the control of particular species of spider mites. Controversy about predator mites has centered on: (1) their synchrony or lack of synchrony with the particular prey species in the way they coinhabit the particular host plants; (2) the question of their prey specificity and use of alternate foods, either other prey species or non-prey materials; (3) the question of their food requirements, termed here their voraciousness; (4) their control or regulatory potential as judged by their responses, both functional and numerical, to increase in prey density; and (5) their erratic or belated occurrence under certain crop conditions.

The present study was undertaken not to answer these questions *per se,* but as a means to develop a practical program of biological control of spider mites occurring on grapes in the San Joaquin Valley of California. However, data obtained for this study do shed light on some fundamental aspects of spider mite predation; at the same time, they point toward possible utilization of an important species, *Metaseiulus occidentalis* (Nesbitt), in the control of spider mites on grape in the study area.

Recently, C. E. Kennett (personal communication) showed that *Metaseiulus occidentalis* is the same species that Kuchlein (1965, 1966, 1967) in the Netherlands referred to as *Typhlodromus longipilus* Nesbitt. Kuchlein's and Chant's (1961) laboratory studies cast much doubt on the efficiency of this predator, based upon studies bearing primarily on its functional response. However, the laboratory work of Waters (1955), Huffaker (1958), Huffaker *et al.* (1963), Laing (1968), Laing and Huffaker (1969), and Sharma (1966) clearly shows that the California stock used in these studies under suitable circumstances has no self-limiting aspects sufficient to render it ineffective in reducing high prey densities, as inferred by the above authors. This aspect is discussed at length by Huffaker *et al.* (1969) and in some respects later in this paper (see also McMurtry *et al.*, 1970).

It is, however, commonly recognized that *Metaseiulus occidentalis* often fails to give adequate control of certain prey species in the field (Huffaker and Flaherty, 1966; Sharma, 1966; and Hoyt *et al.*, 1967). Under certain circum-

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stances, however, it has been considered effective (Smith, 1939; Smith and Stafford, 1955; Hoyt, 1969).

Regardless of the controversy, there is considerable agreement that if predators do have an important role in controlling spider mites, this particular predator species would most likely be the one responsible for maintaining the low prey densities often encountered on certain untreated crops in California. Insectan predators of mites often become effective only at relatively high prey densities (see Huffaker *et al.*, 1969). If this is true, and if *Metaseiulus occidentalis* does lack the ability to control or regulate tetranychid populations on these crops, then it must be assumed that nutritional or meteorological factors are responsible for these low densities. If this latter thesis be accepted, the increased abundance of spider mites so often documented under the use of organic pesticides (see figs. 2, 4, and 5), must be due to improved nutrition, since meteorological factors are largely unaffected by these compounds.

However, aside from the theoretical consideration of population regulation in the absence of reciprocating density-dependent action by an enemy, this thesis poses questions (see later discussion). On the other hand, if *Metasieulus occidentalis* does commonly regulate such spider mite populations, then the chemicals used may contribute the inhibiting ingredient—disturbance of the state of balance. Chemicals can create population imbalance in three ways: (1) the advantage conferred on the prey aside from the differential kill, for example, when the prey population is reproductively stimulated by the chemical; (2) the differential kill alone; and (3) a combination of these two.

In this study, we have examined the total cause and effect relationship—economic and biological—of the increased spider mite abundance that experienced viticulturists have observed, following the general and extensive use of organic pesticides after World War II. It was carried out primarily in the field in order to observe the natural interspecific relationships between the Pacific mite, *Tetranychus pacificus* McGregor, the Willamette mite, *Eotetranychus willamettei* Ewing, and their common predator, *Metaseiulus occidentalis* (Nesbitt) in southern San Joaquin Valley vineyards.

SPIDER MITES ON GRAPES IN THE SOUTHERN SAN JOAQUIN VALLEY

Systematic notes

In their review of the family Tetranychidae, Pritchard and Baker (1955) placed *Tetranychus pacificus* McGregor and *T. urticae* Koch (= *T. telarius* L.) in the *Pacificus* and *Telarius* groups. These two groups are differentiated by the female dorsal integumentary striae. Specific identification within each group requires examination of the male aedeagus. *Tetranychus urticae* is only occasionally found on grapes in the southern San Joaquin Valley.

The genus *Eotetranychus* is differentiated from *Tetranychus* by the possession of an extra pair of setae, the clunals, near the posterior end of the female body, making easy the microscopic differentiation between *Eotetranychus williamettei* Ewing and the above two *Tetranychus* species. With some practice Willamette mite also can be distinguished from Pacific mite by use of a hand lens. Flaherty *et al.* (1966) outlined the field identification of the two species. Two-spotted mite females can also be separated from Pacific mite in the field. Mature females of the latter species possess characteristic caudal spots.

Biological notes

Neither Pacific mite nor Willamette mite has been the subject of a close life history study, but according to Andres (1957), Pacific mite development is very similar in number and appearance of the various stages to the much-studied two-spotted mite, *Tetranychus urticae*. Willamette mite, according to Pritchard and Baker (1952), is similar in life history to the closely related species *Eotetranychus carpini* (Ludemans) and *E. uncatus* Garman. Ubertalli (1955) summarized biological studies of *E. uncatus.*

Colony formation. Willamette mites and Pacific mites feed on the undersurface of the leaf, principally along leaf midribs and veins. Willamette mites, however, tend to disperse more over the leaf surface. Pacific mites tend to aggregate. Both species also show preferences for leaf depressions and folds—Pacific mite, conspicuously so.

Willamette mites produce less webbing on grape leaves than Pacific mites. Heavy webbing by the latter species is often first noted on shoots growing upright from the tops of vines.

Host injury. The feeding of small colonies of both species produces small yellow spots on the leaf surface. Yellowing of the entire leaf is characteristic of high densities of Willamette mites (plate I, photo A).[3] High densities of Pacific mites produce leaf burn (plate I, photo B).

By stunting shoot and leaf growth, the two species may expose the fruit to direct sunlight thus causing sunburned and unsightly bunches. Shedding of leaves may also occur with severe Pacific mite injury, especially during hot weather (plate I, photo E). Leaf shedding along with Willamette mite injury has not been noted.

Overwintering and dormancy. These two spider mites overwinter under grapevine bark as mature females. Clusters of Willamette mites have been noted under loose bark, working their way into tight crevices. Smith and Stafford (1955) maintained that if more than a dozen Pacific mites are found under a single vine arm, a serious infestation may follow the next season. Pritchard and Baker (1952) stated that Pacific mite populations 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. Pacific mite has not been noted to infest winter covercrops in vineyards.

Field studies by Flaherty and Hoy (unpublished data) showed that, from midsummer on, the incidence of diapause in Pacific mite populations increases as foliage feeding-injury increases, a phenomenon similar to that observed for *Panonychus ulmi* Koch on apples (Lees, 1953). In laboratory studies, Flaherty and Hoy also showed that short photoperiods induce Pacific mite diapause; similar results were reported by Lees (1953) for *Tetranychus urticae* and *P. ulmi.*

Both Willamette mite and Pacific mite become active when the grapebuds break in the spring, with Willamette mite appearing more active than Pacific mite during cool, spring temperatures.

Range and hosts. According to Pritchard and Baker (1952), Pacific mite is an important agricultural pest in much of far western United States. It is known to occur in Idaho, Oregon, and California. In California, Mabry and Walton (1939) collected it as far south as Riverside and reported that it attacked some 35 hosts, including cotton, deciduous fruit trees, grapes, melons, beans, berries, alfalfa, clover, and vetch. Pritchard and Baker (1955) also include as hosts trees such as elm and black locust, ornamental shrubs such as

[3] See pages 286 and 287 for color plates.

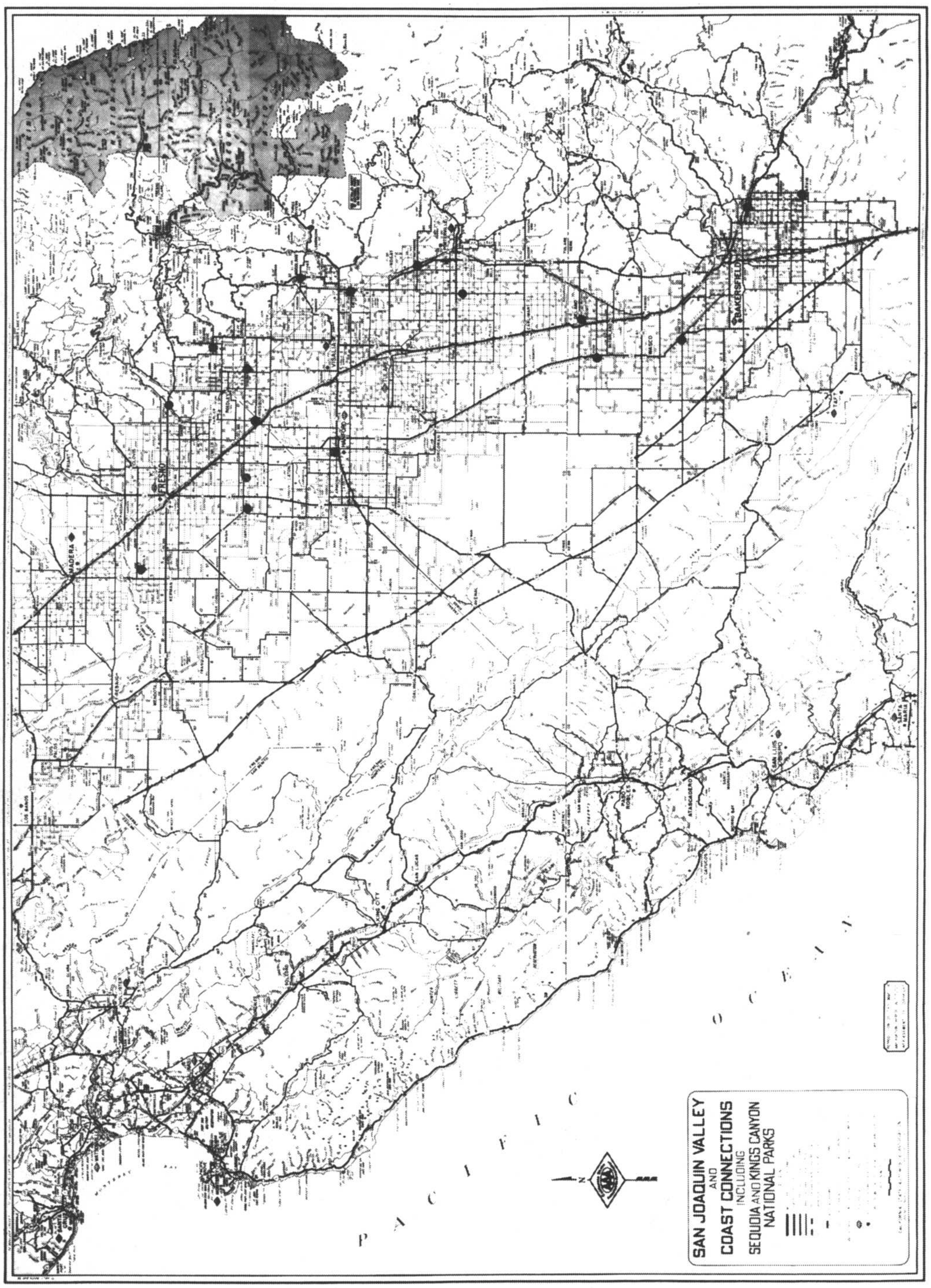

Fig. 1. Map of southern San Joaquin Valley. Dots indicate sampling areas (east and west of U. S. Highway 99).

cotoneaster, and endemic plants such as garrya, ceanothus, sunflower, tarweed, morning glory, California poppy, milkweed, salvia, and pigweed.

Pritchard and Baker (1955) state that Willamette mite is known from southern California northward to Washington, and that it is a serious pest of grapes in California and occasionally infests apples. Other hosts include antelope-brush, box-elder, service-berry, and oak.

Spider mite distributions in the southern San Joaquin Valley, in the vineyard, and on the vine. (Figure 1 shows sampling areas in the Valley.) In general, Pacific mite is favored by hot, dry vineyard conditions. For example, east and west Fresno County have significantly different Pacific mite problems. Observations indicate the differences are largely due to soil type variations. In western Fresno County, the soils are usually lighter in texture and more alkaline; hot, dry, and dusty vineyard conditions are found where these soil types exist. In eastern Fresno County, the heavier soils prevail, and vineyard conditions are somewhat more humid and less dusty. It also seems reasonable that spider mite nutrition would depend upon how soil type affects grapevine chemistry. In any case, the nature of the soil in western Fresno County seemingly dictates the severe Pacific mite infestations often found there, while in large parts of eastern Fresno County — particularly in the Orange Cove area—Pacific mite is absent from vines.

The absence of Pacific mites from grapevines is also conspicuous in eastern Tulare County, more particularly in the Woodlake and Exeter areas. Soils in eastern Tulare County are noticeably heavier than those in western Tulare County, where Pacific mite is often a serious pest.

In those areas of eastern Fresno and Tulare counties where Pacific mite is absent from grapevines, heavy insecticide treatments are often given for the control of grape leafhopper, *Erythroneura elegantula* Osborn. On the other hand, those vineyards that are cultured on the lighter soils in the western parts of these counties are often plagued by Pacific mites following the extensive use of insecticides.

Leigh (1963) also noted the absence of Pacific mite on cotton in certain areas of the eastern San Joaquin Valley. He attributes its absence to higher humidities. This reasoning was derived from Andres' laboratory experiments (1957), in which the Pacific mite was demonstrated to be less tolerant to high humidities than the two-spotted mite, *Tetranychus urticae,* or Atlantic mite, *T. atlanticus* McGregor, both of which are also pests of cotton. Pacific mite, however, can be reared under comparable high humidities in the laboratory and greenhouse, so that other factors related to types of soils in eastern Tulare and Fresno counties could account for its absence.

In the lower end of the San Joaquin Valley—particularly in the Delano and Arvin areas—soil types again seem to play an important role in the ecology of Pacific mite. Although this species has become a serious pest in both areas since the established use of organic pesticides, the greater problem in Arvin apparently is related to the hotter and drier or dustier conditions prevailing. In general, the soils are lighter in Arvin vineyards than in Delano vineyards. Furthermore, non-cultivation or grass-culture is normally practiced during the summer in Delano vineyards, but not in Arvin vineyards. There is little doubt that dust plays an important part in spider mite abundance, and grass-cultured vineyards of Delano are less likely to have dust problems than the clean-cultivated vineyards of Arvin. Also, grass cultivation may play an important role in spider mite abundance by improving vine-water relations during the summer (Flaherty and Lynn, unpublished observations).

Willamette mite also presents some interesting differences in occurrence in the San Joaquin Valley. For example, in eastern Tulare and Fresno counties where Pacific mite is not found on grapevines, Willamette mite is at times abundant. Treatments for control of grape leafhopper are often intense in these areas; yet Willamette mite densities remain conspicuously low, when compared to other areas where similar insecticide applications are associated with Willamette mite outbreaks. As in the case of Pacific mite, one or more factors must be strongly limiting Willamette mites in eastern Tulare and Fresno counties.

In the Biola area of western Fresno County where Pacific mite is a serious pest, high densities of the two species may be found in mixed populations. On the other hand, in the Monmouth area of western Fresno County where Pacific mite is even more serious, Willamette mite is essentially absent. Again, soils differ in the two areas, the Monmouth soils being lighter and more alkaline.

In the table grape area of southern Tulare County and southern Kern County, high densities of Willamette mites are often encountered. Vineyards with pesticide histories, however, harbor the highest densities. Growers in these areas consider Willamette mite a serious pest, and acaracides are freely applied for its control, as preventive measures. Delano table grape growers, in particular, view this species as serious and take measures to reduce dust deposits on vine foliage by oiling well-traveled vineyard roadways.

Unlike Pacific mite, which occurs spottily in the Delano area, Willamette mite is general in its distribution, seemingly showing little varietal preference. Pacific mite is often a serious pest on Almeria and Thompson Seedless table grape varieties but less so on Emperor and Ribier table grapes in the same area.

In the Arvin-Edison area of Kern County, Willamette mite has been the dominant species; however, in recent years the extensive use of synthetic pesticides has resulted in the dominance of Pacific mite in many vineyards. Willamette mite also appears to be more serious in the Arvin area than in the Delano area. As already pointed out, grass-culture is practiced in Delano vineyards and not in Arvin vineyards. Flaherty and Jensen (unpublished data) showed that if grass culture is practiced in vineyards, the abundance of Willamette mite is reduced, possibly because there is less dust where noncultivation is practiced. Willamette mites obviously benefit from roadway dust and there is no reason to believe they would not benefit from dust raised by cultivation equipment. Also, predation may be more effective where grasses or other weeds grow in vineyards (Flaherty, 1969).

Table 1 summarizes the distribution and relative abundance of Pacific mite and Willamette mite in the southern San Joaquin Valley. This table is not in any way intended to be taken at face value, for in recent years the incidence and distribution of Pacific mite and Willamette mite have been changing with increased pesticide usage.

Pacific mites *within* the vineyard have been commonly observed to reach high numbers in the same spot year after year. Often these Pacific mite-susceptible spots consist of obviously weaker vines. Soil differences seem to be correlated with the weaker vines. Water penetration in these outbreak spots may be poor, or the soil is sandy, and dry conditions prevail despite frequent irrigations. In western Fresno County, Pacific mite outbreak spots appear to be related to soil alkalinity and vine-water stress. Table 2 presents population counts on Almeria vines inside and outside a typical outbreak

TABLE 1

SUMMARY OF PACIFIC MITE AND WILLAMETTE MITE DISTRIBUTIONS AND RELATIVE ABUNDANCE IN SOUTHERN SAN JOAQUIN VALLEY VINEYARDS (1964)

Sampling areas	Relative abundance of mites	
	Willamette mite	Pacific mite
Biola, Western Fresno County	Light to heavy	Light to heavy
Monmouth, Southwest Fresno County	Not found	Moderate to severe
Centerville, Eastern Fresno County	Light	Light; some moderate spots
Orange Cove, Eastern Fresno County	Very light	Not found
Kingsburg, Kings County	Light	Light to moderate
Hanford, Kings County	Light	Light to moderate
Dinuba, Northern Tulare County	Light	Light to heavy
Woodlake, Eastern Tulare County	Very light	Not found
Exeter, Eastern Tulare County	Light to moderate	Not found
Strathmore, Eastern Tulare County	Light to heavy	Not found
Poplar, Central-eastern Tulare County	Light to heavy	Light to heavy
Delano, South-central Tulare County	Light to heavy	Light to heavy
Pond, Northern Kern County	Moderate	Not found
Shafter, West-central Kern County	Light to heavy	Not found
Arvin, Southeastern Kern County	Light to heavy	Light to heavy

area. Note that Pacific mite populations were much higher on the weak vines than on the healthy vines.

A number of workers—Garman and Kennedy (1949); Rodriguez (1951, 1958); Le Roux (1954); Fritzche *et al.* (1957); Post (1961); Henneberry (1962)—studied the relationships between plant nutrition and spider mite abundance. Seemingly contradictory results were noted in certain cases. For example, high nitrogen levels in one case would cause higher populations than did nitrogen deficiency; in other cases, the opposite (see van de Vrie *et al.*, in preparation). Watson (1964) suggested some factors which may be responsible for such differences and constructed survival-fecundity tables presenting a more precise picture of the population response under different nutrient levels.

Watson's experiments using ***Tetranychus urticae*** and bean plants suggested that fully nourished, vigorous plants support higher two-spotted mite popu-

TABLE 2

NUMBERS AND DISTRIBUTIONAL PATTERNS OF SPIDER MITES ON UPPER AND LOWER FOLIAGE OF WEAK AND HEALTHY ALMERIA GRAPEVINES IN THE LLOYD GIST VINEYARD (POPLAR, TULARE COUNTY, 1966)

Spider mite	Distribution on foliage* of:			
	Weak vines		Healthy vines	
	Upper	Lower	Upper	Lower
	No.	*No.*	*No.*	*No.*
Willamette	323	2,790	1,030	4,426
Pacific	9,032	758	124	2

* Samples of 30 leaves taken from both upper and lower foliage on healthy and weak vines. Upper foliage on Almeria vines was fully exposed to direct sunlight; lower foliage was shaded.

TABLE 3

INTRA-VINE WILLAMETTE MITE AND PACIFIC MITE DISTRIBUTIONAL PATTERNS ON THOMPSON SEEDLESS GRAPEVINES IN THE MIGUEL VINEYARD
(BIOLA, FRESNO COUNTY, JULY 3 TO OCTOBER 30, 1965)

Item	Area on vine		
	North	South	Top
No. leaves sampled (11 sixty-leaf samples)	660	660	660
Av. leaf area (sq. in.)	19	16	11
Total area sampled (sq. in.)	12,540	10,560	7,260
Pacific mites/660 leaves	3,714	8.902	10,732
Willamette mites/660 leaves	11,391	8,740	6,071
Total mites/660 leaves	15,105	17,642	16,803
Pacific mites/leaf	5.7	13.5	16.3
Willamette mites/leaf	17.2	13.2	9.2
Total mites/leaf	22.9	26.7	25.4
Pacific mites/sq. in. × 10 (av.)	3.0	8.4	14.8
Willamette mites/sq. in. × 10 (av.)	9.1	8.3	8.4
Total mites/sq. in. × 10 (av.)	12.1	16.7	23.1
	Significance level (from paired *t*-test)		
	Top vs North	*Top vs South*	*South vs North*
Pacific mites/660 leaves	.05	NS	.05
Willamette mites/660 leaves	NS	NS	NS
Total mites/660 leaves	NS	NS	NS
Pacific mites/leaf	.05	NS	.05
Willamette mites/leaf	NS	NS	NS
Total/mites/leaf	NS	NS	NS
Pacific mites/sq. in. × 10 (av.)	.05	.05	.05
Willamette mites/sq. in. × 10 (av.)	NS	NS	NS
Total mites/sq. in. × 10 (av.)	.05	.05	NS

NS = not significant at 5% level.
SOURCE OF DATA: Flaherty and Huffaker (Part II).

lations. However, the opposite often appears to be true with respect to Pacific mite on grapes (see table 2). That is, the less vigorous and perhaps nutrient-deficient vines often harbor higher population densities. The physical environment on these vines may be important. Data are presented later showing that this species is sensitive to intra-vine environmental differences related to insolation and heat. This is not to be construed, however, to mean that nutrition is not limiting for Pacific mite, perhaps in a manner similar to that shown by Watson (1964) for *T. urticae,* but it is here emphasized that other factors in the field may override it, or, in fact, be derived from it.

Willamette mite *within* the vineyard generally exhibits a more dispersed pattern than does Pacific mite. Its less damaging nature makes it more inconspicuous than Pacific mite. Buildup and spread of Willamette mite, however, is often noted to occur from vines bordering well-traveled roadways.

Since Pacific mite is favored by hot, dry conditions and Willamette mite by cooler, more humid conditions in the Valley or vineyard, a corollary would be limitation of its distributional patterns on the vine itself by these same factors. Flaherty and Huffaker (part II) found that Pacific mites is considerably more abundant on the south sides and tops of Thompson Seedless vines than on the north sides, or on foliage not receiving full afternoon sun. Table 3 summarizes Flaherty and Huffaker's data.

If spider mites per quare inch is used as a criterion, table 3 illustrates that Willamette mite is more evenly distributed over trellised Thomson Seedless vines and favors the north side much more than does the Pacific mite. The table also shows that when the three areas of the vine are analyzed with respect to each other, there are no significant differences with regard to Willamette mite preferences, while there are significant differences with regard to Pacific mite preferences. On Almeria vines cultured on arbors, Willamette mite conspicuously prefers the shady areas (table 2).

PREDATORS ON GRAPES IN THE SOUTHERN SAN JOAQUIN VALLEY

Insectan predators

This paper (part I) is primarily concerned with predaceous mites (Acarina); insectan predators (Insecta) will be considered only briefly.

Huffaker and Flaherty (1966) discussed the role of insectan predators as regulators of spider mites. They pointed out that in order to survive as searching populations, predatory insects require fairly high densities of prey, at least in some spots. Therefore, if other factors are equal (unlikely), they are less reliable control agents than the predatory mites which work more effectively at low prey densities in preventing outbreaks in the first place.

Huffaker and Flaherty (1966) also state that dependence on repeated reestablishment makes for less reliable control than that which results from persistent presence, which is typical of certain phytoseiid mites. Moreover, a predator's searching power may be sufficiently superior to offset, or more than offset, a high food requirement. Huffaker and Kennett (unpublished results) maintained a population of the phytoseiid, *Amblyseius aurescens* Athias-Henriot, on an isolated, single, potted strawberry plant infested with cyclamen mite, *Steneotarsonemus pallidus* (Banks), for approximately a year. Also, Huffaker and Kennett (1956) showed that *A. aurescens* and *A. cucumeris* (Oudemans) are closely attuned to the life cycle and habits of their common prey which they readily control.

The performance of insectan predators and their contributions to the total machinery of natural control of spider mites in vineyards are little known, but their limitations are obvious. Although six-spotted thrips, *Scolothrips sexmaculatus* (Pergande), at times is quite active, its usually belated appearance and its dispersion pattern relative to that of spider mites are certainly not conducive to regulation at low prey densities. Yet this voracious predator, responding to high density pockets, may serve to greatly impede spread from "outbreak spots." Mr. Curtis Lynn, Fresno County viticulture advisor, has often observed impressive, rapid, late-season destruction of high Pacific mite populations by this predator, but he affirms its shortcomings just described as a low-density regulator on grapes. The belated appearance, however, may have the advantage of aiding *Metaseiulus occidentalis* to restore a state of balance.

Observations for several years in many vineyards throughout the Valley indicate that other insectan predators of spider mites on grapes are even less important than six-spotted thrips as low-density control agents. For example, minute pirate bugs, *Orius tristicolor* (White), usually invade vineyards only after serious outbreaks of Pacific mites occur. They are completely ineffective against their prey because of their limited numbers and very poor distributional patterns. Also, they do not respond reproductively within the required time interval, and Pacific mite populations increase in their presence as if uninhibited.

Insectan predators are often essentially absent where Willamette mites are the sole prey species. Perhaps the dispersion patterns and the small amount of webbing produced by this species on grapes make it less suitable as prey. Moreover, *Metaseiulus occidentalis* does not seem to respond numerically as readily to Willamette mites as it does to *Tetranychus* species (Pacific and two-spotted mites). The authors investigated dispersion patterns of Willamette mites and Pacific mites on grapevines (part II), and concluded that *M. occidentalis* may be a more effective predator of Pacific mites than of Willamette mites, because the former aggregate as populations while the latter disperse as populations. Furthermore, Flaherty (1969) investigated alternate prey and *M. occidentalis* predation, and he considered that this predator's efficiency on Willamette mite populations increases, when tightly-webbed colonies of two-spotted mites (*T. urticae*) are present on grape leaves.

Phytoseiid predators

The classification used herein of genera and species within the Phytoseiidae follow that of Schuster and Pritchard (1963). Their interpretation of generic concepts of species which occur in California adopts an intermediate position between the conservative interpretation of Chant (1959) and the liberal interpretation of Muma (1961).

Metaseiulus occidentalis is by far the dominant species in vineyards throughout southern San Joaquin Valley vineyards. Other species are found in such insignificant numbers that their role in control of spider mites on vines must be even less than that of the insectan predators. Table 4 lists the species collected from grape. Other associated or adjacent vegetation is noted because some species are found more often on vines where this vegetation exists. For example, large numbers of *Amblyseius hibisci* (Chant) were collected on grapevines bordering indigenous vegetation along streams and rivers. The same is true for *M. pomoides* Schuster and Pritchard. Large numbers of these two species were collected on wild grape, *Vitis* sp., and wild blackberry, *Rubus* sp., growing along waterways. *Amblyseius scyphus* Schuster and Pritchard has been collected only in vineyards where weedy grasses are abundant. Schuster and Pritchard (1963) list this species from several grasses.

The absence of some species in vineyards isolated from natural vegetation could be due to the lack of an alternate source of food. *Amblyseius hibisci* has been shown to feed and reproduce on pollen alone (McMurtry and Scriven, 1964). Samples from wild grape and blackberry showed this species, *Metaseiulus pomoides,* and *Typhloseiopsis arboreus* (Chant) to be present in large numbers, yet reproducing in the absence of obvious prey. Possibly, sources of food other than prey are available and important for these phytoseiids.

What role such phytoseiids might have in the natural control of certain acceptable prey species through environmental manipulation is purely speculative. However, it is noteworthy that McMurtry and Scriven (1966) improved the predation by *Amblyseius hibisci* as a population with a liberal use of pollen on avocado leaves. They showed that this predator increased to

TABLE 4
PHYTOSEIIDS COLLECTED FROM GRAPEVINES IN THE SOUTHERN SAN JOAQUIN VALLEY
(1964)

Phytoseiid	Habitat on area of vine, occurrence, and remarks
Amblyseius	
A. asetus (Chant)	Bark. Rare. No association noted.
A. aurescens Athias-Henriot	Bark. Common. Often occurs with *A. brevispinus*.
A. brevispinus (Kennett)	Bark. Common. Often occurs with *A. aurescens*.
A. cucumeris (Oudemans)	Bark. Rare. No association noted.
A. fallacis (Garman)	Bark and foliage. Rare. No association noted.
A. hibisci (Chant)	Foliage. In large numbers on grapevines bordering indigenous vegetation along waterways.
A. palustris (Chant)	Foliage. Associated with fungus-feeding oribatid mites, particularly after rains.
A. scyphus Schuster & Pritchard	Foliage. Occasionally where grasses are associated with grapevines.
Metaseiulus	
M. mcgregori (Chant)	Foliage. Only an occasional specimen collected. No association noted.
M. occidentalis (Nesbitt)	Foliage and bark. By far the most common phytoseiid found on grapevines.
M. pomoides Schuster & Pritchard	Foliage. Found in moderate numbers on grapevines bordering indigenous vegetation along waterways.
Typhloseiopsis	
T. citri (Garman & McGregor)	Foliage. Found on grapevine bordering indigenous vegetation along waterways.
T. arboreus (Chant)	Foliage. Occasionally found on grapevines bordering indigenous vegetation along waterways.
T. smithi (Schuster)	Bark. Common bark species.

abundance on pollen and controlled the avocado brown mite, *Oligonychus punicae* (Hirst), on seedlings to which the pollen was added weekly, while on seedlings having no pollen, the predator reduced the spider mite only slightly below that on the "control" seedlings having no predators. Thus, pollen actually increased the efficiency of this predator as a population, even though an individual predator feeds less on spider mites when pollen is present.

Huffaker and Kennett (1956) discussed the importance of an alternate source of food as a cushion against the hazards of low prey densities. They showed the importance of alternate foods even for species which are primarily predaceous and do not reproduce on non-prey foods.

The main disadvantage of *Metaseiulus occidentalis* as a predator of good economic value is its susceptibility as a population to low prey densities, for it does not reproduce on anything but living prey as food (J. A. McMurtry, personal communication). However, the existence of alternate prey as a cushioning against low pest densities may determine whether or not *M. occidentalis* can effectively regulate the pest at low or non-economic levels (see also Hoyt, 1969).

Thus, alternate foods (prey or otherwise) dictate careful thought when considering phytoseiid predation. Flaherty (1969) considered this in noting that vines infested with weeds harbored lower Willamette mite populations than adjacent weed-free vines. His investigations subsequently showed that small numbers of two-spotted mites moving over from weeds onto the grape foliage favored an earlier predator response with respect to Willamette mites. On adjacent, weed-free vines, a long predator lag period occurred. Subsequently, this paper will show that the continuous presence of Willamette mites may sustain *M. occidentalis* and result in more effective predation of Pacific mites. Moreover, recent studies and observations by Flaherty and Kennett (unpublished) indicate that prey other than spider mites—tarsonemids, eriophyids, and tydeids—may be very important in sustaining *M. occidentalis* during periods when spider mites are not available.

Biological notes on *Metaseiulus occidentalis* (Nesbitt)

Waters (1955), Sharma (1966), Laing (1968), and Lee and Davis (1968) studied the biology of *Metaseiulus occidentalis* under laboratory conditions. Any aspects of the biology in which the investigators differ can be attributed to the conditions under which the experiments were employed. For example, Waters (1955), working with linted oranges as a habitat, observed that the larval stage of the predator attacks and feeds on all stages of the six-spotted mite, *Eotetranychus sexmaculatus* (Riley). The senior author of the present work has also observed the larvae to feed on all stages of Pacific mite and Willamette mite on grape leaves. However, Laing (1968) reported that the larvae do not feed on any stage of two-spotted mite in Munger cells. Laing also reported that cannibalism may be an important survival mechanism during periods of low prey densities. The writers of the present report have not noted much cannibalism in the field.

Kennett (unpublished data) showed that field-collected females overwintering under grapevine bud scales, in some cases, did not lay eggs for a period up to two months after being brought into the laboratory. These overwintering predators, however, were noted to do some feeding. Kennett's data also indicated that the time interval before egg laying occurred was shorter if the females were collected late in the winter, or after a long cold period. Also, Hoy and Flaherty (1970) induced diapause in *M. occidentalis* with short photoperiods. These investigations are continuing.

Chant (1959) reports that *M. occidentalis* was collected from many parts of Canada and the United States, most commonly in the West.

Schuster and Pritchard (1963) report the predator in California on *Acer negundo, Aesculus californica, Convolvulus, Cynodon, Dactylon, Fragaria, Gossypium, Juglans, Magnolia, Malus, Phaseolus, Prunus domestica, Quercus, Salix, Sambucus, Umbellularia,* and *Vitis.* J. A. McMurtry (personal communication) collected it on citrus. The senior author collected it on *Rubus.*

Schuster and Pritchard (1963) report the following prey species associated with *M. occidentalis: Eotetranychus willamettei, Eriophyes vitis, Panonychus ulmi, Steneotarsonemus pallidus, Tetranychus pacificus,* and *T. urticae.* J. A. McMurtry (personal communication) has collected it in association with *Panonychus citri.* The senior author has observed it feeding on a tydeid species on grape.

METASEIULUS OCCIDENTALIS (NESBITT) AS A PREDATOR OF SPIDER MITES ON GRAPES

The controversy and general background

Although laboratory studies by Waters (1955), Huffaker (1958), Huffaker *et al.* (1963), Laing (1968), and Laing and Huffaker (1969) have indicated that *M. occidentalis* possesses many attributes of an effective predator of spider mites, some laboratory and field workers do not encourage reliance on its action. For example, Kuchlein (1965, 1966, 1967) maintains, from consideration largely of laboratory results, that this species can serve as an effective regulator of prey only at low prey densities, if at all. He bases this assumption on its functional response to increase in prey density and to its own density, and a faulty consideration of a presumed "numerical" response. Chant (1961) also casts doubt on its efficacy for related reasons. Moreover, a number of field workers in California have considered that this predator is ineffective against spider mites on grapes and strawberries (Smith, 1939, 1950; Smith and Stafford, 1955; W. W. Allen, personal communication; and R. O. Schuster, personal communication).

Smith (1939) stated that at its best this predator leaves much to be desired, and chemical control is needed, even though the beneficial predator may be sacrificed. Smith and Stafford (1955) stated "... when yellow spots of dime size made by Pacific mite colonies appear on the upper surface of leaves, the time for treatment has arrived." However, the latter writers point out that inspection should be made of these colonies before making such a decision, for the predator may have already eliminated the pest.

Mr. Frederick Jensen and Mr. Curtis Lynn, viticulture farm advisors for Tulare and Fresno counties, respectively, in personal conversation, state that Smith and Stafford's recommendation, which was based on research conducted in the Lodi area, may not apply in the southern part of the San Joaquin Valley. Mr. Jensen and Mr. Lynn feel that grapevine injury does not occur at the injury level at which treatments are recommended by Smith and Stafford. In fact, the recent persistence of infestations associated with development of resistance in these mites to acaracides has led to the discovery that true injury is not readily associated with the low spider mite numbers that Smith and Stafford considered injurious. In addition, the resistance problem has also made acceptance of higher infestations necessary.

R. O. Schuster, acarologist at the University of California at Davis (personal communication), reports that he believes destruction of Willamette mite populations by *M. occidentalis* in the Lodi area occurs only at densities too high and at a time too late in the season to prevent unnecessary grapevine damage. Schuster also expresses the opinion that this predator apparently does not possess the ability to effectively regulate and control Willamette mite at low densities.

Frazier and Smith (1946) and Pritchard and Baker (1952) considered Willamette mite a serious pest of grapes. Smith and Stafford (1955) believed that *M. occidentalis* is a more effective predator of Pacific mite than of Willamette mite. They surmised that agility of the latter species allows more frequent escape from predation. This is a curious presumption, since *M. occidentalis* prefers spider mite eggs to nymphs or adults and since the greater part of a Willamette mite population is usually immobile. The reason that Willamette mite seems better able as a population to escape effective predation than Pacific mite must lie in some population attribute rather than individual agility, an aspect investigated by Flaherty and Huffaker (part II).

With respect to two-spotted mite (*Tetranychus urticae*) on strawberries, W. W. Allen, entomologist at the University of California at Berkeley (personal communication), expressed a view similar to that of Schuster regarding the dependency of *M. occidentalis* on high prey densities. Note that these objections result from conditions quite different form those under which the workers Kuchlein (1965, 1966, 1967) and Chant (1961) assumed the predator to be inadequate. Some field workers have found that *M. occidentalis* performs well at high prey densities (see Huffaker *et al.*, 1969), whereas the above laboratory workers presume it can do so only at low prey densities. Allen also believes that disruption of control by this predator is in part due to necessary chemical applications and cultural practices in strawberry production. Strawberries are a short-lived crop, and this predator is slow to become well distributed in the plantings.

Huffaker and Flaherty (1966) state that rates of increase and predator effectiveness are points often neglected or wrongly viewed in appraising natural enemies. Comparisons of simple reproductive capacities of pest and enemy species are inadequate for judging whether or not an enemy can control the pest. A host may have an inherent reproductive power many times that of the enemy, and yet the enemy may nullify a large part of that potential reproduction. Thus the enemy may have the multiplicative advantage. Laing and Huffaker (1969), using simple mathematical models, showed that this predator can, indeed, nullify much of the reproductive potential of the two-spotted mite. Huffaker and Flaherty (1966) believe that reproductive potential and limited prey consumption should be discounted as reasons for the supposed ineffectiveness of *M. occidentalis* in field strawberries and grapes in California. They stated, "It is not inadequate reproductive capacity or limited prey consumption per individual that may account for a less than adequate control by the predator, if in fact poor control is at all characteristic under undisturbed conditions, once the predator becomes well distributed."

"Well distributed" is a status of dispersion that seems to be a key feature regarding the effectiveness of *M. occidentalis* on grapes, as will be shown, for incipient and increasing prey populations have often been observed to be nearly annihilated by this predator. At other times, prey populations continued to increase or remain at high densities in the obvious absence of the predator. Flaherty and Huffaker (part II) emphasized distributional patterns in their investigations of the effectiveness of *M. occidentalis* on grapes. Using individual vines as study units instead of lumping sampling data from large numbers of vines, their studies indicated that spider mite regulation may depend more upon corresponding predator and prey distributional patterns than on predator or prey densities.

Methods of appraisal

Initially, investigation of the spider mite problem on grapes and the possible role of predation was approached in a broad general way; later studies along specific lines in both the laboratory and field were conducted as the need indicated. Attention has been given to vine-by-vine sampling; distributional patterns in the vineyards and on the vine (see Flaherty and Huffaker, part II); numerical response (and this automatically embracing functional response); the importance of alternate foods (see Flaherty, 1969); and the use of various experimental or check methods in the evaluation of predator action.

For the general studies, samples were taken from vineyards in various parts of the southern San Joaquin Valley in order to get a gross picture of the predator-prey associations and interactions under a wide variety of vineyard conditions. Hopefully, reasons for poor or disrupted action of enemies, if indicated, might be investigated.

Where possible, treated and untreated plots were compared, particularly in vineyards where pesticides, excepting sulfur, had not previously been used as a general practice. The use of carbaryl (Sevin), 1-naphthyl-N-methylcarbamate, proved invaluable in plots where spider mite densities were otherwise low. Spider mite populations may be physiologically stimulated by carbaryl (see van de Vrie *et al.*, in preparation). High numbers of mites can be induced by spraying grapevines with this material even where predators are not involved. On the other hand, *M. occidentalis* is almost annihilated after thorough spraying by this insecticide. Thus, spraying with carbaryl affords a technique whereby the actions of predators and prey at various levels can be observed. Biological check methods also were attempted to supplement the insecticidal check method (also see Flaherty, 1969, and Flaherty and Huffaker, part II).

Population counts were made with a stereoscopic dissecting microscope. Spider mite eggs were omitted in some counts to facilitate the gathering of data in the many vineyards sampled throughout the Valley during the first year, 1964. In 1965 through 1968, when sampling and counting were more limited, all stages of spider mites were counted and lumped. All stages, including eggs, of *M. occidentalis* were lumped together during the five-year period of sampling.

Populations are plotted as spider mites per leaf and *M. occidentalis* per leaf, the latter multiplied by ten to facilitate comparison. Counts were sometimes stopped for various reasons, such as difficulty in securing adequate data and inadvertent destruction of interacting species by chemical treatments applied by growers—whose decisions in this respect could not be controlled. In this manner, some plots in 1964 were ruined. From 1965 to 1968, however, better grower cooperation made possible the collection of data over the entire season. Only a few representative 1964 plots are illustrated and considered here. The data on number of leaves sampled and frequency are given later along with the specific studies.

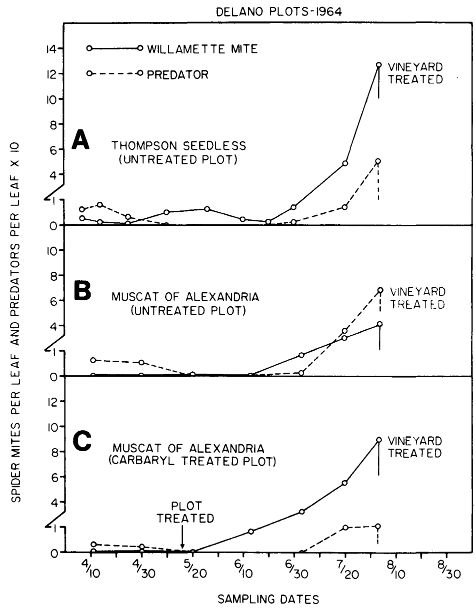

Fig. 2. Typical population trends in vineyards without recent histories of treatments. B and C plots were in same Muscat of Alexandria vineyard. Plot C vines were treated with carbaryl 50W at 2 pounds per 150 gallons of water per acre. When the grower treated the entire vineyard in August, the plots were lost. (Counts were made in 30-leaf samples; spider mite eggs were included.)

Results

Delano plots (carbaryl tests). Figure 2A represents population trends in a Thompson Seedless vineyard, while figures 2B and 2C represent separate trends in the same Muscat of Alexandria vineyard. Neither the Thompson Seedless nor the Muscat vineyard had been treated with pesticide for the previous three-year period. Both vineyards did have a Willamette mite problem before leafhopper treatments were ended in 1961. Although both the Thompson Seedless and Muscat vineyards were finally treated for leafhoppers in early August, 1964, thus disturbing the pest-predator relationships, the trends had progressed far enough into the season for purposes of study.

The population trends in figure 2 illustrate several important points: (1) The predator in both vineyards was active during the early spring, despite the very low prey densities. (2) Although the predator disappeared from the samples during the spring period of rapid vine growth and very low prey densities, seemingly it responded later to prey densities of less than ten mites per leaf. (3) No predators at all were taken in the carbaryl C plot until July 20; while in the untreated B plot, a few predators were taken on July 3. In the B plot, not enough prey were present for a substantial earlier predator response, whereas in the C plot the delay could not be blamed on lack of prey. Moreover, nothing is known about the seasonal biology of this predator that would account for the period of significant increases occurring together. The difference is considered as the effects of carbaryl. Thus, prey increase in the C plot in contrast to the B plot could have been due to an effect of carbaryl stimulation or inhibition of predator action. A *t*-test analysis showed a significant difference (5 per cent level) in number of prey per leaf between the untreated B plot and the treated C plot. The test was made on total prey counts from the date of plot treatment on May 15 to the time of vineyard treatment on August 5.

Arvin plot (typical pesticide history pattern). The population trends shown in figure 3 (see also fig. 4C) illustrate the predator-prey relationships commonly noted in vineyards which have had recent histories of pesticide usage. In these situations, spring predator activity is relatively poor, and a very long predator lag period is exhibited despite the presence of numerous prey.

Figure 3 also indicates that in such vineyards the predator appears to respond only to high prey densities, or responds more readily to Pacific mites than to Willamette mites. In undisturbed vineyards, however, it has already been noted (fig. 2) that the predator seemed to respond to very low prey densities, even to Willamette mites, which Smith and Stafford (1955) suggested were capable of avoiding preda-

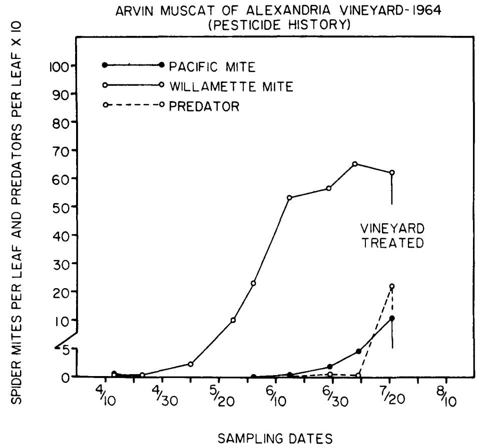

Fig. 3. When grower treated the entire vineyard in July, the plot was lost. (Counts were made in 30-leaf samples; spider mite eggs were not included.)

tion. As seen in figure 3, the response of the predator at the time of rapid Pacific mite increase is possibly no more than coincidental synchrony in recovery of the predator population to a point that it could respond at the time of Pacific-mite increase. Flaherty and Huffaker's studies (part II), however, indicated that the shorter lag period relative to predator response to Pacific mite increases, as contrasted to response to Willamette mite increases, may be due to the greater aggregation and webbing tendencies of Pacific mite.

Biola plots (carbaryl tests). Trends were also observed in mixed Willamette mite and Pacific mite populations in two adjacent Thompson Seedless vineyards, one (the George Miguel vineyard) with a history of pesticide application and the other (the Alex Yost vineyard) without. Both vineyards are located near Biola in west Fresno County. According to Mr. Miguel and other viticulturists in the Biola area, spider mites were not a problem in their vineyards before DDT and other synthetic pesticides were used.

Plate 1, photos G and H, although taken in late August, 1966, illustrate the contrasting spider mite problems in the two vineyards. Photos C and D (the same plate) show carbaryl-induced spider mite damage in the Yost vineyard in 1964. It is clear that differences in spider mite abundance between the two vineyards are closely related to use and non-use of pesticides. Mr. Miguel stated that he used numerous insecticides and acaracides, including carbaryl, over the years.

Figure 4 illustrates population trends on these plots. The absence of Pacific mites in the Yost A plot (untreated vines) until August forms part of the complex of evidence indicating the value of predation in spider mite control in vineyards.

Except for the absence of Pacific mites early in the season in the Yost B plot (treated vines), this population trend was similar to that in the regularly treated Miguel C plot. In the Yost B plot, however, the Pacific mite increase, although earlier than in the Yost A plot, was later than that in the Miguel C plot. The data could be interpreted to mean that the treatments in the Yost B plot were *solely* responsible for the increase; that is, physiological stimulation alone was the reason for the increase in the Yost B plot, and predators played no role in the regulation of the low spider mite densities which were exhibited in the Yost A plot or, for that matter, other untreated vineyards in the San Joaquin Valley. Chaboussou (1965) and Locher (1958) claimed positive evidence of chemically-induced physiological stimulation under the conditions of their studies. However, if stimulation alone was responsible for the increase of spider mites in the Yost B plot, it is difficult here to explain the even earlier increase of both Pacific mites and Willamette mites in the Miguel C plot, unless we assume that such stimulation was still present as a result of treatments in previous years.

The mere fact that predators were more active in the Yost plots than in the Miguel plot, and that predator

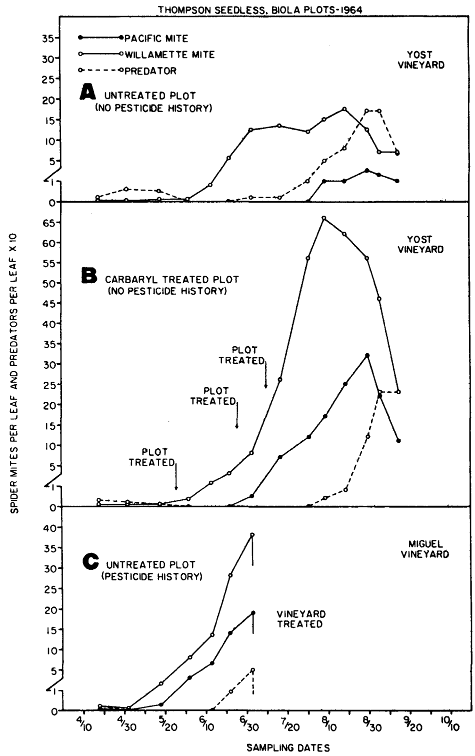

Fig. 4. B-plot vines treated with carbaryl 50W at 2 pounds per 150 gallons of water per acre, May 26, June 26, and July 10. The Miguel C plot was lost when the grower treated the entire vineyard. Spider mite and predator counts were made in 40-leaf samples; spider mite eggs were not included.

trends were delayed by carbaryl treatments in the Yost B plot (see also fig. 2C), suggest that current or past chemical control programs may reduce effective predator action. Moreover, the data from the Yost A plot indicate that *M. occidentalis* is capable of responding to very low prey densities. Thus, even if stimulation of spider mite fecundity is important in this case, it is not known if the predator population would have increased sufficiently to curtail much of the prey increase—if the chemical had not at the same time prevented effective predation. It is not to be construed here, however, that stimulation alone would not cause a significant increase in spider mite abundance under other conditions where poor predator-prey relationships are exhibited.

Finally, in the 1964 plot studies, it appeared that Pacific mites in the Yost A plot were not allowed to increase significantly, because the predator, already active on Willamette mites, had attained sufficient numbers and distribution to prevent it. That is, Willamette mite, in this case, acted as an alternate prey and thus increased the effectiveness of *M. occidentalis* on Pacific mites, which it appears to attack more readily. It is noteworthy that a predator lag period occurred with Pacific mites in the Yost B plot where carbaryl was used, but no lag period occurred with Pacific mites in the Yost A plot. In the latter plot, the predator responded to Willamette mite increase with a lag. However, this response occurred prior to a significant Pacific mite increase. Even though the predator inherently responds more readily to Pacific mite increases, it did not so respond in the carbaryl-treated B plot, despite high numbers of this species being present in July and still higher numbers of Willamette mites much earlier. Carbaryl had so nearly annihilated the predators that they required a long period of time to recover.

Miguel and Yost vineyards compared (1965 and 1966)

Population trends were followed in the Yost vineyard on vines with no pre-experimental history of pesticide treatments. They were treated with carbaryl in 1964 and again in 1965. Control vines were untreated (see fig. 5A and B). In the Miguel vineyard, population trends were followed on vines which were not treated for the first time in many years and on vines which were treated as usual by the grower (see fig. 6A and B).

Unlike the 1964 counts, spider mite eggs were included in the 1965 and 1966 counts. Also, samples in 1964 were taken strictly at random in both vineyards, but in 1965 and 1966, sampling was more selective. Because spider mites were scarce both years in the Yost vineyard, an attempt was made to choose leaves which showed some indication of spider mite activity. Thus, the densities indicated were considerably higher than the actual densities that occur during low-density periods. In the Miguel vineyard, leaves were chosen in relation to areas of the vines and to positions on the canes, because predator and prey dispersion data were also being collected (see Flaherty and Huffaker, part II). The densities in this case were not exaggerated as they were in the Yost data.

Figure 5B shows that the Yost vines, treated with carbaryl in 1964, had a small carryover in 1965 of Pacific mite (black circle in early April), unlike the untreated vines 5A. The Miguel vineyard in 1965 (fig. 6A) had its usual early spring Pacific mite carryover. This indicates that the previous year's imbalance in the Yost plot (fig. 5B) was carried over to some extent into the next season in a manner similar to that in the Miguel vineyard. Imbalance in the Yost B plot, consisting of only a single row treatment for one year, of course, is slight when compared to that in the Miguel vineyard plot, where the entire vineyard had been treated regularly for a number of years. Predators, moreover, in both Yost A and B plots in 1965 were active during the early spring, and all prey populations were reduced even further, with evidence of shriveled and sucked-out spider mites bodies. As in 1964, early spring predator-to-prey ratios in 1965 were obviously higher in the Yost vineyard than in the Miguel vineyard; this provides further evidence that lack of effective predation permitted the prey populations in the Miguel vineyard to persist at higher levels and to increase at a more rapid rate in the spring than did those in the Yost vineyard. The more effective, early-season predation

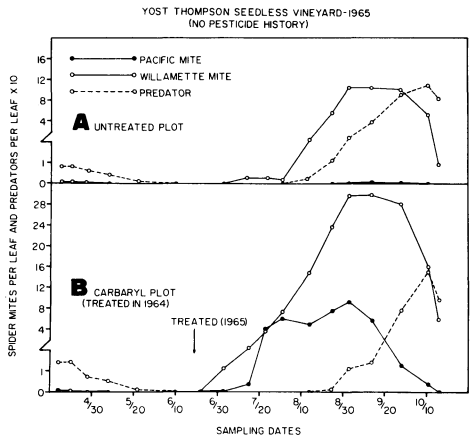

Fig. 5. Counts were made in 80-leaf samples; spider mite eggs were included.

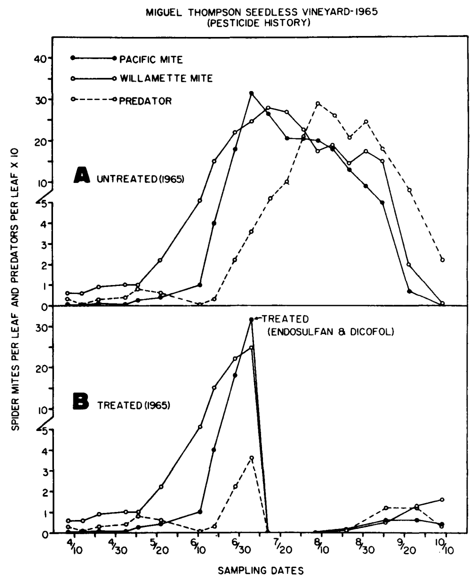

Fig. 6. Pre-treatment densities in B are assumed from A. Counts were made in 60-leaf samples; spider mite eggs were included.

in the Yost vineyard will be discussed later.

Again, as in 1964, vines treated in the 1965 Yost B plot showed an increase of both prey species and lagging predation. Carbaryl stimulation again might have been solely responsible for the greater abundance of spider mites in the B plot as contrasted to the A plot, but this hypothesis ignores the chemically-caused lag period in predation in the B plot and the undisturbed response of the predator to very low prey densities (less than four Willamette mites per leaf) in the A plot.

The 1965 A plot (fig. 5) again suggests that the predator actively preyed on Willamette mites before any significant increase of Pacific mites occurred. Figure 5B, on the other hand, indicates that Pacific mite was capable of taking advantage of any absence of effective predation at that time of the year. It is significant that the predator-Willamette mite interaction may serve to augment total predator activity on the more serious Pacific mite. If Willamette mite were not a factor in this activity, it is likely that Pacific mite populations would fluctuate more widely and cause more damage than they do, even in untreated vineyards. The absence of Willamette mite, in part at least, may be the reason why Pacific mite populations fluctuate so much more widely in untreated vineyards in the Monmouth area of west Fresno County than in these untreated Biola vineyards where Willamette mite is present. (See next section on Monmouth plots.)

Finally, the 1965 study (fig. 6) showed what can happen to populations as a result of pesticide treatments. The counts in the Miguel plot B were made after the grower treated the vineyard with endosulfan and dicofol. The data previous to the treatment (indicated by the arrow) are assumed equivalent to the data in plot A. Note that the untreated A-plot prey populations were disappearing because of intense predation simultaneously with a resurgence of prey and predators in the treated B plot. However, the resurgence of the predators as shown here (data lumped from leaf samples collected from a large number of vines) can be misleading; for Flaherty and Huffaker (part II), who studied population trends on individual vines in this plot, showed that

Plate I

Photo A. Right, yellowing of grape leaf due to Willamette mite injury; left, undamaged leaf.

Photo B. Thompson Seedless foliage severely burned by Pacific mites.

ERRATUM: photo B, plate I, was printed upside down.

Photo C. Willamette mite damage envelops Thompson Seedless vines. Vine's were treated with carbaryl.

Photo D. Severe Pacific mite damage of upper foliage on Thompson Seedless vines: Vines were treated with carbaryl.

Photo E. Thompson Seedless leaf shedding because of Pacific mite injury.

Photo F. Right, typical yellowing foliage caused by Willamette mite on untreated row; left, acaricide-treated, no mite damage. John Enns vineyard.

Photo G. Undamaged by mites; no history of treatment. Yost vineyard, 1966.

Photo H. Severe Pacific mite injury; long history of treatments. Miguel vineyard, 1966.

resurgence of predators did not occur on most of the vines after a dicofol treatment. Their studies form part of a complex of evidence that chemically-induced imbalance in vineyards is partly due to disruption of predator-prey distributional patterns, and not (as is often thought) just destruction of predators.

The 1966 population trends (figs. 7 and 8) in the Yost and Miguel vineyards are somewhat similar to the 1964 and 1965 trends (figs. 4, 5, and 6). Figure 7A in the Yost vineyard again showed better early-spring predator-to-prey ratios than the Miguel vineyard (fig. 8A). Spring prey populations in the Miguel vineyard persisted as usual, particularly the Pacific mite, while Yost prey populations apparently were further decimated from initially very low levels. Although the Miguel predator population trend (fig. 8) again indicates that *M. occidentalis* cannot respond to low prey densities, the predator trend (fig. 7) in the Yost vineyard continues to show that *M. occidentalis* can respond to low prey densities.

Since, however, a downward trend of the Willamette mite population (fig. 7A and B) occurred in the absence of meaningful predation, the ability of *M. occidentalis* to regulate Willamette mites, at least, is subject to question. That is, can Willamette mite densities support or limit *M. occidentalis* populations on grapevines, with the prey themselves not reciprocally regulated by the predators? R. O. Schuster (personal communication) suggests that this predator is found on grapevines only because Willamette mite is present as a food source. That is, the predator is dependent on the prey, but it does not control their numbers. His studies in the Lodi area indicated no significant differences in numbers of Willamette mites on grapevines, whether predators were present or absent.

However, the trends in figure 7 do not suggest that *M. occidentalis* lacks ability to respond numerically to very low prey densities, even if, in this case, belatedly. But Schuster and the other field workers cited previously subscribe to the view that this predator is inherently unable to respond to increases at low prey densities, and that it is, therefore, an inefficient predator, at least under the conditions of their studies.

Just because the predator did not respond to and control Willamette mites during any one seasonal period does not necessarily mean that it is incapable of regulating this prey species over the long run—or from season to season. This paper will show later that the action of this predator in one season has an important bearing on its action and control of the prey the following season. Thus, it seems likely that the lack of any early-summer predator response to increasing Willamette mites, as depicted in figure 7, was due to the low number of prey and their erratic distribution in the vineyard. For example, on July 9, 120 Willamette mites were counted in an 80-leaf sample, but only three of these leaves had prey; moreover, one of them had 116 prey. A similar prey distributional pattern was found in the B plot. Thus, predator response was expected to be poor or delayed with so few foci of prey. Later in the season the searching predator population apparently had greater chances for prey contacts. For example, on September 20, 14 of 80 leaves held prey in plot A, although the total number of spider mites was only 67. The possible importance of tydeid mites as supplemental prey will be discussed later.

The downward trend in figure 7 of Willamette mites in the absence of much predation seems to emphasize the role of other population-depressive factors. Smith (1950) also observed declining Willamette mite populations in the absence of predation. He attributed

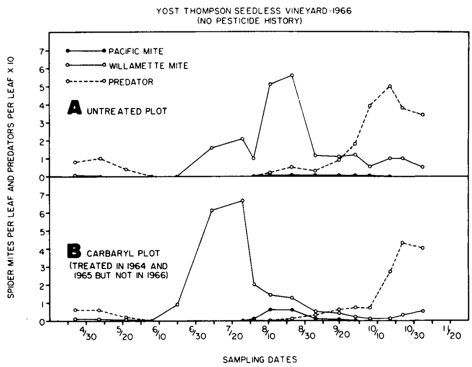

Fig. 7. Counts were made in 80-leaf samples; spider mite eggs were included.

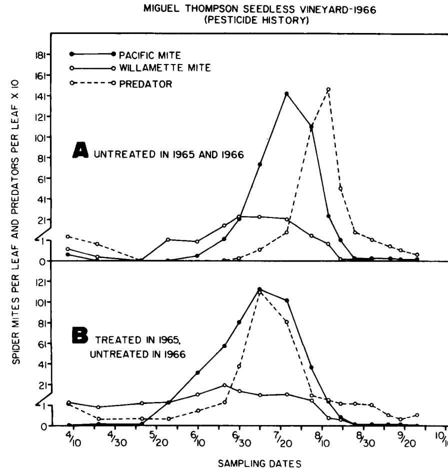

Fig. 8. Counts were made in 108-leaf samples; spider mite eggs were included.

these declines to sulfur programs. Whatever the reason, Willamette mite populations did decline or remain low in Biola vineyards in 1966. Yet, Pacific mites, which remained at even lower levels than Willamette mites in the untreated Yost vineyard, caused severe and widespread damage in treated vineyards in the Biola area in 1966 (plate I, photos G and H). Therefore, if *M. occidentalis* lacks the ability to maintain spider mites at low densities, then we must conclude that factors other than predation suppressed both species in the Yost vineyard, while suppressing only Willamette mite in adjacent treated vineyards. A more reasonable hypothesis is that *M. occidentalis* exerted a dynamic effect (not necessarily continuous for all seasons) in the control of spider mites in the Yost vineyard; and the use of pesticides disrupted, or made inefficient, this predator's action in adjacent vineyards. Moreover, population suppression by factors other than predation is not discounted by this hypothesis, for this paper (part I) and Flaherty and Huffaker's paper (part II) stress the importance of abiotic actions in the overall natural control of spider mites in vineyards.

The 1966 trends in the Yost vineyard again suggested the importance of a short lag period for Pacific mite. That is, the continued presence of Willamette mites helped to maintain active predation of the seasonally more restricted, but explosive, Pacific mites. Also, data from the 1966 plots further suggest that although the predators and prey in the Yost vineyard interacted late into the fall, vine injury and heavy predation caused early prey population crashes in the Miguel vineyard, thus causing predator populations to dwindle. Perhaps good spring predator activity depends upon late-season diapause development of this species. Table 5 presents predator and prey counts made during the spring in the two vineyards. The table shows that prey was less abundant, while predator activity was generally greater in the Yost vineyard than in the Miguel vineyard. A *t*-test analysis showed significant differences among predators per leaf, predator-to-prey ratios, and prey per leaf in the two vineyards during the early spring period. Perhaps the predators were more effective in the Yost vineyard, not only because they had less prey to handle in the early spring, but because the predators and prey coinhabited the limited plant parts. (See later studies in Peterson vineyard on predator distributional patterns during the early spring.)

TABLE 5
SUMMARY OF AVERAGE SPRING PREDATOR AND PREY INCIDENCE IN THE YOST AND MIGUEL VINEYARDS
(BIOLA, FRESNO COUNTY, 1964 TO 1966)

Date	Number mites		Number predators	
	Willamette	Pacific	Per leaf	Per prey
Miguel vineyard				
1964				
April 10	0.13	0.05	0.04	0.22
April 24	0.10	0.04	0.00	0.00
May 10	0.04	0.01	0.00	0.00
Average	0.09	0.03	0.01	0.07
1965				
April 16	0.61	0.01	0.01	0.02
April 28	1.10	0.04	0.04	0.04
May 8	1.28	0.05	0.05	0.04
Average	1.33	0.03	0.03	0.03
1966				
April 16	0.46	0.03	0.02	0.04
April 22	0.17	0.00	0.08	0.47
May 13	0.00	0.00	0.00	0.00
Average	0.22	0.01	0.03	0.17
Grand average (Miguel)	0.55*	0.02*	0.02*	0.09*
Yost vineyard				
1964				
April 10	0.10	0.00	0.03	0.30
April 24	0.01	0.00	0.01	1.00
May 10	0.10	0.00	0.10	1.00
Average	0.07	0.00	0.05	0.77
1965				
April 16	0.07	0.00	0.10	1.43
April 28	0.05	0.00	0.07	1.40
May 8	0.06	0.00	0.05	0.83
Average	0.06	0.00	0.07	1.56
1966				
April 16	0.04	0.00	0.04	1.00
April 22	0.03	0.00	0.12	4.00
May 13	0.00	0.00	0.08	—
Average	0.02	0.00	0.08	2.50
Grand average (Yost)	0.05	0.00	0.07	2.42

* Significantly different from incidence in the Yost vineyard at the .05 level.

Monmouth area population trends

Figure 9B shows predator-Pacific mite population trends in a vineyard with no pesticide history in the Monmouth area. Willamette mite is not found on grapevines in this area. When compared to trends in the Yost vineyard (figs. 4 and 5), the predator-Pacific mite trends shown in figure 9B are similar to those in the Yost carbaryl-treated plots (see figs. 4B and 5B). That is, unlike the Yost untreated vines (figs. 4A and 5A), where Willamette mite acted as an alternate prey and helped to maintain an active predator population without much Pacific mite lag, a predator-lag period was exhibited in the Monmouth vineyard in a manner similar to the carbaryl-treated Yost vines (figs. 4B and 5B). The chemically-induced lag period in predation was exhibited on the latter vines, despite an abundance of Willamette mites.

A number of vines were also damaged by Pacific mites in the Monmouth vineyard in contrast to the Yost vineyard, where populations of this mite are low. However, unlike the Miguel vineyard (which has had a long history of treatments), serious vine damage in the Monmouth vineyard (which had had no history of treatments) was restricted to a fairly small number of vines. In the Miguel vineyard serious vine damage is more general (see plate I, photo H).

Figure 9 clearly suggests why Pacific mite damage in the Monmouth vineyard was restricted. It shows population trends on undamaged vines (A) and on damaged vines (C). It is obvious that predator action was delayed on the latter vines, which were not numerous in this vineyard. Population trends for the vineyard in general were noted in counts during the April-to-August period. Then they were determined from the average of damaged and undamaged vines during the August-to-September period. The actual vineyard averages from August until September would have been lower than for the trends in the vineyard in general as shown in figure 9B.

Figure 10 shows population trends in a Monmouth area vineyard which has experienced a history of very heavy pesticide treatments, but with no treatment during the period of study (1966). Similar population trends also were observed in 1967. The absence of predation early in the spring and the high Pacific mite population at that

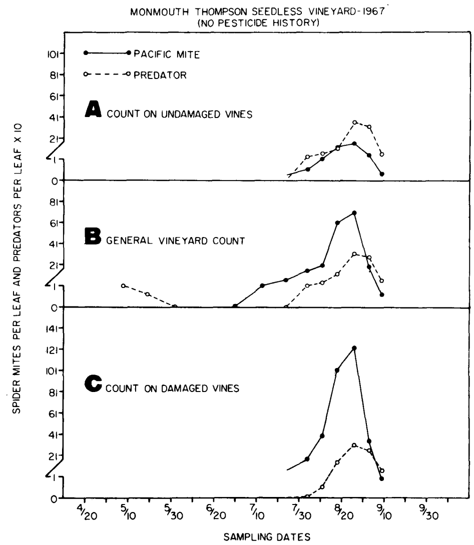

Fig. 9. Counts were made in 30-leaf samples; spider mite eggs were included.

time are noteworthy. Now, if a comparison can be made between population trends represented by figure 9B, and that represented by figure 10—both vineyards are in the Monmouth area but not adjacent—the importance of *M. occidentalis* is evident, even in an area where the environmental conditions are highly favorable for Pacific mite increases.

Predator-release studies

The importance of the late fall and early spring predator-prey interactions mentioned above was tested in the fall of 1966. Twenty-four vines in the Peterson vineyard near Poplar, Tulare County, were treated with carbaryl on July 27, August 16, and September 1, of 1966, in order to annihilate *M. occidentalis* and increase the abundance of Willamette mites. Predators were reared on soy bean plants infested with two-spotted mites for use in stocking the experimental vines. On October 9, the soy bean plants with predators were placed on each of 12 of the 24 vines. The numbers of predators placed on each vine could not be counted, but one

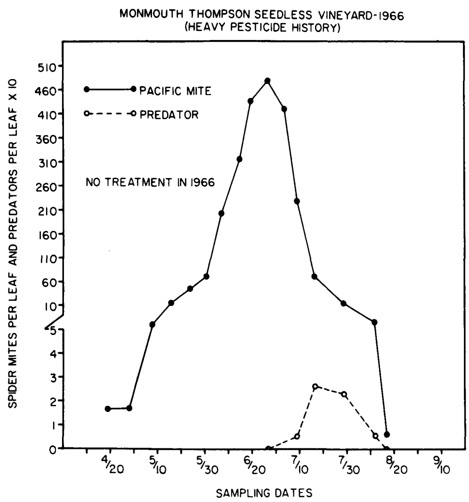

Fig. 10. Counts were made in 20-leaf samples; spider mite eggs were included.

week later there were about 60 predators per 30 grape leaves. Thus, two Willamette mite plots, contrasting in their fall populations of predators, were established—both of which had been treated with carbaryl. In the spring of 1967 when the consequent data were obtained, the only difference in the two plots was the presence or absence of the predators during the preceding fall. Any delayed stimulation of prey fecundity that might have resulted in the spring would have been equally inherent to both carbaryl-treated plots.

Figure 11 and table 6 show that the two Willamette mite populations were declining at the time of predator stocking. A slightly faster decline occurred where the predators were present; but how much was due to the predators is questionable, because little predator reproduction was taking place. The predator, however, was feeding and surviving on the prey late into the season. (Shriveled prey bodies were observed.) A fairly slow decline was taking place—not a drastic reduction. This was similar to the late-season Yost interaction. A large number of the predators survived the overwintering period.

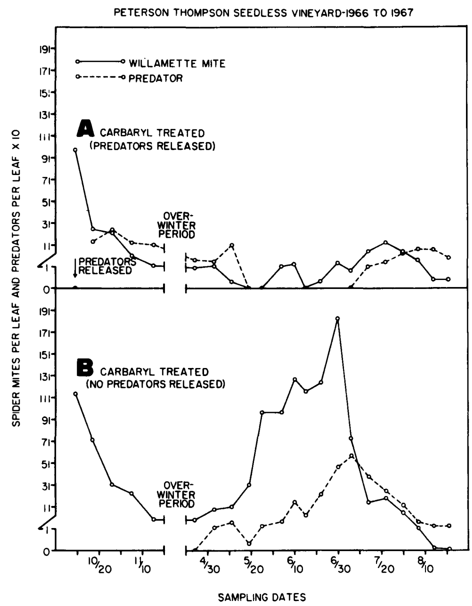

Fig. 11. Counts showing the importance of late fall and early spring predator-prey interactions. Predators in A and B vines eliminated by carbaryl treatments on July 27, August 16, and September 1, 1966. Predators resupplied to A vines on October 9, 1966. Overwinter period was from November 1966, to April, 1967. Counts were made in 30-leaf samples; spider mite eggs included.

In the predator release plot, *M. occidentalis* maintained efficient control of the prey population the following spring, while the Willamette mite population increased, largely uninhibited, in the plot where predators were not released, until a natural invasion and buildup of predators occurred. Predators then responded to the high prey populations and rapidly increased. The inadequate predator-to-prey ratios and the poor synchrony in predator and prey distributional patterns in this latter plot during the spring are worth noting (table 6). As pointed out previously, synchrony in predator and prey distributional patterns may, in part, be the reason why early-season predation in the Miguel vineyard was ineffective.

TABLE 6

COMPARISON OF LATE-FALL AND EARLY-SPRING INCIDENCE OF WILLAMETTE MITES AND PREDATORS ON VINES WHERE PREDATORS WERE VIRTUALLY ELIMINATED BY CARBARYL TREATMENTS WITH THE INCIDENCE ON VINES ALSO SO TREATED BUT TO WHICH PREDATORS WERE ADDED

(PETERSON VINEYARD, POPLAR, TULARE COUNTY, 1966 TO 1967)

Date of count	Predators not added					Predators added				
	Willamette mites on 30 leaves	Leaves (out of 30) with Willamette mites	Predators on 30 leaves	Leaves (out of 30) with predators	Predators to prey (ratio)	Willamette mites on 30 leaves	Leaves (out of 30) with Willamette mites	Predators on 30 leaves	Leaves (out of 30) with predators	Predators to prey (ratio)
	No.	*No.*	*No.*	*No.*		*No.*	*No.*	*No.*	*No.*	
1966:										
Oct. 9*.......	3,435	29	0	0	0.00	2,947	27	0	0	0.00
Oct. 17.......	2,160	21	0	0	0.00	779	21	41	12	0 05
Oct. 26.......	942	24	0	0	0.00	672	23	76	14	0.11
Nov. 5.......	682	30	0	0	0.00	145	17	40	19	0.27
Nov. 15.......	155	21	0	0	0.00	46	12	33	11	0.72
Overwintering period										
1967:										
April 24......	145	18	0	0	0.00	27	7	13	5	0.48
May 3........	293	21	4	1	0.01	38	7	11	7	0.29
May 11.......	321	17	11	3	0.03	10	3	33	10	3.30
May 19.......	922	21	1	1	0.00	1	1	0	0	0.00
May 25.......	2,921	25	7	2	0.00	0	0	0	0	0.00
June 4........	2,976	26	12	5	0.00	30	1	0	0	0.00
June 10.......	3,845	27	44	10	0.01	60	1	0	0	0.00
June 15.......	3,555	30	20	9	0.01	0	0	0	0	0.00
June 22.......	3,721	29	65	17	0.02	10	3	0	0	0.00
June 30.......	5,506	30	141	21	0.03	77	4	0	0	0.00
July 6........	2,204	30	171	27	0.08	24	4	0	0	0.00
July 14.......	440	20	115	23	0.26	243	9	3	1	0.01
July 21.......	557	21	76	19	0.14	380	13	7	4	0.02
July 30.......	240	18	33	17	0.14	246	14	22	11	0.08
Aug. 5........	40	7	13	8	0.32	94	11	27	13	0.30
Aug. 14.......	6	4	8	8	1.33	13	6	27	15	2.07
Aug. 21.......	2	1	7	6	3.50	13	5	16	10	1.23
Aug. 28.......	2	1	5	4	2.50	0	0	7	5	——

* Predators released on October 9, 1966.

Reestablishing predator effectiveness

The results in the Miguel vineyard represent the difficulty that may be experienced, in the Biola area at least, in attempting to reestablish predator effectiveness in disturbed vineyards. Data for 1966 (fig. 8) show the effects of cessation of organic pesticide treatments in the Miguel vineyard. Plot A had not been treated since July, 1964, while plot B was treated as usual in 1965. Through 1966, no shift occurred towards the balanced condition that apparently existed in the Yost vineyard. In 1966, plot A (untreated in 1965) fared worse than plot B, which was treated in 1965. In 1967, poor predator-prey relationships were still the rule on vines untreated since 1964, and considerable vine damage was again noted. Table 7 presents data collected in 1967 at approximately the time Pacific mites peaked in abundance in the Miguel vineyard. Contrasting data for the Yost vineyard are also presented. The poor predator-prey relationships in the Miguel vineyard are again noteworthy.

TABLE 7

DISTRIBUTION OF PEAK *METASEIULUS OCCIDENTALIS* AND SPIDER MITE POPULATIONS IN THE YOST VINEYARD (NO HISTORY OF PESTICIDE) COMPARED WITH THOSE IN THE MIGUEL VINEYARD (PESTICIDE HISTORY—LAST TREATED JULY, 1964). DATA COLLECTED ON AUGUST 19, 1970

Item—number of:	Miguel vineyard (treatment history)	Yost vineyard (no treatment history)
Willamette mites on 40 leaves	9,846	1,500
Leaves (out of 40) with Willamette mites	40	27
Pacific mites on 40 leaves	3,668	10
Leaves (out of 40) with Pacific mites	35	5
M. occidentalis on 40 leaves	67	29
Leaves (out of 40) with *M. occidentalis*	10	8
M. occidentalis to prey (ratio)	0.005	0.020

As in 1965 and 1966, population crashes were observed during the summer of 1967 in the Miguel vineyard, while predator-prey activity continued late into the season in the Yost vineyard. The late-season predator-prey activity in the Yost vineyard must have improved chances for good numbers of predators to hibernate; for in December, 1967, nine predators were found overwintering under the scales of 30 buds in this vineyard, while only one predator was found overwintering under the scales of 30 buds in the Miguel vineyard. Predator-prey relationships were again poor in the Miguel vineyard the following spring (1968); on April 8, a leaf count in the Yost vineyard showed a predator-to-prey ratio of 2.5, with only Willamette mite as prey. In the Miguel vineyard the ratio was 0.1, with Pacific mite as the dominant prey species.

In 1968, however, restoration of balance in the Miguel vineyard appeared to be forthcoming in 1969. Figure 12 illustrates how imbalance might be corrected: First, very effective predation took place during July of 1968, the month when Pacific mites in this vineyard usually inflicted heavy vine damage. (The damaging population may extend late into August.) Figures 6 and 8, and table 7, show that lagging predator populations enabled damaging Pacific mite populations to persist on the vines for extended periods in 1965, 1966, and 1967. Therefore, since predation was effective and vines showed little injury in 1968, one would suspect that fewer Pacific mites would enter diapause and escape to the bark for hibernation than the number that entered diapause and hibernated the previous three years. During 1965, 1966, and 1967, effective predation occurred only after considerable vine injury. Flaherty and Hoy (unpublished data) consider vine injury caused by Pacific mites an important factor for inducing diapause in this species.

Second, although late-season predator activity had not occurred in the previous three years in the Miguel vineyard, it did occur in 1968—as it had year after year in the Yost vineyard. Moreover, in December, 1968, approximately the same number of cane buds with predators were observed in the two vineyards—a condition not encountered before.

Why predators were active late into the season in the Miguel vineyard in 1968, and not in the previous three years, is not clear. Late-season predator activity in the Yost vineyard seemed to depend upon the presence of Willamette mites, although small numbers of other prey may have served as supplemental food. On the other hand, in the Miguel vineyard where prey populations crashed each year, the absence of

Willamette mites seemingly precluded much late-season predator activity, and 1968 was no exception (see fig. 12). Late-season predator activity in the Miguel vineyard in 1968, therefore, must have been supported by tydeid mites, upon which they are known to feed. Possibly, tydeids were unimportant in 1965, 1966, and 1967, for not until 1968, was this prey species believed numerous enough to affect late-season activity appreciably. An occasional abundance of tydeids may be an important factor in the maintenance of balance over the long run. However, much study is needed in what appears to be a subtle, predator-prey relationship.

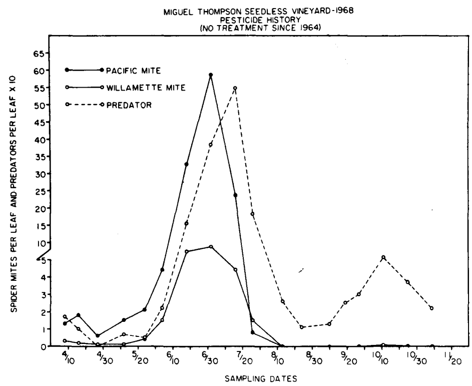

Fig. 12. Counts were made in 120-leaf samples; spider mite eggs were included.

The combination of Pacific mite injury that is slight and late-season predator activity in 1968 may be the necessary ingredients for the long overdue correction of imbalance in the Miguel vineyard. However, until populations in this vineyard exhibit trends similar to those that occur in the Yost and other untreated vineyards in the Biola area, one cannot assume the reestablishment of balance—assuming that Yost population trends (figs. 4, 5, and 7) are models for natural conditions in the Biola area. Further studies on the correction of imbalance in the Miguel vineyard are underway.

EFFICACY OF *METASEIULUS OCCIDENTALIS*

Data for 1965 and 1966 in the Miguel and Yost vineyards (figs. 5, 6, 7, and 8) indicate why late-fall predator activity contributes to effective spring predation. In both years, the spider mite populations in the Miguel vineyard crashed to very low levels by the end of September. Heavy predation, reduced fecundity and diapause induction because of vine injury, and the normal seasonal decline probably all contributed to sharp population crashes. Those prey that escaped predation went into hibernation, and the survivors served as the spring carryover population.

The 1966 Miguel plot results (fig. 8) clearly illustrate such a drastic population crash. Note that the Willamette mites declined even earlier than the Pacific mites and did not recover as they did in the Yost vineyard (fig. 7). Therefore, for all practical purposes, in the Miguel vineyard, spider mites on which predators could feed were scarce from the beginning of September through the late fall. Early spring counts in 1967 were similar to those from 1964 to 1966 (table 5); that is, there were fewer predators, and more prey occurred in the Miguel samples than in the Yost samples—although greater numbers of predators were present in the Miguel vineyard the previous summer (1966).

In 1965 (fig. 6) the predator-prey interactions in the Miguel vineyard continued longer into the season than in 1966 (fig. 8). But again, the predator population seemed short-circuited by an early prey decline.

(Contrast the predator-prey interaction in the Miguel vineyard as shown in fig. 6 with that which occurred in the adjacent, balanced Yost situation as shown in fig. 5.)

In contrast to the severe predator-prey interactions which occurred in the

Miguel vineyard, a more moderate or efficient predator-prey relationship occurred in the Yost vineyard. The moderate interaction in the Yost vineyard thus allowed an extended fall-season predator activity, and this, in turn, produced a well sychronized predator action in the following spring.

Extremely rapid growth of grapevines during the early spring may have further disrupted the already ineffective action of the few predators which overwintered in the Miguel vineyard. During the early-spring period, exceptional opportunity for prey to escape from the few predators on a given vine may have been provided by the rapid elongation of vine shoots and the great expansion of vine and leaf surfaces. The data in table 5 indicate that prey and predators may have actually declined in density (per leaf, but not per vine) during this period of rapid vine growth. Later, the number of prey per leaf, as well as the number per vine, increased, as subsequently did the predators—but with some lag.

It should be clear that although the number of spider mites per leaf on rapidly growing vines was decreasing, their absolute numbers may well have been increasing. The problem of effective predator contact was therefore increased. An unfavorable lagging response occurred; for the greater part of the numerical response resulted from high-density pockets of prey populations, rather than through an effective, wide-ranging type of searching on the part of the predator.

Vine injury by Pacific mites and over-exploitation by the predators may not fully account for the late-season inactivity of Willamette mite in the Miguel vineyard. The late-fall activity of Willamette mites in the Yost vineyard as contrasted to that in the Miguel vineyard may have been due to the different nutrition afforded by the vines for mites in the two vineyards. The effect of vine nutrition on predator-prey relations needs to be investigated. The effects of high Pacific mite populations on Willamette activity also need study.

From these considerations, we might now say that effective predation in the Yost vineyard depended on the subtle interactions of many mechanisms—all in rather precarious balance. Density-independent actions disproportionately favorable to the prey or unfavorable to the predator would explain occasional, sharp, prey population increases. The use of pesticides, for instance, would tend to promote greater fluctuation by disrupting a normal readjustment. Density-dependent actions—vine injury by Pacific mites and over-exploitation of prey by predators—may perpetuate disruptions of predator-prey interactions for some years. For example, localized leaf injury would tend to force dispersion of the prey over a wider area and continually away from the foci of most effective predation, with lagging readjustment on the part of the predator. If the injury were severe enough, increased numbers of spider mites would go into hibernation early and escape predation. The predator population would also destroy itself by annihilating the prey on the foliage too early in the season. Hypothetically, a disruption of the predator-Willamette mite interaction by use of pesticides in the Yost vineyard could lead to a less effective control of Pacific mites. The latter species would then be allowed to increase to abundance, and the severe density-dependent repercussions thus described might produce a condition like that in the Miguel vineyard.

The data presented so far are offered to support the hypothesis that the high degree of natural control of spider mites exhibited in the Yost vineyard year after year was due to density-dependent action, in this case by the predator, *M. occidentalis.* Since the prey populations remained too low for the vine injury itself to serve as the density-dependent mechanism of natural regulation, the only alternative is to consider density-independent forces.

If we consider the latter possibility, then the abiotic forces must constitute the principal restraints against population increase. However, such density-independent forces are considered incapable of *regulating* densities on a long-term basis, since they are not geared to density (Nicholson, 1933; Smith, 1935; Solomon, 1957; Huffaker and Messenger, 1964). But since the use of carbaryl was associated with a severe population increase in the Yost vineyard, such a pesticide must in some way relax, or alter, the regulating action of such abiotic forces, or the population would not increase. This hypothesis assumes that these abiotic forces provide the high degree of control in this vineyard in the absence of the pesticide. It is not supposed here that the pesticide is capable of altering abiotic forces such as the meteorologic or edaphic features of the vineyard; thus, the pesticide would have to act in such a manner that the spider mites are stimulated to increase through its direct action on the mites or through induced changes in the plant affording nutrition to the mites. But stimulation would seem to be largely ruled out in the case at hand, for it is not to be expected that such an effect would persist and be so serious four years after the use of the chemicals. Heavy applications of carbaryl, a chemical suspected of having stimulatory effects (Chaboussou, 1965) did not produce results suggesting a lasting effect from test plots in the Yost vineyard (see figs. 4, 5, and 7).

We are talking now about a *carryover* in the stimulating potential of the pesticide itself on the spider mites that appear later—not an effect from the resulting larger carryover population into the next season, as may be caused by the *immediate* stimulating effect. If abiotic actions were solely responsible for the regulation at low densities in the first place, then these high populations that were prompted by use of pesticides would later subside and remain low in subsequent seasons. In the Miguel vineyard, 1965 through 1968, they did not; this is consistent with the view that such abiotic factors did not act as density-dependent forces, but as forces independent of density. Hence the data are contradictory to the hypothesis: that such forces alone may be responsible for Pacific mite regulation at the low densities observed over long periods in the Yost vineyard.

Considering the predator hypothesis, it may seem difficult to comprehend that long-term action of the predator, *M. occidentalis,* can control spider mites at low densities. Yet, its response to, and destruction of, low-density, incipient outbreaks of Willamette mites and Pacific mites are evident (figs. 4, 5, 7, 9, and 11). Also, considerable laboratory evidence (Waters, 1955; Huffaker, 1958; Huffaker *et al.,* 1963; Laing, 1968) has been gathered to attest to the ability of *M. occidentalis* to regulate spider mites at low densities in a density-dependent manner.

ARE PESTICIDES NECESSARY TO CONTROL SPIDER MITES?

Lynn *et al.* (1965) and Flaherty *et al.* (1966) recommended that application of chemicals for the control of grape leafhopper be made only when populations reach economic levels. Chemical treatments for this pest often aggravate spider mite problems. But more often than not, grape leafhopper control has been conditioned by the philosophy of precautionary chemical treatment without regard to injury levels. In fact, for some time, such information and tools as described in the following paragraphs have been available to curtail or greatly reduce chemical programs to control the grape leafhopper.

Mr. Curtis Lynn, Fresno County viticulture farm advisor, recently recommended that the number of leafhoppers per leaf in the second (July) brood be raised from five to 10 nymphs per leaf, if the egg parasite *Anagrus epos* Girault is active in the vineyard (personal communication). His recommendation for Thompson Seedless raisin and wine grapes was based on yield data obtained under different densities of grape leafhopper.

With table grapes, unlike raisin and wine grapes, appearance and quality, as well as yield, are at stake if table fruit is heavily spotted from leafhopper droppings. However, growers interested in the philosophy of integrated pest control for table fruit have now begun to realize that preventive chemical programs are often unnecessary. For instance, it has been shown that under commercial conditions, Thompson Seedless vines for table production often can be left untreated for grape leafhoppers for the entire season without any loss of fruit quality.

Varietal differences may affect leafhopper preferences—an aspect of vineyard pest control not previously considered, but observed in the field by Mr. Frederick Jensen, Tulare County viticulture farm advisor, and the senior author of this paper. Late-variety, table-grape vineyards, such as Ribier and Emperor, often swarm with leafhoppers during mid-season, while adjacent Thompson Seedless vineyards carry only low, non-spotting populations.

Jensen *et al.* (1965) outlined a field technique for sampling so that low leafhopper populations will not be treated unnecessarily. Jensen and Flaherty (unpublished data) have gathered information which indicates that the amount of leafhopper spotting may be predictable before the Thompson Seedless table grape harvest, so that it may be possible to tell whether or not a given population will lower fruit quality. Treatments can thus be made on the basis of this prediction.

Finally, Doutt and Nakata (1965) emphasized the importance of blackberry (*Rubus* sp.) plantings as refuges for the leafhopper egg parasite. They stressed the importance of this parasite's early-season activity for effective control.

As for spider mites, experienced viticulturists in the San Joaquin Valley have generally acknowledged that they increased to abundance with the use of modern organic pesticides. Flaherty *et al.* (1966) considered the misuse of such pesticides for the control of grape leafhopper as the contributing factor. Also, too little information is available on the possibility of curtailing acaracide treatments—for many of these organic acaracides are just as disruptive to natural control mechanisms as are organic insecticides.

The southern San Joaquin Valley yield studies described in the following section may help answer the question of whether or not pesticides are necessary to control spider mites.

Biola yield studies (1964)

This study was conducted in the Alex Yost vineyard at Biola, Fresno County, with the cooperation of Mr. Curtis Lynn, farm viticulture advisor of that county. The vineyard had no pesticide history. Tests in randomized block conditions were as follows:

Six-vine row replicates each treated for:	Spray treatment	Rate of application/ 150 gal./acre
Leafhopper	Carbaryl 50W	2 lb.
Spider mite	Tedion 4F	1 qt.
Leafhopper }	Tedion 25W }	2 lb.
Spider mite }	Endosulfan 50W }	4 lb.

TABLE 8

SPIDER MITE DAMAGE COMPARED ON UNTREATED AND CARBARYL-TREATED VINES IN THE YOST VINEYARD (FRESNO COUNTY, 1964)

Treatment	No. vines damaged by spider mites*		Avg. vine injury index†
	Severely	Moderately	
Carbaryl	69	117	0.47
Control (untreated)	2	37	0.08

* 540 treated and 540 untreated vines scored.
† Vine injury index: 1 = moderate; 2 = severe.

Six vine rows—one replicate in each block—were left untreated (for control purposes). Each vine row consisted of 90 vines. Sprays were applied May 25, June 26, and July 10, with 3 pounds wettable sulfur per 150 gallons treatment in May and June. Leafhoppers were controlled to eliminate their possible effect on yield, and the like. Carbaryl was used for "leafhopper (alone)" to increase spider mites.

Three hundred berries were randomly taken from each replicate and weighed to determine average weight per berry. After crushing, a hydromater was used to determine total solids. Yield was measured by weighing the harvested raisins. Spider mites and predator counts were made on those replicates where the acaracide (tedion) was not applied. Each vine was rated as follows for spider mite injury at harvest time: 2 = severe damage; 1 = moderate damage; and O = light damage. Vines taking on a yellowish tint might be maturing or lightly damaged by mites. An index rating was given only if there was no question of mite injury.

Figure 4A and B illustrate the population trends on the check and on carbaryl-treated vines. Table 8 presents the vine-injury index. Plate I, photos C and D, show the actual vine damage by mites on a carbaryl-treated row. "C" shows Willamette mite injury, and "D" shows Pacific mite injury. Such vines would have been indexed 1 and 2, respectively. The vine-injury index data illustrate the significant relationship between carbaryl use and spider mite abundance; 69 of these treated vines were severely damaged, while only two of the check vines suffered severe spider mite injury.

Analysis of variance of the test data summarized in table 9 showed no significant differences in average berry weight, Balling degree, or yield among the four treatments. The average yield for the untreated vines was 6 per cent greater than for the vines treated with carbaryl. (Jensen and Flaherty, unpublished data, showed in their field studies of leafhopper economic levels that carbaryl may significantly reduce yields.) On the other hand, and most important, no significant reduction in yields, berry sizes, and total solids occurred because of Willamette or Pacific spider mites on either the heavily infested, carbaryl-treated, or moderately infested, control vines. Also, studies the following year (1965) showed no significant reduction in yield, berry size, or total solids from the previous year's (1964) spider mite damage.

Although Pacific mites obviously injured the foliage on the carbaryl-treated vines, this damage did not occur until late in the season. Berry weight and Balling degree remained the same, indicating that populations were active, for the most part, after the fruit was well developed. However, it will be shown later that Pacific mite does reduce berry weight and balling degree,

TABLE 9
SUMMARY EFFECTS OF SPIDER MITES ON THOMPSON SEEDLESS GRAPES AND RAISINS IN THE YOST VINEYARD
(BIOLA, FRESNO COUNTY, 1964)

Treatment	Peak spider mite densities*		Grapes†		Raisins†
	Pacific mites per leaf	Willamette mites per leaf	Mean berry wt.	Specific gravity	Mean raisin yield/90 vines
	No.	*No.*	*gm*	*° Balling*	*lb.*
Check	5	18	1.90	18.93	825
Tedion	none	none	1.91	18.83	834
Carbaryl	35	68	1.97	19.12	780
Tedion plus Thiodan	none	none	1.99	18.71	815

* Spider mite eggs not included in these counts.
† Analysis of variance (.05 level) showed no significant effects of spider mites or treatments on grapes or raisins.

when foliage injury occurs before the berries are mature.

Shafter vineyard yield studies (1964)

This study was conducted in the John Enns vineyard, Shafter, Kern County, with the cooperation of Mr. Donald Luvisi, viticulture farm advisor for Kern County. The Enns vineyard had a history of treatments. Test conditions were as follows:

Four-vine row replicates each treated for:	Spray treatment	Rate of application/ 120 gal./acre
Spider mites	Tedion 4F	1 qt.
Leafhoppers	Carbaryl 80W	5 lb.*
Spider mites Leafhoppers	Carbaryl 80W Tedion 4F	5 lb.* 1 qt.

* High rates of carbaryl used due to a mixing error.

The Enns plot was similar to the Yost plot except that the design was completely randomized rather than randomized in a block design. There were four replicates, with 91 vines per row; four rows were untreated. Only carbaryl was used to control leafhoppers. Carbaryl was applied May 24, and tedion was applied May 24 and July 20. Methods of obtaining the yield data were similar to those used in the previous test.

Table 10 presents a summation of the harvest data, and figure 13 illustrates the population trends. Mites were almost nonexistent on treated vines. Plate I, photo F, shows the Willamette mite injury on a check row as compared to an adjacent tedion-treated row. The uninjured vines treated with the acaracide are evident. No injury estimates were made. Pacific mite was absent, and foliage was not burned, although Willamette mite was abundant. Injury between individual vines did not vary greatly. Heavy "yellowing" injury by Willamette mites was widespread in both the check and carbaryl-treated plots. Figure 13 shows that population differences between check and carbaryl-treated vines were slight. Spider mite eggs were not included in these counts.

The harvest data were similar to those of the Yost trial. Again, Willamette mite injury did not significantly reduce production. Berry weight and total solids also did not differ. However, significant differences in yield did occur when

TABLE 10

SUMMARY EFFECTS OF WILLAMETTE SPIDER MITES ON THOMPSON SEEDLESS GRAPES AND RAISINS IN THE JOHN ENNS VINEYARD (SHAFTER, KERN COUNTY, 1964)

Treatment	Densities* per leaf	Grapes†		Raisins‡
		Mean berry weight	Specific gravity	Mean raisin yield/vine
	No.	*gm*	° *Balling*	*lb.*
Check	92	2.08	19.4	9.93
Tedion	none	2.11	19.6	10.31
Carbaryl	95	2.15	20.1	9.01
Tedion plus carbaryl	none	2.10	20.5	8.98

* Spider mite eggs not included in counts.
† Analysis of variance (.05 level) showed no significant effects of spider mites or treatments on grapes.
‡ Analysis of variance (.05 level) showed the raisin yields were significantly affected by carbaryl but not by tedion or spider mites.

vines treated for leafhoppers alone and vines treated for both leafhoppers and spider mites were compared with untreated vines. In the Yost and Enns vineyards, vines treated with carbaryl showed the lowest mean yield, but the Enns test showed a statistical difference (5 per cent level). Thus, in two widely different areas of the southern San Joaquin Valley, it was shown that Willamette mite is an innocuous pest and that chemical treatments may reduce yield.

Further studies and comments on Pacific mite injury

The Biola test showed that Pacific mites probably did not significantly reduce yield, because the full impact of the population came after the crop had largely matured. If, however, this same population had peaked in abundance earlier, the crop would have suffered. Table 11 shows that this species can materially reduce yield and quality in a short period of time. The population on the burned vines began to increase rapidly about the first of August, and within 10 days it defoliated approximately 50 per cent of the top foliage. By August 15, very few spider mites were left on the leaves, probably because of severe vine injury and active predation by six-spotted thrips. Although the grapes from the burned vines made acceptable raisins, a loss in quantity and quality was reflected by reduced berry weight, Balling degree, and raisin quality (B+ grade constituting 65 per cent in the unburned vines and only 34 per cent in the burned vines). If the population had peaked

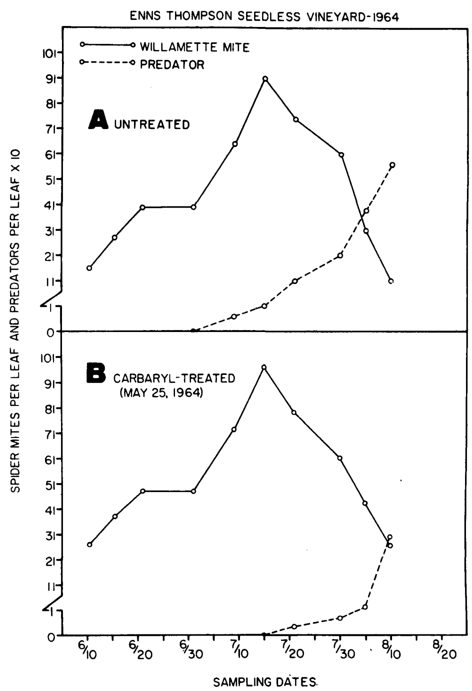

Fig. 13. Counts were made in 80-leaf samples; spider mite eggs were not included.

TABLE 11

EFFECTS OF PACIFIC MITES ON THOMPSON SEEDLESS GRAPE BERRIES AND RAISINS IN THE BARR VINEYARD (DINUBA, TULARE COUNTY, 1966)

Factor	From vines	
	With Pacific mite damage	Undamaged
Berries: *		
Balling degree	19.5	21.5
Av. wt./berry (grams)	1.96	2.02
Raisins (grade): †		
B+ (per cent)	34	65
C (per cent)	56	30
C− (per cent)	10	5

* Three hundred berries were sampled.
† Raisin samples were run through the California Raisin Advisory Board Air Stream Sorter. B+ = above average heavy); C = minimal requirement; C− = not acceptable (too light). Sorter measures raisin meatiness, which correlates with berry size and sugar content.

even earlier, it is likely that little crop would have been acceptable. Longer exposure to the sun on defoliated vines would have resulted in many bunches drying on the vines.

Control of Pacific mites combined with attempts to restore vineyard balance poses some special problems. For the most part, Pacific mite problems are pesticide-induced, but is some cases, imbalance is not readily corrected by merely curtailing the use of chemicals. For instance, Pacific mite was still a serious pest in the Miguel vineyard four years after chemical treatment was terminated. Tolerating even low numbers of Pacific mites can be precarious, due to this species' enormous biotic potential and its ability to quickly inflict severe vine injury. Control difficulties may also arise quickly, because resistance and spray coverage problems are exaggerated when Pacific mite densities are high.

Thus, once imbalance is in effect, treatments may be necessary for Pacific mite populations that are well below economic injury levels. Yet, if imbalance is to be corrected, treatments of low densities may preclude the reestablishment and redistribution of natural enemies. Therefore, in order to avoid the hazards of prey explosions or treatments which may perpetuate imbalance, the problem of preventing Pacific mite injury and correcting imbalance must be attacked in a broad general fashion; this does not, however, preclude the use of chemicals.

Recent field studies by Flaherty and Lynn (unpublished data) suggest that a number of techniques which themselves do not interfere with natural enemies may be used to reduce Pacific mite population explosions. For example, in contrast to clean, cultivated vineyard plots—the normal practice in many vineyards—Sudangrass vineyard plots required fewer treatments for Pacific mites. The need for fewer treatments in grass plots may be related to less dust on vine foliage, better soil-water penetration, and generally higher vineyard humidities. More irrigations may be necessary when grass culture is practiced during the summer.

Flaherty and Lynn (unpublished data) showed that sprinkler irrigation may be used as a method of restoring balance. Pacific mite populations are kept below economic levels when sprinklers are used, while predator populations are undisturbed. Although sprinkler systems, portable or permanent, are costly, the benefits derived should more than offset the original investment. For instance, these initial studies indicate that grape quality and production are improved with the use of sprinkler systems in contrast to furrow irrigation practices. Moreover, sprinkler systems effectively reduce spring frost, summer heat, and powdery mildew problems. Of course, the elimination of costly acaracide treatments helps to pay for the original sprinkler investment.

Flaherty and Lynn (unpublished data) also showed that the selective acaracides, e.g., TEPP (tetraethylpyrophosphate), may be used as a tool for restoring balance. *Metaseiuslus occidentalis* is tolerant to TEPP, while Pacific mites in their active stages are fairly susceptible. Timely applications of this material were used to check damaging Pacific mite increases, while the predator was slowly regaining control in the vineyard.

Finally, Flaherty and Lynn have observed that cultural practices which improve vine vigor tend to inhibit Pacific mite outbreaks. Sometimes, vine-water stress seemed to account for such outbreaks. Winter and spring covercrops have been noted to improve soil-water penetration and lessen Pacific mite outbreaks. Several covercrops—Sudangrass, subclovers, and rye grasses—are presently being tested. The judicious use of fertilizers, new pruning techniques, and nematode control, all aimed at improving vine vigor, need investigating.

Some educational experiences concerning Willamette injury in table grape vineyards

Although Willamette mites have little effect on raisin and wine quality, they may reduce table grape quality. Reduced foliage growth exposes bunches to direct sunlight. The berries on these bunches are discolored. Even light populations may cause a yellowish tint (premature maturity) in Thompson Seedless berries, when the market calls for a light green berry. Grapes on vines with dense foliage would suffer less than those on lightly foliated vines, if both had equivalent Willamette mite populations.

In 1965 the senior author and Mr. Frederik Jensen, Tulare County viticulture advisor, in cooperation with the owner of Elmco vineyards (5,000 acres of fancy table grapes) initiated efforts to show growers that treatments for Willamette mites on table grapes are often unnecessary. Previously, Willamette mites were considered serious pests by Elmco personnel and low populations were treated, usually in a preventive control program.

The first steps in our program were to acquaint the five Elmco foremen, each of whom was in charge of about 1,000 acres of table grapes, with the differences between Pacific mites and Willamette mites, their damage potentials, and their population habits on vines. Flaherty *et al.* (1966) control techniques were suggested. Most of the effort was aimed at reassuring the foremen that populations were, in fact, Willamette mite, and not Pacific mite, and vine damage would be comparatively minor. When vine injury reached levels where any further increase might have a deleterious effect on fruit quality, judgment of whether or not to treat was based on spider mite and predator counts. Such counts had to be made only in a few cases.

Only one vineyard population of spider mites in this program was treated in 1965, and that treatment was directed against Pacific mites. In 1966, no vineyards had to be treated, although Willamette mites were abundant in many of them. According to all concerned, no loss in quality was experienced. During both years, considerable apprehension was shared among foremen, owner, and ourselves. We were gratified in the end, to learn that Willamette mite is not, indeed, the pest it was believed formerly to be on table grapes.

TABLE 12

PREDATOR AND PREY POPULATION COUNTS ON TABLE GRAPE VINES AT A STAGE OF WILLAMETTE MITE DAMAGE WHEN FRUIT QUALITY COULD BE AFFECTED, IN THE EDWARD MERZOIAN VINEYARDS (POPLAR, TULARE COUNTY, 1966)

Vineyard	Leaves sampled	Date of count	Willamette mites*	*M. occidentalis*
	No.		*No.*	*No.*
Emperor	30	Aug. 2	18	45
Thompson Seedless	20	July 22	8,499	328
		Aug. 5	21	72

* Spider mite eggs included in these counts.

Table 12 presents the pest and predator status in two vineyards at a time when the foremen were apprehensive because of vine damage and were willing to apply treatments. In the Emperor vineyard, a count showed only a few spider mites. In fact, there were more predators than prey on August 2. A count on July 22 in the Thompson Seedless vineyard showed good predator-prey relationships. Because of these counts, no treatments were given, and fruit quality in neither vineyard suffered.

What actually worried the foremen was the yellowing of the foliage by Willamette mites. In the Emperor vineyard, the population had already been annihilated by predators and any treatment would have been wasted, even if damage was economic. Treating vine damage instead of spider mite populations is a common error in vineyard pest control. Predator and prey counts in the Thompson Seedless vineyard revealed that annihilation would occur shortly, and no treatment was necessary.

Willamette mites should not be considered so innocuous that treatment should simply be discontinued. Control, however, depends on many complex factors. In the vineyards described here, mite control was contingent on the grape leafhopper chemical control program. The latter was carefully coordinated with the activity of the leafhopper egg parasite (*Anagrus epos*). Chemicals that do no aggravate spider mite problems were selected, e g., endosulfan was used instead of carbaryl. Once these measures were taken and pesticide disturbances in the Elmco vineyards were reduced, nondamaging populations of Willamette mite could be tolerated.

SUMMARY

The spider mites, *Tetranychus pacificus* McGregor and *Eotetranychus willamettei* Ewing have increased to abundance in grape vineyards since World War II. Viticulturists have observed this increase to be correlated with the use of organic insecticides. In at least some cases, chemicals appeared to cause an imbalance of spider mite populations with their natural enemies, particularly *Metaseiulus occidentalis* (Nesbitt), by differentially killing predators and prey; by conferring advantage to the prey through reproductive stimulation; or by a combination of the two.

These studies in the southern San Joaquin Valley showed that, in general, the distributional patterns of Willamette mites and Pacific mites differ in the Valley, in the vineyard, and on the vine itself. Pacific mite prefers hot, dry conditions and foliage exposed to direct

sunlight; it congregates noticeably on shoots growing upward from the tops of vines. Apparently for this latter reason, they are more attractive to predators than the dispersed Willamette mites (which prefer cool, humid conditions).

Both species are conspicuously limited in eastern Tulare and Fresno counties—the Willamette mite, less so—probably due to soil conditions. Pacific mite, in particular, appears quite responsive to soil changes. Outbreaks of this species are often noted to occur year after year in the same vineyard spots; vine vigor or soil-water penetration in these spots is often poor.

Vineyards with no history of pesticide treatment often had better early-season predation by *Metaseiulus occidentalis* than vineyards treated in the past. Predation was more efficient in the untreated vineyards, although larger numbers of prey occurred in the treated vineyards. Also, contrary to claims that *M. occidentalis* needs an abundance of prey to be effective, data showed active predation at very low densities. The present study also discounts a more recent hypothesis that this predator is only effective, if at all, at low densities because of its self-limiting aspects.

When regulating low Pacific mite densities under undisturbed conditions, the predator appears to benefit from the fairly innocuous, but often abundant, Willamette mite. When Pacific mite (an explosive and serious pest that is often more seasonally restricted than Willamette mite) begins to increase significantly during hot summer days, the lag in predator response is usually short. Sufficient numbers and effective distribution of predators have been maintained by the ever-present, but low, numbers of Willamette mites. Without these attributes, the Pacific mite population can "escape" to inflict quick and serious damage to vines. Thus, these studies support the view that a complex community, including alternate prey, offers the possibility to stabilize spider mite populations at economically tolerable levels.

Mild summer and fall predator-prey interactions are conducive to late-season activity of the predator. This, in turn, can lead to effective early-spring predator action. On the other hand, when predator and prey populations crash during the summer or early fall (because of vine injury or over-exploitation of prey), late-season predator activity is reduced. The mild, predator-prey interaction desired was consistently exhibited in untreated vineyards, in contrast to the violent interaction that occurred in vineyards with long histories of pesticide treatment. Therefore, either violent, density-independent actions (pesticide treatment) or violent, density-dependent actions (Pacific mite vine injury and overexploitation of the prey by the predator) may lead to or help perpetuate imbalance.

Large commercial vineyard areas in the southern San Joaquin Valley, including fancy table grape acreage, are commonly and needlessly treated for Willamette mite. Yield and fruit quality data showed that this species is not often a significant pest. Little differentiation has been made in the past between Pacific mites and Willamette mites, and treatments have been applied without discrimination as if both were serious pests.

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II. Influence of Dispersion Patterns of *Metaseiulus occidentalis*

This study revealed that prey population attributes, not individual attributes, dictate the efficiency with which *Metaseiulus occidentalis* (Nesbitt) (Acarina: Phytoseiidae) responds to and controls populations of given spider mite species *(Eotetranychus willamettei* Ewing and *Tetranychus pacificus* McGregor) on grapevines.

The study also showed that under vineyard conditions, *M. occidentalis* has the ability to respond numerically to low or high prey densities. Using individual vines as study units, the length of the lag in predator response to low or high prey densities was shown to be mainly a function of absence or poor distribution of the predator relative to its prey.

Individual vine studies may delineate not only the importance of predation (delayed density-dependent action) but the importance of abiotic factors (density-independent actions), as well. Lumping of sampling data from large groups of vines precludes the appraisal and separation of these two equally important facets of natural control.

Finally, the studies indicate that chemical treatments may disrupt predator and prey distributional patterns, either directly by annihilating the predators or indirectly by annihilating their prey, or a combination of the two.

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