HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 30 JUNE, 1960 NUMBER 2

TEMPERATURE AND HUMIDITY RELATIONSHIPS OF TETRANYCHUS DESERTORUM BANKS WITH SPECIAL REFERENCE TO DISTRIBUTION

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The desert spider mite, *Tetranychus desertorum* Banks, has been reported as an important agricultural pest in Paraguay and the cotton belt of the southern United States. In California, however, it is found occasionally on weeds and becomes a pest of cultivated crops only rarely and in isolated localities. Experimental studies to ascertain the reason for these differences in economic severity were undertaken for the purpose of applying ecological principles to the theoretical question of why a pest is severe in one place and not in another as well as obtaining specific biological data for this species.

Differences in climate, host plants, natural enemies, cultural practices, and intrinsic physiologies of the mite populations were considered as possible explanations for the differences in economic severity in the various parts of the distribution of this species. Of these, climatic differences appeared to be the most marked. It was noted that this spider mite is an important pest only in areas in which normal spring and summer rainfall exceeds one inch per month.

The hypothesis attributing lack of economic severity of *T. desertorum* in central California to the aridity of this region was supported by laboratory studies demonstrating a higher rate of reproduction and a faster rate of development at high, as compared to low, relative humidity. This view was further supported by laboratory data showing *Tetranychus telarius* Linnaeus, an important spider mite pest in central California, to have a lower rate of reproduction and a slower rate of development at high, as compared to low, relative humidity.

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TEMPERATURE AND HUMIDITY RELATIONSHIPS OF *TETRANYCHUS DESERTORUM* BANKS WITH SPECIAL REFERENCE TO DISTRIBUTION[1]

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INTRODUCTION

THE DESERT SPIDER mite, *Tetranychus desertorum* Banks, was first described from weed hosts in New Mexico (Banks, 1900).[3] It has since come to be recognized as one of the major species of mite pests over most of the cotton belt of the southern United States. Also, in Paraguay, Nickel (1958) observed that this species of mite was a widespread and serious pest on a number of crops. In California, however, this same species exists on weed hosts in isolated localities, moving onto cultivated crops in injurious numbers only in rare instances and in restricted areas. In this same region, however, *Tetranychus telarius* (Linnaeus), *Tetranychus pacificus* McGregor, and *Tetranychus atlanticus* McGregor are important pests of cotton and other crops. These phenomena suggested an ecological study of *T. desertorum* in an attempt to determine what factors make it a serious pest in Paraguay and Texas but not in California. Such an investigation would indicate whether or not it presents a threat to California agriculture by focusing some light on the more basic question of what factors may limit the economic distribution of a pest.

Iglinsky and Rainwater (1954) described the life history and habits of *T. desertorum* in Texas, and Smith (1958) thoroughly studied the field ecology of this species on cotton in Georgia. A field study of spider mites on cotton in Texas by Hightower and Martin (1956) provided quantitative information on the distribution and abundance of *T. desertorum* on various host plants as well as observations regarding its dispersion.

Detailed presentations of the systematics of *T. desertorum* and its taxonomic relationship to other species have been given by Pritchard and Baker (1955), Iglinsky (1951), and Smith (1958); hence this aspect will not be covered in the present study.

The following investigation was undertaken to contribute additional in-

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

formation on the general biology of *T. desertorum* and, if possible, to find the most important causal factors determining its economic distribution. Necessary components of such an investigation include: (1) the compilation of data regarding the distribution, hosts, and natural enemies of *T. desertorum;* (2) the formulation, on the basis of this information, of a hypothesis to explain its economic severity or lack of it in the various regions; and (3) laboratory trials designed to test the hypothesis and supply basic biological information on the species.

FIELD OBERVATIONS

Distribution

When studying the distribution of an agricultural pest one must consider the fact that it may occur and be collected in regions in which it is not normally economically important. Such collections may represent local pockets of favorable conditions outside the generally favorable range, temporary distribution as a result of fortuitous dispersal outside the favorable range, or populations existing at a low level of subsistance under conditions of marginal favorability, erupting to economic levels only rarely when favorable conditions occur. Thus Cook (1929) differentiated between "systematic or absolute distribution" and "economic distribution." Such a division is employed below with the **total distribution** giving all places in which *T. desertorum* has been collected and the **economic distribution** considering levels of economic severity in various regions.

Total Distribution. In the United States, *T. desertorum* has been reported from California, Arizona, New Mexico, Texas, Oklahoma, Louisiana, Mississippi, Georgia, Florida, South Carolina, and North Carolina by Pritchard and Baker (1955), and from Alabama by Arant (1954). This species has also been collected in Mexico, Argentina, Peru (Pritchard and Baker, 1955), Paraguay (Nickel, 1958), and Australia (Dodd, 1940).

Figure 1 shows all states in the United States in which *T. desertorum* has been collected. It should be noted that this does not necessarily give the exact distribution of this mite, for entire states are shaded even though collections may have been made only in limited areas.

California records are:

Alameda County: Berkeley, VIII-26-58, *Erigeron canadensis* L. (J. L. Nickel, J. L. Nickel collection, Berkeley, California).

Colusa County: Williams, IX-6-58, *Erigeron canadensis* L. (J. L. Nickel, J. L. Nickel collection, Berkeley).

Contra Costa County: Antioch, VIII-9-52, grass (W. C. Bentinck, A. E. Pritchard collection, Berkeley).

Fresno County: Selma, VI-51, cotton (G. L. Smith, A. E. Pritchard collection, Berkeley).

Kern County: Bakersfield, VIII-11-49, legume, A. E. Pritchard, A. E. Pritchard collection, Berkeley), Shafter, VII-19-50, sunflower (G. L. Smith, A. E. Pritchard collection, Berkeley), Cawelo, 3 mi. W., *Erigeron canadensis* L., *Eremalche kernensis* C. B. Wolf, *Tribulus terrestris* L. (J. L. Nickel, J. L. Nickel collection, Berkeley).

Los Angeles County: Crystal Lake, VI-29-50, *Eriodictyon* sp. (J. W. MacSwain, A. E. Pritchard collection, Berkeley).

Orange County: Newport Beach, VIII-18-52, *Distichilis* sp. (R. E. Beer, A. E. Pritchard collection, Berkeley).

Stanislaus County: Patterson, VII-11-52, melons (A. E. Michelbacher, A. E. Pritchard collection, Berkeley).

Tulare County: Tipton, 2 mi. N., VII-16-51, cotton (T. F. Leigh, A. E. Pritchard collection, Berkeley), Traver, VII-13-58, *Erigeron canadensis* L.,

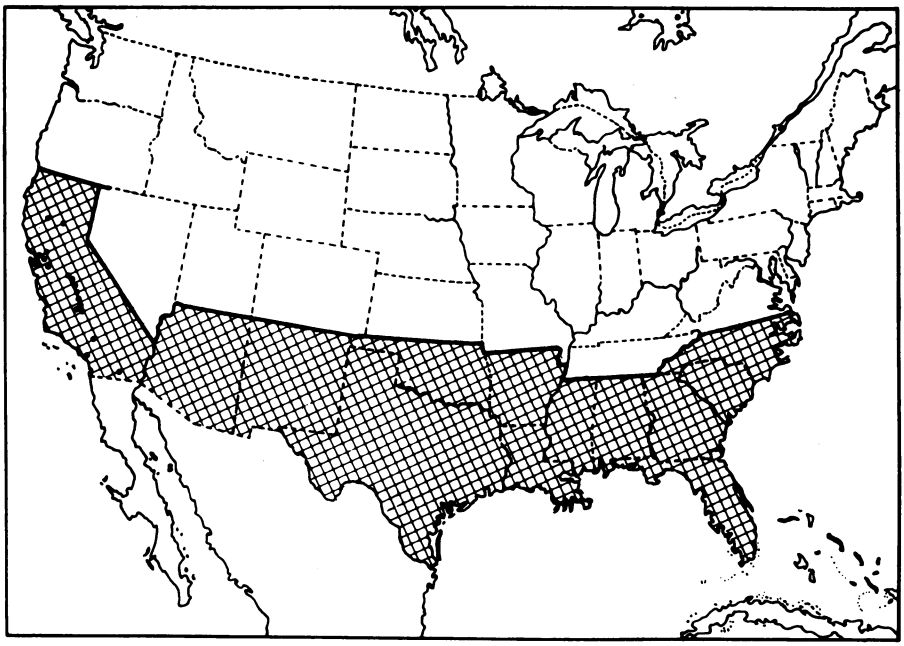

Fig. 1. Total distribution of *T. desertorum* in the United States. Crosshatched area represents states in which this species has been collected. California localities are indicated by dots.

Centromadia sp. (J. L. Nickel, J. L. Nickel collection, Berkeley). In addition to these records, *T. desertorum* has been reported as a pest of melons at Live Oak (Sutter County) and in the Imperial Valley by Michelbacher *et al.* (1954) and infesting weeds at Tipton, Delano, MacFarland, and Famoso, by T. F. Leigh (*in litt.*, August 25, 1958). The distribution in California is indicated by dots on the map in figure 1.

Economic Distribution. Comparison of relative economic severity in various areas presents a more difficult problem since records of spider mite infestations frequently do not give species, and detailed field studies have been reported from only Texas and Georgia. Outside these two states and Paraguay, and California, in which this study was made, the information has been assembled from correspondence with workers in other states, references to *T. desertorum* in control trial reports, and from field observations reported by various workers in the United States Department of Agriculture Coöp-

erative Economic Insect Report. Most of these reports are not quantitative and often refer to *T. desertorum* together with other species, but should give some indication of the states in which economic infestations have occurred.

A survey of the agricultural insects in the Chaco region of Paraguay (Nickel, 1958) showed *T. desertorum* to be the most important mite pest of this region. It was seen on many hosts throughout the year, becoming particularly severe as an agricultural pest in the spring and early summer months.

In California, *T. desertorum* has been observed infesting crops in very localized areas in occasional years. Michelbacher *et al.* (1954) reported it as a pest of melons near Live Oak and in the Imperial Valley. It appears that serious infestations occurred only during certain years and it is not considered a serious pest in these localities now. Gordon L. Smith, University of California entomologist at the Shafter Cotton Field Station for more than twenty years, indicated (in personal conversation, August, 1956) that he had observed *T. desertorum* in destructive numbers on cotton only rarely and in isolated and restricted localities. He also reported having seen this mite on weeds for several consecutive years in the same small area about 14 miles northwest of Bakersfield. When this area was visited in the summer of 1956, a moderate population was found on horseweed, *Erigeron canadensis* L. A cotton field nearby was not infested. Two attempts to initiate an infestation in a small, untreated cotton field by placing infested portions of horseweed on the cotton plants were unsuccessful. In the summer of 1957, the mite could not be found in this location. However, in the summer of 1958, after an unusually wet spring, a very heavy infestation (see figure 2)

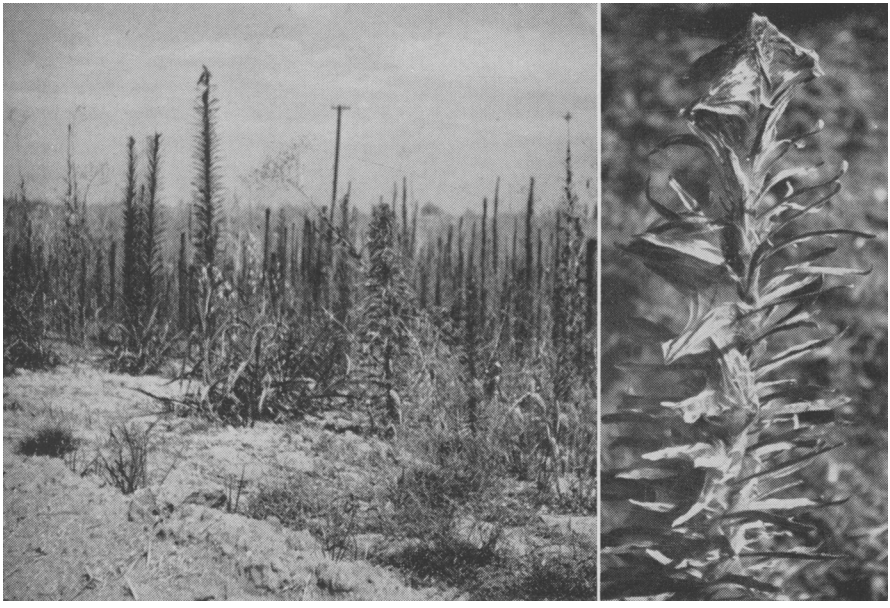

Fig. 2. Left, horseweed, *Erigeron canadensis* L., infested with *T. desertorum* in weedy spot 14 miles northwest of Bakersfield, California, July, 1958. Right, webbing produced by heavy *T. desertorum* infestation on horseweed.

was observed in July on horseweed at this same spot. A light infestation was seen in the margin of an adjacent castor bean field but this did not reach economic proportions during the remainder of the growing season. Horseweed about a mile away from this spot was free of *T. desertorum* and no infestation was found in a cotton field within a half mile of this heavy weed infestation. At this same time, dense but very localized populations on weed hosts were observed at a number of localities between Bakersfield and Fresno. No crop infestations were reported, however. During the years in which the above observations were made, *T. telarius,* and, to a lesser extent, *T. atlanticus* and *T. pacificus* were serious pests throughout this area.

D. M. Tuttle (*in litt.,* September 16, 1958) reported that *T. desertorum* has occurred in Arizona as a pest but is probably not so prevalent as *T. telarius.* He also indicated that *T. desertorum* has been more abundant around Phoenix than Yuma and that in any particular year either species might be most abundant.

Spotty infestations were reported in the cotton-growing areas of New Mexico for 1956 and 1957 by Durkin (1957, 1958).

There are many reports of *T. desertorum* on cotton in Texas. Iglinsky (1951) made a field survey of cotton in the 1948 and 1949 growing seasons at many localities in eastern and central Texas and found *T. desertorum* to be the only species of spider mite attacking cotton. He reported that collections by U. S. Department of Agriculture entomologists in the lower Rio Grande Valley and at El Paso during this same period were also all *T. desertorum.* Gaines, King, and Fuller (1952) reported it to be the species of mite most prevalent in the area around College Station, Texas. Hightower and Martin (1956), in field studies of mites on cotton in central Texas, found *T. desertorum* to be predominant in spring and early summer whereas *T. telarius* became predominant in August and September. They considered *T. desertorum* to be the most important mite on cotton in this area. Martin (personal conversation, May, 1958) stated that *T. desertorum* used to be the only important mite on cotton in southern Texas, but that *T. telarius* has increased in importance recently and is now the most serious mite pest because it is more difficult to control.

According to T. F. Leigh (personal conversation, July, 1958) *T. desertorum* infestations have been spotty in Arkansas and limited mainly to the southern portion of the state.

H. B. Boudreaux (*in litt.,* April 16, 1958) reported having seen *T. desertorum* throughout Louisiana and in isolated localities in Arkansas. Oliver (1955, 1956) reported infestations on strawberries in Tangipahoa Parish, Louisiana.

In Mississippi, Harned (1952*a*) reported *T. desertorum* infesting cotton and pigweed in July and August.

Robertson and Arant (1956) indicated that *T. desertorum* is the principal species of spider mite on cotton in Alabama. They reported that *T. desertorum* and *T. atlanticus* were present in abundance in 1954 and that *T. telarius* was also present but caused little, if any, damage.

Smith (1958), in a thorough field study of *T. desertorum* in Georgia, found 80.6 per cent of all mites on cotton in 1955 to be this species. He reported

T. desertorum present in 96.5 per cent and *T. telarius* in 26.3 per cent of the counties in Georgia, and found that usually only one species was involved in any infestation.

In the Carolinas, Harned (1952*b*) and Fife and Walker (1954) reported *T. desertorum* and *T. telarius* from cotton in South Carolina while Harned (1952*b*) and Mistric (1955) indicated these two species present in considerable numbers in several counties in North Carolina.

The above information, though scattered and incomplete, indicates a general pattern for the United States in which *T. desertorum* appears to be a moderate to serious pest in New Mexico, Texas, southern Arkansas, Louisiana, Mississippi, Alabama, Georgia, South Carolina, and North Carolina, and, to a lesser extent, in central Arizona. Information from Florida is lacking. In California and western Arizona economic infestations are rare and isolated. Apparently the primary region of economic severity in the United States, that region in which the heaviest infestations most generally occur, is central Texas, probably extending eastward into Louisiana. Thus California and central Texas would appear to represent examples of fringe and primary regions of economic distribution, respectively.

Climate and Distribution. The distribution of *T. desertorum* would seem to indicate its limitation to the southern portion of the United States and similarly warm regions in other countries. *T. desertorum* has not been collected in the more northerly states and its economic distribution is limited mainly to the region south of the isotherm for a January mean temperature of 40°F (4.4°C) (Harbridge, 1941, p. 704). This is not surprising considering that *T. desertorum* is active in all stages throughout the winter, having no resistant or dormant stage, whereas in species of spider mites which are found in more northerly regions, as *T. telarius,* the adult females go into diapause under cold temperature conditions (Andres, 1957).

Within this warmer region, the economic distribution as described above appears to be limited to the area of significant spring and summer rainfall. The climographs in figure 3 contrast the climates of two areas in which *T. desertorum* is an economic pest (Blumental, Paraguay, and Waco, Texas) with that of an area of rare and spotty outbreaks (Bakersfield, California). In figure 4 the Bakersfield temperature and rainfall of the season in which *T. desertorum* was not found there (1956–57) are contrasted to that of the subsequent season (1957–58) in which is was very abundant in the same area on horseweed.

These climographs, particularly in figure 3, represent a high degree of integration, since they do not indicate the extremes or annual or daily fluctuations in temperature and rainfall. Humidity data are not available in many of the climatological summaries, hence rainfall is plotted against temperature and it is assumed that there is a correlation of higher humidity with greater rainfall. In spite of the limitations of climographs they do give a general picture of the seasonal march of temperature and moisture. In summary, long-term climographs do not clearly indicate the weather, but they do give an indication of certain important factors in the climate. It is recognized that, whereas weather influences local or seasonal abundance,

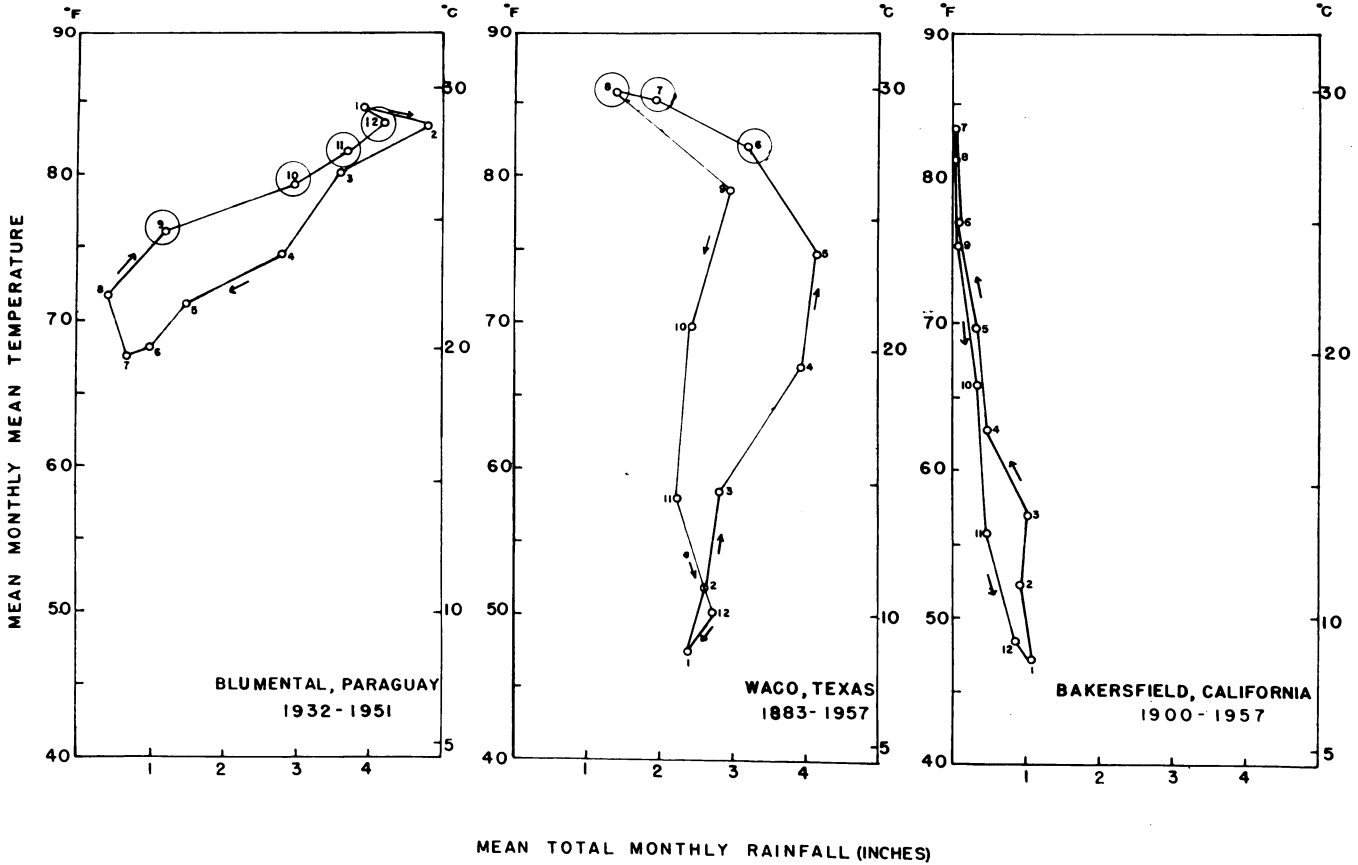

Fig. 3. Climographs of two areas (Paraguay and Texas) in which *T. desertorum* is an important crop pest and one (California) in which it is not. Numbers 1 to 12 indicate months of January to December. Circled numbers indicate months in which these mites were most severe on crop plants.

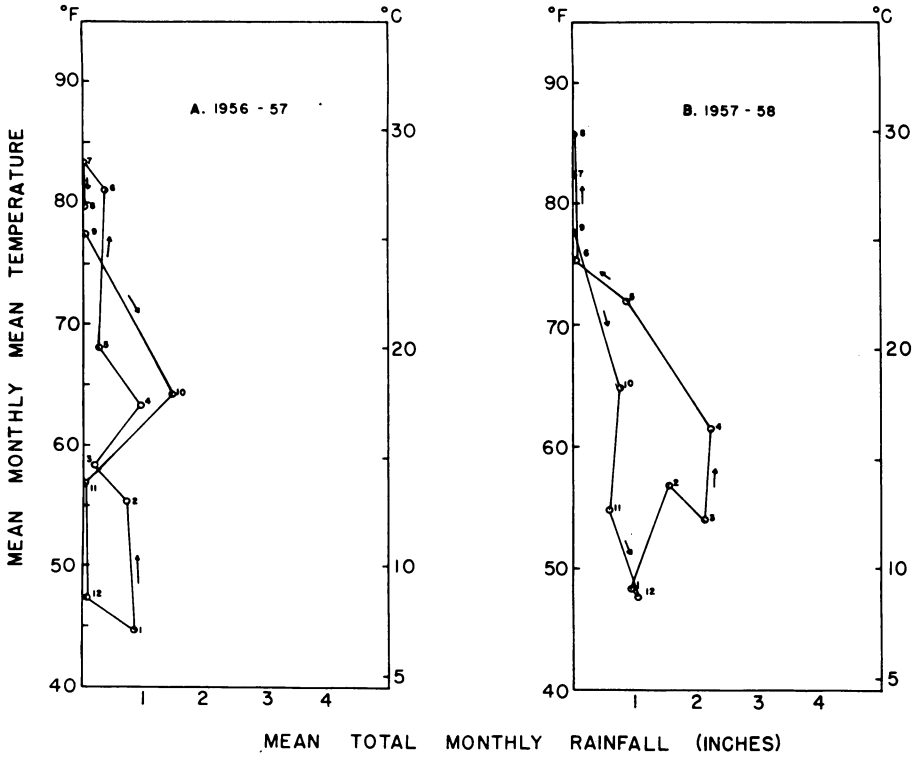

Fig. 4. Climographs for Bakersfield, California, for one season in which *T. desertorum* was not found on horseweed (1956–57) and one season in which it was abundant (1957–58). Numbers 1 to 12 indicate months of January to December.

climate may be the important factor in distribution. To the extent that this is true, climographs will prove useful in this consideration.

In the comparison of the long-term Texas and California climographs as shown in figure 3, there appears to be little difference between the two areas in the mean monthly temperatures throughout the year. Rainfall, however, especially in the summer, is much higher in Texas. Similarly, the Paraguay climograph indicates a moderately high summer rainfall. The circled numbers indicate that this species is of greatest importance in the late spring and early summer months (June through August in Texas; September through December in Paraguay). Figure 4 indicates that the abundance of *T. desertorum* on weeds in California is possibly correlated with above-normal spring rainfall. The very low summer rainfall normally experienced in this region was evident, even after the abnormally wet spring of 1958, but above-normal humidities prevailed throughout most of the summer.

Based on the economic distribution and the climograph comparisons given above, there appears to be a correlation between summer rainfall and economic severity of *T. desertorum*. Such a correlation, however, presents an

apparent paradox in the light of previous investigations. It is well established that *T. desertorum,* like most other species of spider mites, is most severe, in areas where it is a pest, during drought years (McGregor, 1950; Cassidy, 1952). The fact that this species is more abundant in areas with summer rainfall and yet within this range is most severe in drought years may be partially explained by the indications that, even in drought years, summer relative humidities in central Texas are higher than normal humidities in the Central Valley of California. Cassidy (1952) reported that spider mites caused severe damage in 1951 from the Atlantic to the Pacific in one

TABLE 1

COMPARISON OF NORMAL SUMMER HUMIDITIES IN BAKERSFIELD, CALIFORNIA, AND WACO, TEXAS, WITH SUMMER HUMIDITY AT WACO IN A YEAR WITH BELOW-NORMAL RAINFALL

Month	Mean noon relative humidity (per cent)*			
	Bakersfield, California		Waco, Texas	
	1957	Normal†	1951	Normal‡
June	25	27	57	55
July	27	26	44	51
August	27	29	37	47

* Bakersfield: 12:00; Waco: 12:30.
† 18-year means. Interpolation from 10:00 a.m. and 4:00 p.m. means.
‡ 11-year means.

of the driest summers on record. The relative humidities in Waco, Texas, for the early summer months of 1951 are compared with normal humidities for these months in this locality and in Bakersfield, California, in table 1. These data indicate that relative humidities were near normal in the drought year in Texas, and were consistently higher than normal for corresponding periods in California.

Further explanation for spider mite severity in drought periods is given by the well-known fact that spider mite infestations frequently begin and are most severe in the dusty margins of fields. Such dusty conditions would be more widespread in droughts. Also, Eaton and Ergle (1954) have demonstrated that higher hexose sugar concentrations are found in cotton leaves under drought conditions. This factor, with its possible effect on reproduction and development of mites, may also have an important bearing on mite abundance in drought years. Rain *per se,* however, mechanically reduces infestation and/or their spread. Thus it appears that in spite of the temporary adverse effects of rain or favorable effects of drought on mite populations, a consideration of long-term climate and the economic distribution of *T. desertorum* points to the conclusion that this species may be favored by and have been selected under the generally higher humidity conditions of the areas with summer rainfall.

Iglinsky (1951), on the other hand, reported that a temperature of 85°F and a relative humidity of 40 per cent were nearly optimum for *T. desertorum* and believed that this might explain why this species was of more

importance than other species of mites in the "arid Southwest." He further stated that limited observations indicated that different conditions may be optimum for other species of mites attacking cotton. He reported that *T. telarius* was more often of economic importance in the southern and southeastern states and believed that this was because it required higher humidity conditions. The information regarding economic distribution and climate reported above does not support Iglinsky's observations. *T. telarius* is the most important species of spider mite on cotton in the arid Central Valley of California, while *T. desertorum* is important in southern states having a considerable amount of summer rainfall. The optimum temperature and humiditiy for this species need to be determined by additional laboratory studies.

Host Plants

In Paraguay, *T. desertorum* was collected from alfalfa, barley, beans, grass (*Bromus* sp.), clover, corn, cotton, dill, eggplant, onion, muskmelon, papaya, watermelon, and several winter weed hosts, among which *Verbena tenuisecta* Briquet[4] was the most important.

Pritchard and Baker (1955) reported cultivated crops damaged by this pest to be melons, cantaloupe, cucumber, celery, carrot, turnip, and alfalfa. Other hosts reported by these workers were *Larrea tridentata* (DC.), *Stillingia* sp., *Opuntia* sp., *Mimulus guttatus* DC., *Tribulus terrestris* L., *Eriodictyon* sp., *Erigeron canadensis* L., *Helianthus* sp., grass, wild tomatoes (Peru), and gladiolus.

In the course of this study, it was observed that the dominant summer host in California was horseweed, *E. canadensis*. Other California hosts were *Eremalche kernensis* C. B. Wolf, *Trichostema lanceolatum* Benth., puncture vine (*Tribulus terrestris* L.), and *Centromadia* sp. These other plants, however, were always less severely infested than the horseweed near them. Robbins (1940) reported this weed to be a common native of the eastern states and indicated that it was probably introduced into California sometime prior to 1876. Overwintering populations of *T. desertorum* in California were found on mallow (*Malva parviflora* L.) and Australian saltbush (*Atriplex semibaccata* R. Br.). The latter appeared to be the more important winter host.

In Texas, Hightower and Martin (1956) found summer hosts included cotton, bloodweed (*Ambrosia aptera* (D.C.)), tievine (*Impomoea* sp.), and cocklebur (*Xanthium* sp.), and heavy populations on bur clover (*Medicago hispida* Gaertn.) in March and April. The most important winter hosts were evening primrose (*Oenothera* sp.), sow thistle (*Sonchus asper* (L.) Hill), and wild verbena (*Verbena bipinnatifida* Nutt.).

In Georgia, Smith (1958) reported geranium (*Geranium carolinianum* L.) and wild violets as major winter hosts.

Cotton is the major economic host throughout the cotton belt. In Louisiana, Oliver (1955) reported *T. desertorum* infesting strawberries.

A consideration of the host plants in these several regions indicates that *T. desertorum* can develop on a variety of hosts, most of which are relatively

[4] Identification by Harold N. Moldenke, Trailside Museum, Yonkers, N.Y.

low-growing plants. Its dominant summer host in Texas is cotton and, in California, horseweed, though both of these plants are present in each of these two localities.

Natural Enemies

In Paraguay, the predaceous mite, *Typhlodromus* (*Amblyseius*) *longispinosus* Evans (identified by D. A. Chant, Department of Agriculture, Science Service, Belleville, Ontario) was collected in association with *T. desertorum*. Laboratory feeding tests definitely demonstrated this species to be a predator of *T. desertorum*. Predaceous thrips identified as *Scholothrips* sp. (identified by Stanley F. Bailey, University of California, Davis) were likewise observed feeding on *T. desertorum* in Paraguay.

In California the predaceous mite, *Typhlodromus* (*T.*) *occidentalis* Nesbitt (identified by D. A. Chant), the predaceous thrips, *Scolothrips pallidus* (Beach) (identified by Stanley F. Bailey), and the anthocorid bug, *Orius tristicolor* (White), were collected in *T. desertorum* colonies in the field and demonstrated by laboratory feeding experiments to be predators of this species.

Iglinsky (1951) considered *Orius insidiosus* (Say) to be the most important predator of *T. desertorum* in Texas. Smith (1958) observed predation by the coccinellids *Hippodamia convergens* Guerin and *Ceratomegilla maculata* (DeGeer) and thrips but reported finding no predatory mites. Robertson and Arant (1956) reported the predaceous thrips *Scolothrips sexmaculatus* (Pergande) feeding on *T. desertorum* in Alabama, but considered it doubtful whether it was important in the decline of the mite population.

McGregor and McDonough (1917) reported 31 species of arthropod natural enemies of spider mites in the southeastern United States. Of these they considered *S. sexmaculatus, Typhlodromus* sp., itonidid midges, *Geocoris punctipes* Say, and *Orius insidiosus* to be the most important.

This consideration of the natural enemies of *T. desertorum* in the various regions indicates that about the same taxonomic groups of predators are represented in each locality.

Summary of Field Observations

In studying why a species is economically important in one portion of its geographic range and not in another many factors are involved. Most important among these might be: available host plants, parasitism, cultural practices, chemical control measures, competition, and climate. The existence of physiological differences between the mite populations is also a possibility.

Host plants and predation of *T. desertorum* in the several localities have been discussed above. Although these factors may be quite important in the seasonal history of this mite in these areas there is nothing to indicate that these factors differ between the localities involved in a manner that would greatly influence its economic distribution. Likewise, it is considered unlikely that differences in the cultural practices between the regions under consideration would be responsible for the differences in economic severity of this mite, though this aspect has not been thoroughly investigated in this study.

The observations that *T. desertorum* in California can attain very high population levels in localized weed patches without becoming important on adjacent crops would suggest the possibility that chemical-control practices for other pests in the California crops affect its abundance. This view is strengthened by the knowledge that *T. desertorum* is more easily controlled by sulfur, often included in insecticide applications to crops, than is *T. telarius* (Gaines, King, and Fuller, 1952; Nickel, 1958), and also that *T. desertorum* is generally more susceptible to other acaricides than *T. telarius* (Mistric and Rainwater, 1952). This inadequately explains the lack of economic severity of *T. desertorum* in California, however, because *T. atlanticus,* a mite species which is also susceptible to sulfur, is often a serious pest of cotton in this region.

Another explanation for the lack of severity of *T. desertorum* on cotton in California in spite of occasional high populations in weed patches might be the existence of a physiological race in California with different host preferences from populations of this species in Texas. This appears to be unlikely since some heavy infestations on cotton have occurred in California and greenhouse and laboratory studies have demonstrated that the California *T. desertorum* mites do very well on cotton.

Competition, particularly with *T. telarius,* may be of considerable importance. When greenhouse stock cultures of *T. desertorum,* maintained in the course of these studies, became contaminated with *T. telarius,* the ratio of the two species gradually changed until *T. desertorum* constituted only a very small portion of the mites present. Field reports indicated that although *T. desertorum* and *T. telarius* were both important cotton pests, one species or the other would usually be prevalent in any one field (Smith, 1958) or year (D. M. Tuttle, *in litt.,* September 16, 1958). It would, therefore, appear that the species of spider mites on cotton have broadly overlapping niche requirements so that one or another becomes predominant, depending on environmental factors which favor one or another.

Of all the limiting factors mentioned, climate appears to present the most obvious differences between central Texas and central California. Of the climatic factors, humidity stands out as the most apparent differential factor. The hypothesis is therefore set forth, to be tested by laboratory experiments, that high relative humidity is more favorable than low relative humidity for *T. desertorum* so that the arid climate in central California is at least one important factor preventing its being a widespread pest in this region. Confirmation of this hypothesis would require data demonstrating high relative humidity to be more favorable than low relative humidity for *T. desertorum* while data for another species of mite which is important in California, such as *T. telarius,* should not show such a relationship; or, at least, *T. desertorum* should be shown to be more favorably affected by high, and/or less favorably affected by low relative humidities than is *T. telarius.*

LABORATORY STUDIES

T. desertorum was studied in the laboratory under simulated field conditions in Paraguay and California, and under conditions of controlled temperature and relative humidity in California in order to learn more about its general

biology in these regions and the relative effects on it of different temperature and moisture conditions.

General Life History Studies

Preliminary tests were conducted to determine the duration of the various stages, the longevity, and the fecundity of the Paraguay and California populations of *T. desertorum* under temperature conditions approaching those experienced under summer field conditions. By conducting these trials in California with temperatures and methods as similar as possible to those in the Paraguay trials, it was intended that some indication would result as to whether or not these distant populations were biologically similar.

The general biology of *T. desertorum* in the southern United States has been amply covered by Iglinsky (1951) and Smith (1958), including a description of the various stages. Iglinsky (1951) also reported the duration of the different stages of *T. desertorum* and *T. telarius,* at variable temperatures of different means. *T. desertorum,* like other spider mites, passes through the following developmental stages: egg, larva, protonymph, and deutonymph. Approximately one half of the duration of each of the immature stages is spent in quiescence. The progeny of unfertilized females develop only into males. This species spins a copious amount of webbing and generally feeds on the ventral surfaces of leaves, but will spread over onto the dorsal surfaces more readily than do most species of *Tetranychus.* The eggs are laid singly and the preponderance of oviposition as well as quiescence take place near leaf veins.

Methods. These studies were conducted under variable temperature conditions; in Filadelfia, Paraguay, inside a residence, and, in Berkeley, California, inside a greenhouse. Temperature records in Paraguay consisted of recorded daily high and low temperatures, as indicated by a Six's combined maximum and minimum thermometer located on the wall near the test cells. In the California trials, hygrothermograph records were kept, with the cells and hygrothermograph inside an aluminum screen shelter, as shown in figure 5. In both regions daily means were calculated from the maximum and minimum temperatures. The ranges and means of the daily means for the various experiments are given in table 2. These indicate very similar mean temperatures for the experiments in the two localities; however, it should be noted that the daily march of temperature was possibly quite different. The Paraguay temperatures occurred naturally in a hot climate, whereas the California temperatures were the result of artificial manipulations in a greenhouse in a cooler climate. Thus the lows in the latter case, maintained by thermostatically controlled heat, fluctuated near the minimum temperature for several hours each night, compared with the natural condition of gradually being depressed to and rising from the minimum. Unfortunately, thermograph records from Paraguay are not available, but if they were, it is very possible that they would show the total heat experienced in the Paraguay trials to be greater.

Humidity was not controlled in these tests; however, it was affected by leaf transpiration into the relatively closed system of the cell and was thus quite high and fairly constant. Several checks, using cobalt thiocyanate

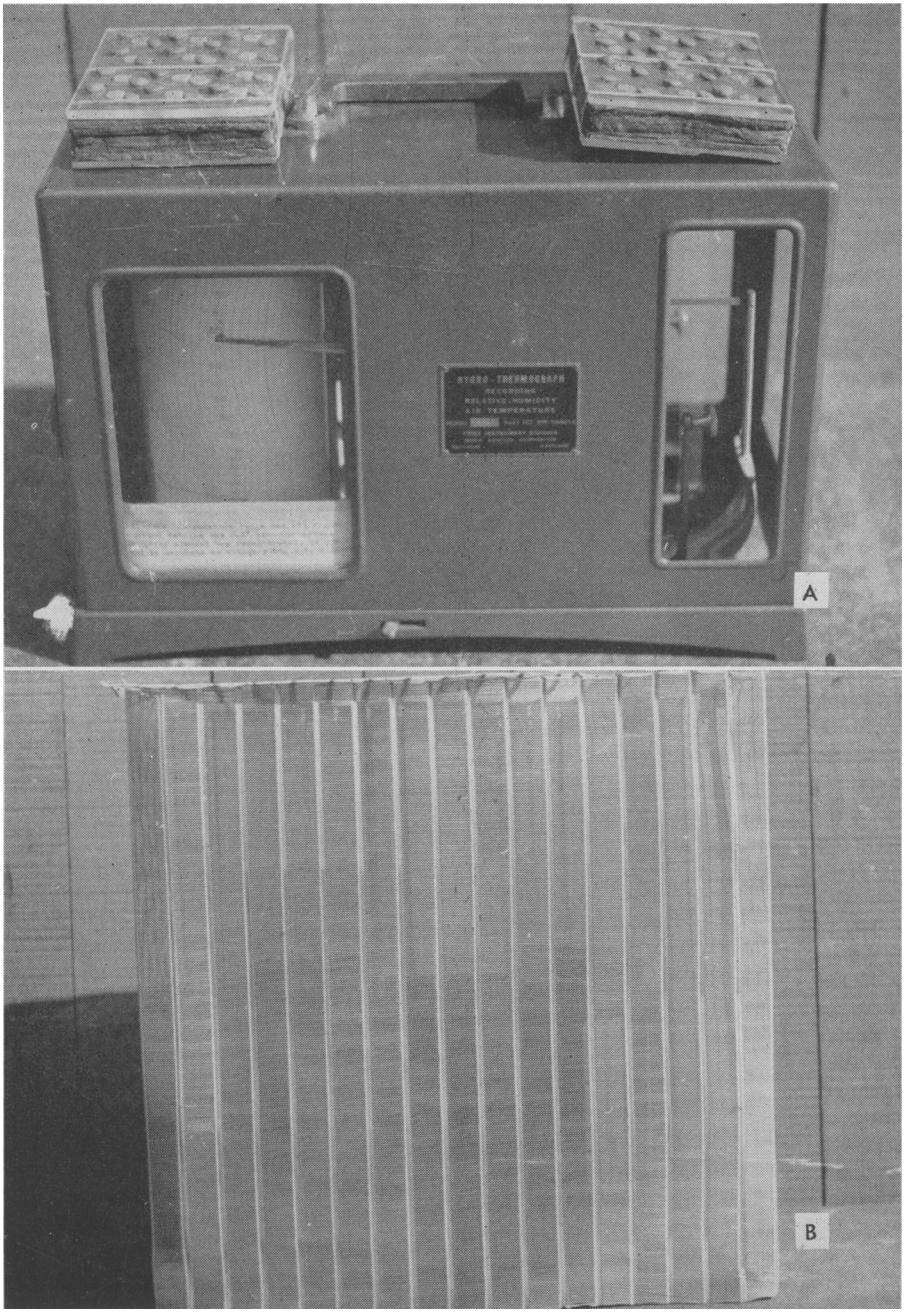

Fig. 5A. Mite rearing units and hygrothermograph as used in California variable temperature experiments. 5B. Aluminum screen shelter used to cover hygrothermograph and rearing units in California variable temperature experiments.

TABLE 2

VARIABLE TEMPERATURES RECORDED IN THE GENERAL LIFE-HISTORY STUDIES

Location	Expt. no.	Number days	Temperatures				
			Extremes, ° F		Daily means*		
					Range	Mean for Expt.†	
			Low	High	° F	° F	° C
Paraguay	1	26	75	104	82.5–95.0	88.5	31.4
	2	24	73	100	82.0–93.0	87.4	30.8
California	1	12	73	103	80.0–88.0	85.1	29.5
	2	29	72	107	84.0–90.5	87.1	30.7
	3	20	74	105	82.0–90.5	87.1	30.7

* Daily means: averages of maximum and minimum temperatures for each 24-hour period.
† Mean temperature for experiment: average of daily mean temperatures.

humidity indicator paper as described by Solomon (1957), showed the relative humidity in the cells to be near 90 per cent.

In all the trials the mites were confined to the dorsal surface of cotton leaves in cells ¼-inch in diameter and ⅛-inch deep. Figure 6 shows mites feeding in such a cell. Twelve-cell rearing units, 4-inches long, 3-inches wide, and approximately 1-inch thick, as pictured in figure 7, were used. Components of such units are shown in figure 8. In preparing the rearing units a cotton leaf (C), selected for uniformity in healthy green color and smoothness, was placed on a ½- to ¾-inch-thick layer of wet, cut, blotter paper (B), which in turn was supported on a Plexiglass plate (A). The top Plexiglass plate (D) was then placed on the leaf and the unit held together with rubber bands. The individual cells were closed by cover-glasses which were held in place with plastic modeling clay (F). The blotting paper was moistened with water daily.

Fig. 6. Close-up view of a single cell showing adult female *T. desertorum* with feeding injury visible. (Approx. 40X)

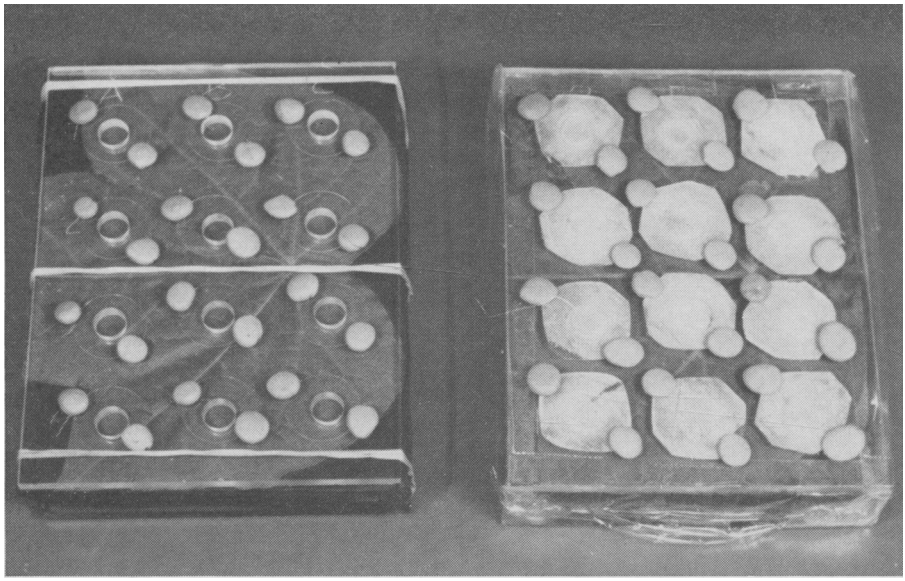

Fig. 7. Left, rearing units showing glass covers used in the variable temperature experiments. Right, silk covers used in the constant temperature and humidity experiments.

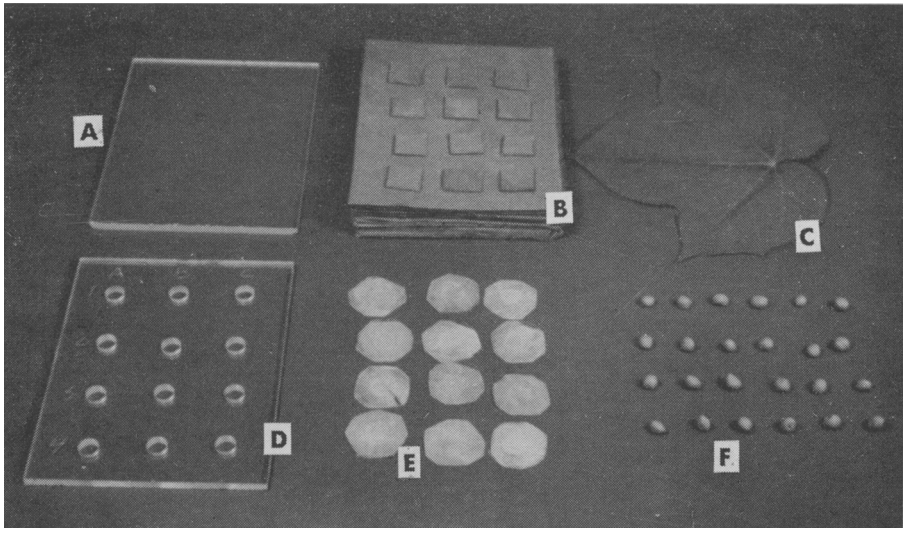

Fig. 8. Component parts of a 12-cell rearing unit showing: (A and D) plexiglass plates; (B) blotter paper; (C) cotton leaf; (E) plastic-cloth covers; and (F) plastic clay.

Mites used in these experiments were taken from infested cotton plants in the field (Paraguay tests) or stock cultures on Henderson dwarf lima beans in the greenhouse (California tests—see figure 9). These latter colonies were established from mites originally collected in September, 1957, near Tipton, California. Experiments were initiated by placing one quiescent deutonymph female and an active adult male in each cell. Additional males were supplied if any died or escaped. In tests with unfertilized females, the males were omitted. When the adult female mites emerged they were observed

Fig. 9. Stock cultures of mites on Henderson dwarf lima beans.

daily for longevity and egg production. Some of their eggs were separated for use in the developmental studies. Eggs of known age were obtained by allowing the females to oviposit for brief periods in separate cells and then transferring the females to other cells. The duration of these periods was the same as the interval between subsequent observations in the development studies, i.e., Paraguay—24 hours, California—12 hours. In the Paraguay tests, some adult females reared in the developmental studies were utilized in subsequent experiments. Observations for the development data were made daily in Paraguay and at 12-hour (± 1 hour) intervals in California. Mites were transferred to cells with fresh leaves at first evidence of leaf yellowing. In the longevity and fecundity experiments in California, the adult mites were routinely transferred to new cells every two days. Transfer of mites was accomplished by means of a fine, dental, root canal broach.

Rate of Development. The results of the developmental studies are given in tables 3, 4, and 5. In table 3 the totals for the several replications indicate that, under summer conditions in Paraguay, the mites completed their immature development in approximately 8½ days. Mites from California, however, under conditions aimed at duplicating those experienced in Paraguay, required almost a day longer to complete their total development.

TABLE 3

TOTAL DEVELOPMENT TIMES (EGG TO ADULT) OF *TETRANYCHUS DESERTORUM* IN PARAGUAY AND CALIFORNIA AT VARIABLE TEMPERATURES WITH MEANS NEAR 30°C

Experiment	Duration in days					
	Females			Males		
	Number mites	Range	Mean ± SE_m	Number mites	Range	Mean ± SE_m
Parag. No. 1	13	7–11	8.07±0.29	8	8–9	8.75±0.19
Parag. No. 2	49	7–10	8.63±0.09	3	8	8.00±0.00
Parag. Total	62	7–11	8.52±0.07	11	8–9	8.55±0.16
Calif. No. 1	9	8.5–9.5	8.64±0.21	3	8.5–10.0	8.87±0.44
Calif. No. 2	15	8.5–11.0	9.67±0.19	38	8.0–11.0	9.39±0.10
Calif. No. 3	62	8.0–13.0	9.47±0.12	56	8.0–12.0	9.35±0.11
Calif. Total	86	8.0–13.0	9.44±0.10	97	8.0–12.0	9.37±0.07

TABLE 4

DURATION OF VARIOUS STAGES IN THE DEVELOPMENT OF *T. DESERTORUM* MITES IN PARAGUAY AND CALIFORNIA UNDER VARIABLE TEMPERATURES WITH MEANS NEAR 30°C

Stage	Duration (days)						t*
	Paraguay			California			
	Number mites	Range	Mean ± SE_m	Number mites	Range	Mean ± SE_m	
Egg	129	2–4	3.00±0.03	309	3.5–5.5	4.08±0.02	17.43†
Larva	117	1–3	1.82±0.04	223	1.0–3.0	1.87±0.02	0.77
Protonymph	87	1–3	1.77±0.06	204	0.5–3.0	1.47±0.03	3.26†
Deutonymph	73	1–3	1.90±0.06	180	1.0–5.0	1.98±0.03	0.90
Total (egg–adult)	73	7–11	8.52±0.75	183	8.0–13.0	9.40±0.06	5.76†

* t values calculated for differences between mean durations for Paraguay and California.
† Statistical separation between localities at the 0.01 level of significance.

TABLE 5

DURATION OF PREOVIPOSITION PERIODS FOR FEMALE *T. DESERTORUM* MITES IN PARAGUAY AND CALIFORNIA UNDER VARIABLE TEMPERATURE CONDITIONS WITH MEANS NEAR 30°C

Locality	Preoviposition period			
	Immature development on stock or field plants		Immature development in cells in laboratory	
	Number mites	Mean duration (days) ± SE_m	Number mites	Mean duration (days) ± SE_m
Paraguay	4	1.75±0.50	12	0.92±0.29
California	39	1.91±0.73	51	0.94±0.33

A separation of the developmental periods for each of the immature stages, with the sexes combined, is given in table 4. This gives evidence that the difference in total development time between the two localities can largely be attributed to the egg stage. In fact, the difference is slightly greater than that indicated by the totals because of a significant reversal in the protonymph stage.

The question arises whether this significant difference in incubation period was due to intrinsic biological differences in the populations of the two areas, or whether it can be explained in terms of the possible differences in the daily march of the temperatures and the consequent differences in total heat as described above. It would appear logical that a temperature difference between the rearing conditions in the two areas should affect all stages. However, Iglinsky and Rainwater (1954), in their studies on the development of *T. desertorum,* demonstrated a marked shortening of the egg stage and a lesser change in duration of the other stages with a slight elevation of the mean temperatures. Since both of these studies were conducted at variable temperatures, a definite conclusion cannot be drawn, though constant temperature studies (below) should shed more light on the matter.

As indicated in table 5, there was no significant difference in preoviposition periods between the two localities. A marked difference was observed, however, between females taken as quiescent deutonymphs from infested plants and those having been reared from the egg stage in the cells. It would appear that this shortening of the preoviposition period in cell-reared females reflects the ample food supply and lack of crowding under the artificial conditions.

Longevity and Fecundity. The egg-laying capacity of these mites and their adult mortality are shown graphically in the age-specific fecundity and survivorship curves in figure 10. The combined effects of these values are tabulated in table 6 as the net reproduction rate (R_0)—the multiplication per generation. These are modified tables in that the immature mortality, which was low, is ignored, and the calculations are based on a 100 per cent female sex ratio. A more detailed presentation as to the calculation and significance of this figure is given in the section reporting the constant temperature and humidity studies.

These results indicate that, though the R_0 is very similar for the two samples, the Paraguay females laid a greater number of eggs per day but that the effect of this was offset by an earlier mortality. This combination, as well as the acceleration of incubation period discussed above, could possibly be due to warmer temperatures in Paraguay rather than inherent differences between the two populations of mites.

The California experiments indicated that both food and spatial factors during the development of the immature stages can greatly affect the fecundity and longevity of adult females. It was necessary to conduct several series of longevity-fecundity trials to obtain data on sufficient numbers. Generally the quiescent deutonymphs to be used in these trials were taken from heavily infested bean plants. In one instance they were taken instead from fresh, healthy bean plants on which only a light population of mites had fed. The fecundity and survival of this series, here referred to as the "vigorous" group, are shown in figure 11A. This combination of higher

TABLE 6

MODIFIED LONGEVITY (l_x), AGE-SPECIFIC FECUNDITY (m_x), AND NET REPRODUCTION RATE (R_0), OF *T. DESERTORUM* MITES IN CALIFORNIA AND PARAGUAY UNDER VARIABLE TEMPERATURE CONDITIONS WITH MEANS NEAR 30°C

Age (days)	Paraguay*			California†		
	l_x	m_x	l_xm_x	l_x	m_x	l_xm_x
1	1.00	2.8	2.80	1.00	0.5	0.50
2	1.00	7.8	7.80	1.00	3.6	3.60
3	1.00	9.4	9.40	1.00	5.3	5.30
4	1.00	10.9	10.90	0.96	5.7	5.47
5	0.88	5.9	5.19	0.96	5.8	5.57
6	0.88	5.9	5.19	0.91	5.9	5.37
7	0.88	4.6	4.05	0.91	6.1	5.56
8	0.50	10.3	5.15	0.86	6.2	5.33
9	0.50	9.8	4.90	0.86	5.8	4.99
10	0.50	7.4	3.70	0.86	5.9	5.07
11	0.38	8.3	3.15	0.82	6.2	5.08
12	0.38	8.0	3.04	0.73	5.0	3.65
13	0.25	3.7	0.93	0.68	5.1	3.47
14	0.25	3.3	0.83	0.55	4.2	2.31
15	0.25	0.0	0.00	0.46	4.1	1.89
16	0.13	0.0	0.00	0.36	4.4	1.58
17	0.13	6.0	0.78	0.14	5.6	0.78
18	0.13	0.0	0.00	0.05	3.6	0.18
19	0.00	0.0	0.00	0.05	4.7	0.24
20	....	....	....	0.05	5.0	0.25
21	....	....	....	0.05	3.0	0.15
22	....	....	....	0.00	0.0	0.00
	R_0 = 67.81			R_0 = 66.34		

* Paraguay results tabulated from both fertilized and unfertilized females; initial number of mites for l_x = 8, m_x = 14.

† California results tabulated from fertilized females only; initial number of mites for l_x = 22, m_x = 36.

fecundity and greater longevity resulted in a R_0 of twice that of the mites in the other series (table 5, figure 10B).

Another interesting characteristic demonstrated in the California studies was that unfertilized females have a lower age-specific fecundity but a greater longevity than fertilized females, as evidenced in comparing figure 11A with figure 11B. For this reason, only fertilized females are included in the California R_0 calculations. The Paraguay studies did not appear to show this difference and the numbers were too small to separate the groups, so both fertilized and unfertilized females, as well as females reared on infested plants and those reared in cells are included in the Paraguay data.

Sex Ratio. Iglinsky (1951) reported that eggs taken on the day of mating from females mated one to two days after emergence resulted in a ratio of three females to two males and that the total progeny over the life span of 11 females mated immediately after emergence was 399 females and 113 males. Smith (1958), in a field survey, found 86.4 per cent of *T. desertorum* mites to be females.

In the course of the above California life-history studies, eggs laid by females of various ages were separated and the sexes of the resulting adults

recorded. Males were kept in the cells with the parent females from shortly prior to emergence until death of the females. Copulation was not observed but it was assumed that it took place in most cases immediately after emergence because of the males' habit of hovering over the quiescent deutonymph females waiting to copulate as soon as the adult females emerge. The results of these observations are given in table 7 and graphically presented in figure 12. The rapid rise of per cent female offspring with the age of the mother until a plateau of approximately 85 per cent is reached is probably due to a combination of occasional delay in mating, with the methods described, and the possible lack of fertilization of early eggs passing through the oviduct at the time of mating and shortly thereafter. Delayed mating would rarely occur in the field, as there are usually a number of males waiting by each quiescent deutonymph. If such a sex ratio gradation should be demonstrated under field conditions, however, the effect of this third variable should be reflected in net reproduction rate calculations. Such a correction would probably reduce this figure by about 25 per cent.

Constant Temperature and Humidity Studies

Experiments at variable temperatures provide useful information about the general life history of a species and the approximate duration of the various stages. For more accurate and reproducible information regarding temperature relationships and optima, however, constant temperature studies are essential. To test the hypothesis regarding the relative favorability of high-versus-low humidities, these studies were also conducted under conditions of controlled relative humidity.

When conducting laboratory studies to determine favorable or optimal conditions, a basic question concerns the criteria for favorability. Conditions most favorable for survival may be quite different from those favoring numerical abundance. However, since the purpose of this study was to determine factors influencing economic severity of *T. desertorum,* rapid numerical increase was an important criterion. Conditions favoring population increase of a pest, resulting in densities which bring about damage and

TABLE 7

SEX RATIOS OF PROGENY OF ADULT FEMALE *T. DESERTORUM* MITES IN VARIOUS AGE GROUPS IN CALIFORNIA UNDER VARIABLE TEMPERATURE CONDITIONS WITH MEANS NEAR 30°C

Age of mother (days)	Number offspring		Per cent female offspring
	Female	Male	
1.5–2.5	13	19	40.6
2.6–3.5	19	20	48.8
3.6–4.5	16	8	66.7
4.6–5.5	10	7	58.8
5.6–6.5	10	2	83.4
6.6–7.5	7	3	70.0
7.6–10.5	18	3	85.8
10.6–16.5	15	3	83.3

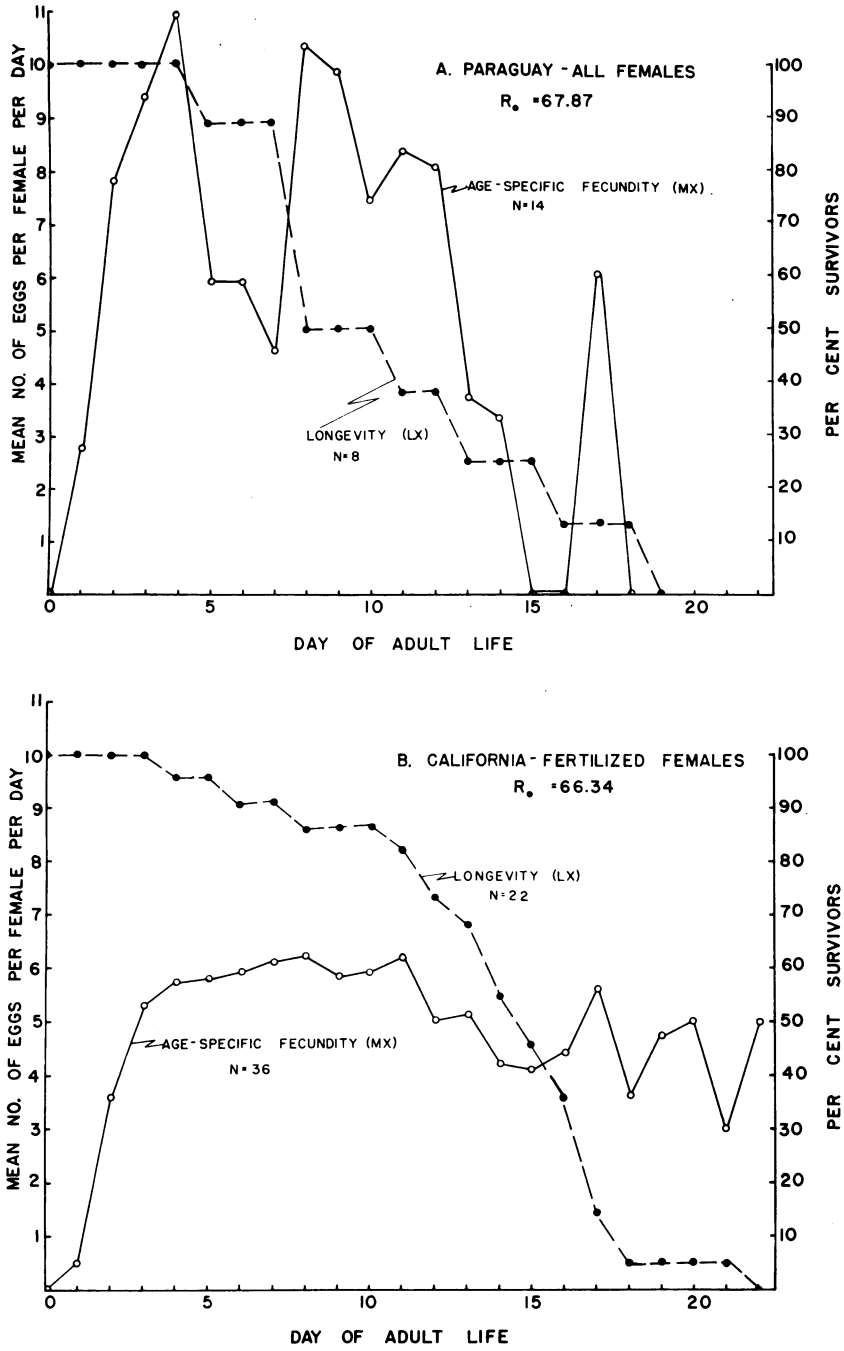

Fig. 10. Age-specific fecundity and survivorship of *T. desertorum* mites in California and Paraguay under variable temperature conditions, with means near 30°C.

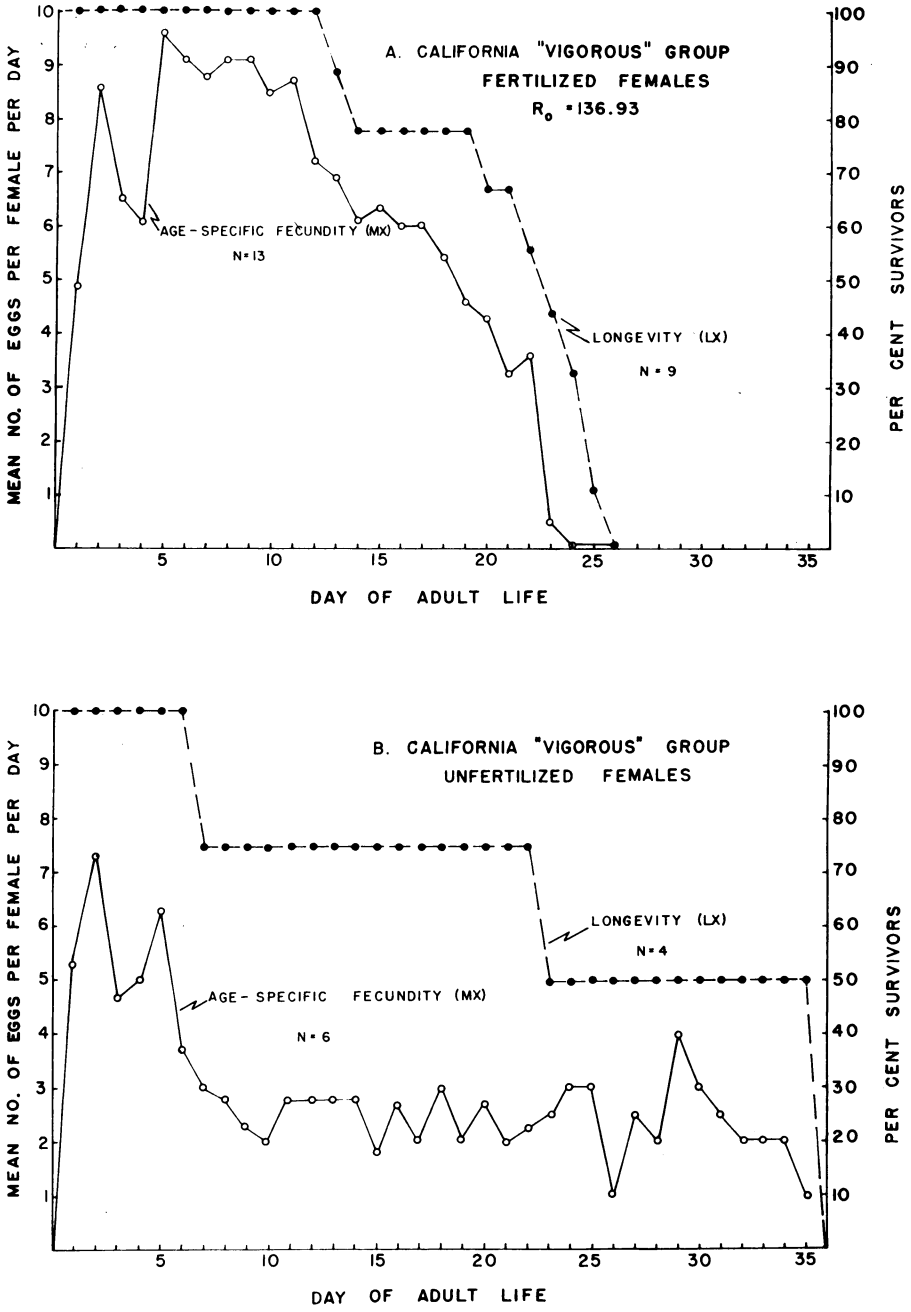

Fig. 11. Age-specific fecundity and survivorship of fertilized and unfertilized adult female *T. desertorum* mites in California under variable temperature conditions with means near 30°C.

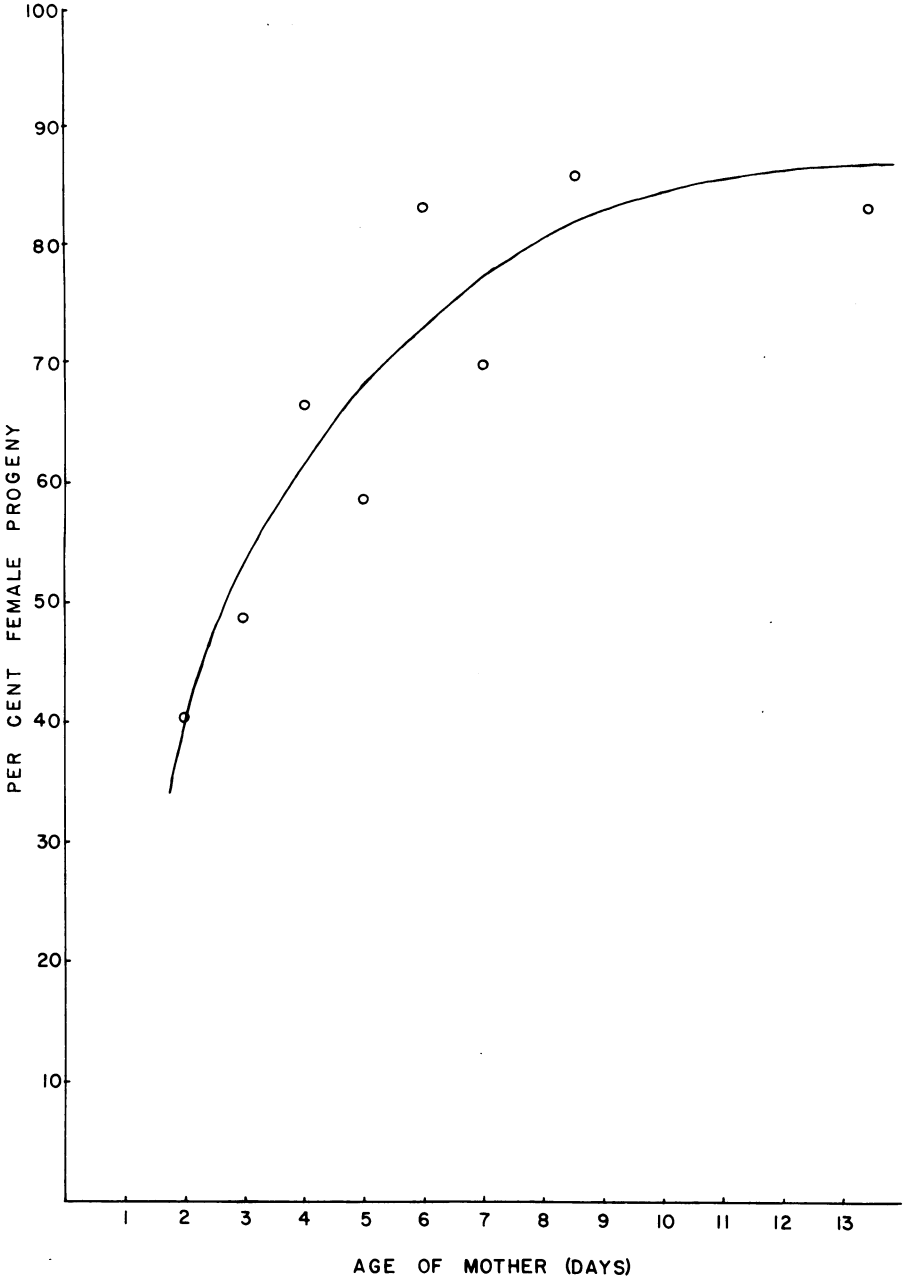

Fig. 12. Effect of age of mother on sex ratio of progeny of *T. desertorum* mites in California under simulated summer field conditions. Curve fitted to points visually.

spread, would be those favoring a high rate of reproduction. The reproduction rate, in turn, is influenced by the rate of development, fecundity, and longevity of the species. Environmental factors affecting these aspects include the physical factors of temperature, humidity, light, and air movement, and the biotic factors of natural enemies and inter- and intraspecific competition for food and space. Since it would be impossible to study all of these factors in detail at the same time, it is best to study them separately, under laboratory conditions designed to keep the other factors as constant as possible, and then relate the information thus obtained back to the entire ecosystem.

Of the environmental factors listed, the effects of temperature and humidity levels were selected as the subject of these experiments with *T. desertorum,* because these two physical factors seemed to offer the most likely explanation for differences in economic severity as discussed in the section on climate and distribution. Temperature and humidity are closely interrelated and their effects on reproduction and development must be considered together. The purposes of the studies which follow were to determine the most favorable temperature and humidity combination under laboratory conditions for *T. desertorum* in terms of rate of development, longevity, and fecundity, and to compare these results with the temperature and humidity relationships of *T. telarius.*

Methods. Procedures employed in these experiments were the same as those described for the general life-history studies except for the modifications necessary to maintain controlled temperatures and humidities, and the refinements dictated by experience gained in the variable temperature studies.

The rearing units were kept in standard, glass desiccator jars placed one above the other, two per temperature cabinet, as shown in figure 13. Temperature cabinets were modified, 7-cubic-foot refrigerators, each with six 15-watt fluorescent lamps as a constant light and heat source. Temperature was controlled thermostatically and air movement maintained by means of a small circulating fan. The position of the desiccators was rotated at each inspection (daily or twice daily). Temperatures were determined by placing thermocouples, just above the leaf surface, in the cells in the various desiccators, and measured by a recording potentiometer over a period of several days. The different positions of the desiccators plus slight temperature fluctuations resulted in some variation. The mean temperatures and ranges are given in table 8. At the time of the thermocouple temperature measurements the temperatures indicated by mercury-in-glass thermometers located outside the desiccators at the bottom of the cabinets were also determined and these reference thermometers were checked daily to insure that the temperatures remained the same throughout the experiments.

Humidity was controlled by the use of various saturated salt solutions in the bottom of the desiccators. The two main relative humidity levels used were low (25 to 30 per cent) and high (85 to 90 per cent). In a few trials an intermediate relative humidity of approximately 45 per cent was employed. The salts used in maintaining these levels were: low-potassium acetate, intermediate-potassium carbonate, and high-potassium nitrate. At high temperatures the humidities tended to be at the low ends of the ranges,

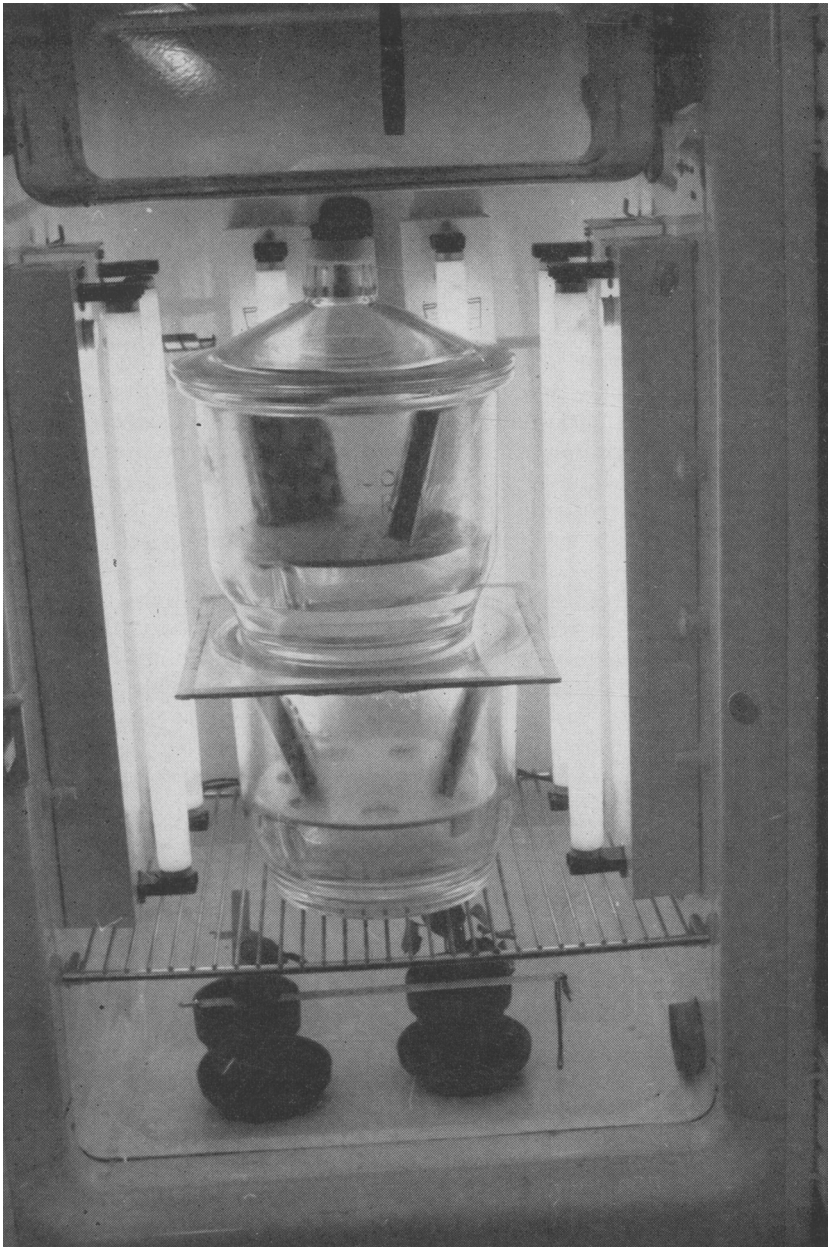

Fig. 13. Temperature cabinet and humidity chamber used in constant temperature and humidity studies. Cotton seedlings were placed in lower portion of cabinet for standardized rearing of mites used in these studies.

TABLE 8

TEMPERATURES USED IN CONSTANT TEMPERATURE AND HUMIDITY LABORATORY STUDIES (TO NEAREST 0.5 DEGREE)

Range* °C	Mean temperature	
	°C	°F
8.5–11.0	10.0	50.0
15.0–17.5	16.5†	61.5
24.0–26.0	25.0	77.0
29.5–30.5	30.0	86.0
35.0–37.0	36.0	97.0

* Measured in cells by thermocouples and recording potentiometer.
† Referred to in text as 16° C.

whereas at low temperatures they were at the high ends of the ranges. Humidity readings were made by placing small pieces of cobalt thiocyanate indicator paper inside the cells and making colorimetric humidity readings as described by Solomon (1957). Larger pieces of indicator paper were placed on the cell units, outside the cells, to give a visual indication of proper humidity maintenance. It was observed that there was very little, never more than 5 per cent, difference in the relative humidity at the leaf surfaces in the cells from that of the ambient air in the desiccators.

Maintenance of constant relative humidity levels dictated two changes in the construction of the cell units from those used in the earlier tests. The evaporation of water from the exposed wet blotting paper had to be eliminated. This was accomplished by wrapping each rearing unit with "Saran Wrap" (Dow Chemical Company, Midland, Michigan) attached with cellophane tape, leaving only the cell-opening surface uncovered—as shown in figure 7B. Also the cover-glass cell covers had to be replaced by covers which would allow free exchange of water vapor in and out of the cell. These covers, as shown in figure 8E were constructed by covering holes bored in plastic coverslips with fine bolting silk.

The general life-history experiments had demonstrated the importance of food and spatial factors during the development of the females used in the tests, hence all quiescent deutonymph females used in these trials were reared under standardized conditions. They were taken from seedling cotton plants on which they had developed from eggs deposited by adult female mites which had been placed on the plants and allowed to oviposit for 5 days, 9 to 14 days prior to selection of the quiescent deutonymphs. The adult females were placed on the cotton when the plants had developed two true leaves. Five females were placed on each true leaf. These mites were taken from stock cultures on Henderson dwarf lima bean plants which had been started from mites taken off horseweed near Tipton, California, in July, 1958. The developing mites on the cotton seedlings were kept at the bottom of the 30°C box, as shown in figure 13B. Thermocouples placed at leaf level on these plants indicated the mites were reared at a temperature of 26°C. Humidity readings indicated a relative humidity in this part of the cabinet of approximately 50 per cent. The cotton plants were watered with ½-strength Hoag-

land's solution during the period in which mites were on them. Thus all the mites used in the tests which follow were reared under conditions of controlled temperature and humidity on a relatively uniform food supply.

Leaves used in the rearing units were taken from among the top three pairs of fully expanded leaves of cotton plants which were reared in the greenhouse and fertilized weekly with ½-strength Hoagland's solution. These leaves were selected for uniformity and rinsed thoroughly in tap water before use.

Adult female mites in the longevity and fecundity trials were transferred to fresh leaves every five days at 16°C, every three days at 25°C and every two days at 30°C and 36°C. Transfer of mites was accomplished by means of a number 00 sable hair brush.

Low Temperature Survival. Preliminary experiments indicated that quiescent deutonymphs placed in cells at temperatures below 10°C died before emergence and that some at temperatures slightly above 10°C emerged and oviposited. These early tests also indicated that few eggs could survive 20 days at slightly below 10°C. The following trials were conducted to test the effect of low temperature on adult females, quiescent deutonymph females, and eggs under more exact temperature conditions and at both low and high humidities.

Adult survival at 10°C (8.5 to 11.0) was determined by placing quiescent deutonymphs in cells, allowing them to emerge and pass through the preoviposition period at 25°C and approximately 50 per cent relative humidity, then transferring the rearing units to 30 and 90 per cent relative humidity desiccators in the low-temperature cabinets. At each humidity each of the females laid a few eggs. The total number of eggs deposited at the cold temperature averaged approximately 5 per female. Twenty-one days after placing the females at 10°C, they were transferred to fresh cells and kept at the low temperature while the eggs which had been laid under these conditions were placed at 25°C and approximately 50 per cent relative humidity to determine viability. These eggs had been exposed to the low temperature for 12 to 19 days (high humidity) and 2 to 19 days (low humidity) before the transfer. The percentage which hatched was 42.6 for those laid at the high humidity and 9.5 for those laid at the low humidity. The adult females were kept at the cold temperature and observed daily until all were dead. Survivorship curves for females at this temperature for the two humidities are given in figure 14. Though the numbers were quite small, a modifying effect on cold temperatures by high humidity was strongly indicated.

Quiescent deutonymphs were placed in cells at 10°C at high and low humidities, left there for 15 days, and transferred to 25°C and approximately 50 per cent relative humidity conditions to test viability. Some emerged at the low temperature and others emerged after transfer to the higher temperature. The results are given in table 9. Though all of the quiescent deutonymphs exposed to 10°C at the high humidity survived to emerge and oviposit, only 18.2 per cent of those exposed to the same temperature at the low humidity survived.

The effect of cold temperature on eggs of *T. desertorum* was also investigated. Female mites were permitted to oviposit over a 24-hour period in six

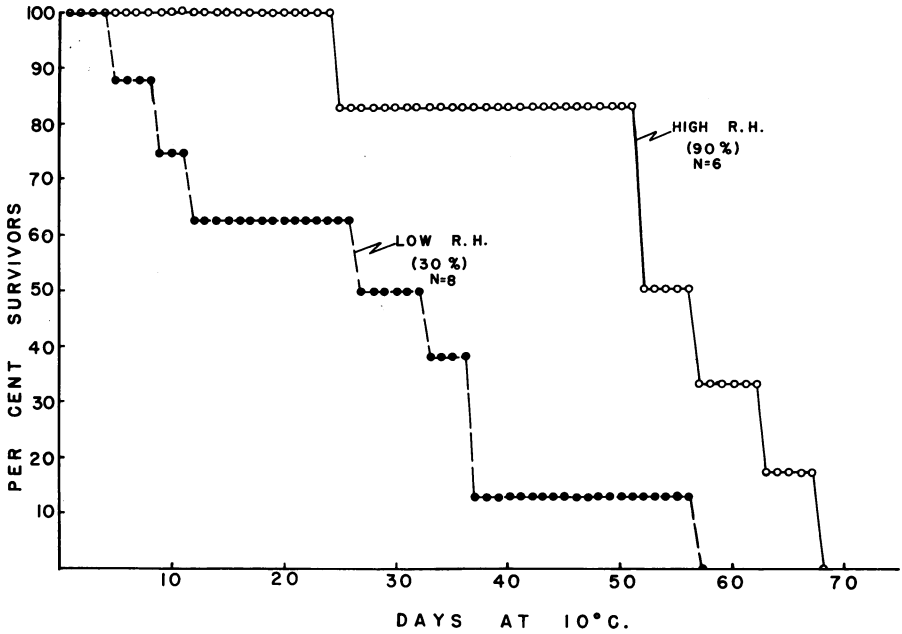

Fig. 14. Survivorship of adult female *T. desertorum* mites at 10°C and at low (closed circles) and high (open circles) relative humidity levels after a preoviposition period at 26°C and 50 per cent relative humidity

rearing units at 25°C and approximately 50 per cent relative humidity. Three units containing the newly laid eggs were then placed in each of the high and low humidity desiccators at 10°C. At the end of 5, 15, and 25 days of cold-temperature exposure, one rearing unit from each humidity was transferred to the standard 25°C, 50 per cent relative humidity condition and the number which hatched recorded. The egg mortalities at the low temperature are given in table 10 and graphically presented in figure 15. Whereas almost all of the eggs were killed by a 25-day exposure to 10°C at low humidity, less than a third were killed at high relative humidity. None of the eggs hatched at either humidity during the 25 days at 10°C,

TABLE 9

EFFECT OF LOW TEMPERATURE (10°C) ON EMERGENCE AND SURVIVAL OF QUIESCENT DEUTONYMPH FEMALES OF *T. DESERTORUM* AT LOW AND HIGH HUMIDITY LEVELS

Relative humidity	Number mites	Number emerged during 15 days at 10° C	Number emerged after transfer to 25° C	Per cent survivors*
Low (30%)	11	2	0	18.2
High (90%)	12	6	6	100.0

* Survivors: those which emerged and oviposited.

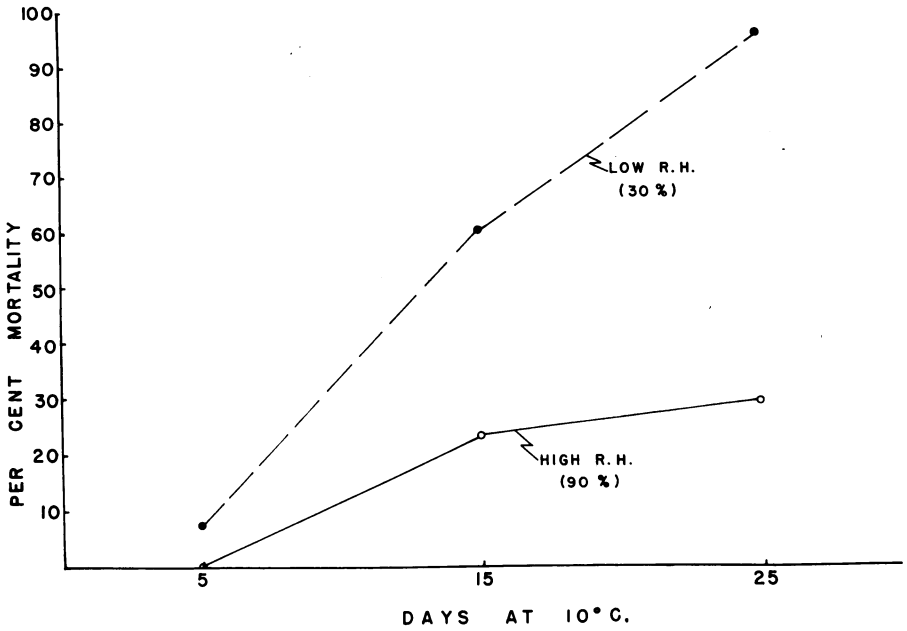

Fig. 15. Effect of various periods of exposure on mortality of *T. desertorum* eggs at low (closed circles) and high (open circles) relative humidity levels.

but those hatching after this period did so approximately a day sooner at 25°C than the normal incubation rate at this temperature, indicating that some development, though slight, had occurred during the cold-temperature exposure.

The results of these cold-temperature studies indicate that 10°C is very near the threshold of temperature for development for *T. desertorum* eggs and that there is considerable mortality from exposure to this low temperature. Further, these results demonstrated that the lethal or retarding effects of low temperature are considerably lessened by high humidity.

TABLE 10

EFFECT OF LOW TEMPERATURE (10°C) ON MORTALITY OF *T. DESERTORUM* EGGS FOR VARIOUS EXPOSURE PERIODS AT LOW AND HIGH HUMIDITY LEVELS

Days at 10° C	Mortality					
	Low R. H. (30%)			High R. H. (90%)		
	Number eggs	Number dead	Per cent dead	Number eggs	Number dead	Per cent dead
5	55	4	7.3	66	0	0.0
15	111	67	60.3	120	28	23.3
25	45	43	95.6	34	10	29.4

TABLE 11

MORTALITY AND SURVIVAL OF IMMATURE STAGES OF *T. DESERTORUM* AT DIFFERENT TEMPERATURE AND RELATIVE HUMIDITY LEVELS

Temp. °C	Stage	Low humidity (25–30%)				High humidity (85–90%)			
		Number mites	Number dead	Mortality (Per cent)	Survival*	Number mites	Number dead	Mortality (Per cent)	Survival*
16	Egg	92	9	9.8	902	85	2	2.4	976
	Larva	60	2	3.3	872	61	1	1.6	960
	Protonymph	44	1	2.3	852	58	0	0.0	960
	Deutonymph	41	0	0.0	852	55	0	0.0	960
25	Egg	129	8	6.2	938	96	1	1.0	990
	Larva	95	3	3.2	907	76	1	1.3	977
	Protonymph	89	1	1.1	897	74	0	0.0	977
	Deutonymph	84	1	1.1	887	68	0	0.0	977
30	Egg	103	9	8.7	913	142	5	3.5	965
	Larva	50	0	0.0	913	113	0	0.0	965
	Protonymph	49	0	0.0	913	110	0	0.0	965
	Deutonymph	49	0	0.0	913	105	0	0.0	965
36	Egg	113	94	83.2	168	147	58	39.5	605
	Larva	8	0	0.0	168	24	3	12.5	529
	Protonymph	8	0	0.0	168	19	1	5.3	501
	Deutonymph	8	2	25.0	126	9	4	44.0	279

* The estimated numbers of individuals completing any stage, assuming an initial number of 1,000 eggs.

Immature Mortality. In the course of the developmental studies the number of mites dying in each stage was recorded at 16°C, 25°C, 30°C, and 36°C, and at high (85 to 90 per cent) and low (25 to 30 per cent) relative humidities for each temperature. The results of these observations are given in table 11. Survival for any stage was calculated my multiplying the per cent surviving by the number entering that stage, assuming an initial number of 1,000 eggs for each condition. The total mortality of all immature stages is plotted in figure 16. These results showed that the major source of immature death was in the egg stage with the least mortality at 30°C and a very high mortality at 36°C. The number of eggs hatching at this high temperature was so low and so many of those which did hatch escaped the cells that the data on subsequent stages are inadequate. Those which hatched at 36°C and did not escape the cells appeared to develop normally until they reached the deutonymph stage. In this stage the females seemed to have great difficulty in assuming pre-adult quiescence. They would go on for days becoming more and more turgid and often die before becoming quiescent. Some of those which were successful in going through to the adult stage died before ovipositing. Thus it is apparent that this temperature is very detrimental to *T. desertorum.*

In considering the immature mortality, humidity differences are striking. At all temperatures, egg mortality at low humidity was more than twice that at high humidity.

Adult Longevity. The longevity of mated adult female *T. desertorum* mites was determined by observing them daily from emergence until death.

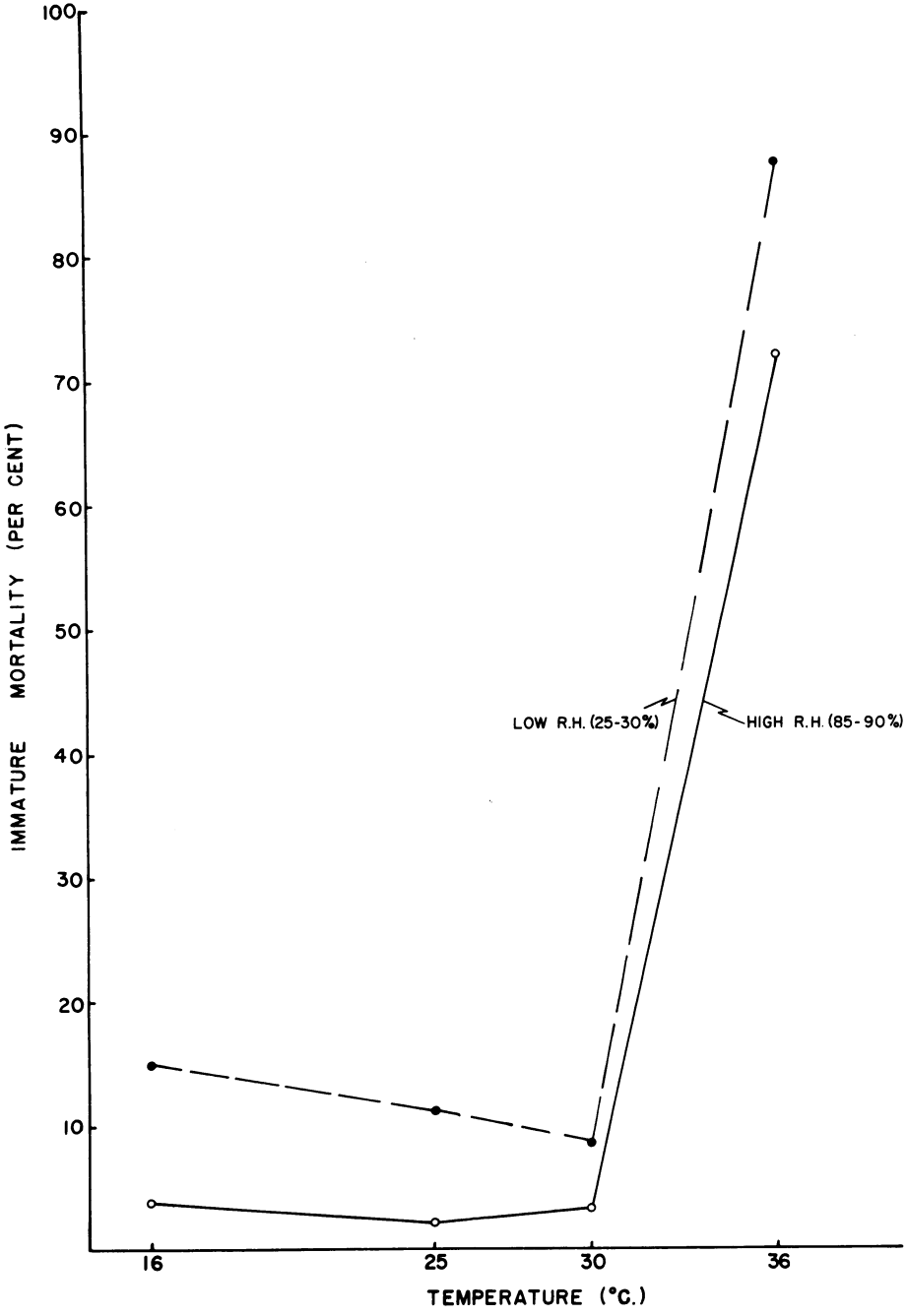

Fig. 16. Combined mortality of the immature stages of *T. desertorum* at different temperature and relative humidity levels.

Quiescent deutonymphs used for these observations were reared on cotton seedlings under the standardized conditions described above. These data were collected at the temperatures of 16°C, 25°C, 30°C, and 36°C and at low (25 to 30 per cent) and high (85 to 90 per cent) relative humidities at each temperature. Mites obviously injured in transfer and those escaping in the course of these observations were not included in the longevity results. Therefore, since the chance of being injured or escaping was greater with longer life, the results tend to be somewhat biased in the direction of lesser longevity. Such a bias could not be avoided but should not seriously affect comparisons between different temperatures and humidities as it was present under all conditions.

The mean adult longevities and ranges observed are given in table 12. These results, expressed as the probability of any adult female being alive at any given age under these combinations of temperature and humidity are given in the columns labeled "adult l_x" in tables 14, 15, 16, and 17, and plotted in figures 17A, 18A, 19A, and 20A. As is apparent from the broad ranges and high standard errors, a great deal of variability in length of adult life was observed. For this reason, statistical analysis indicated no significant differences as a result of humidity at the 5 per cent level of significance, but the results in table 2 as well as the survivorship curves indicate a trend of generally shorter adult life at the low humidity level for all temperatures tested except 36°C. At 30°C the difference due to humidity was large enough that a "t" value of 2.00 was obtained with a "t" of 2.02 needed for significance at the 5 per cent level, so that for practical purposes this can be considered a significant decrease in the length of adult life by the low humidity.

A definite diminution in adult life was indicated with increase in temperature.

TABLE 12

LONGEVITY OF *T. DESERTORUM* ADULT FEMALES AT DIFFERENT TEMPERATURE AND RELATIVE HUMIDITY LEVELS

Temp. °C	Low humidity (25–30%)			High humidity (85–90%)			t*
	Number mites	Longevity, in days		Number mites	Longevity, in days		
		Range	Mean ± SE_m		Range	Mean ± SE_m	
16	27	13–46	23.45±1.76	23	14–61	27.35±0.94	1.35
25	21	9–28	16.90±1.02	22	11–30	17.55±1.09	0.32
30	24	4–23	13.17±0.78	24	4–27	17.42±1.27	2.00
36	18	3–14	8.33±0.79	17	4–13	8.25±0.70	0.10

* t values calculated for differences between mean longevities at low and high humidities are not significant at the 5 per cent level.

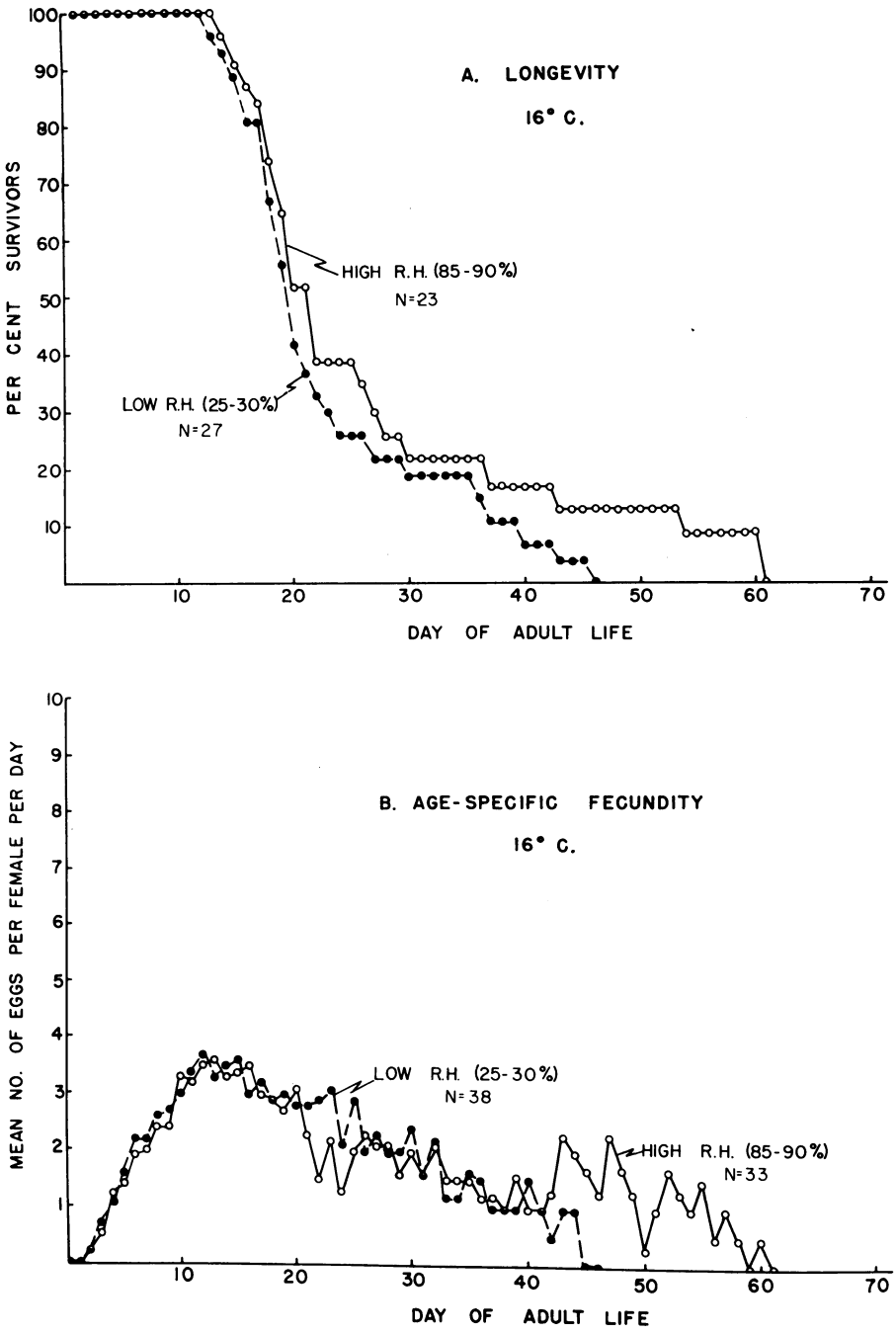

Fig. 17. Longevity and age-specific fecundity of adult *T. desertorum* females at 16°C (15 to 17.5°) and at low (closed circles) and high (open circles) humidity levels.

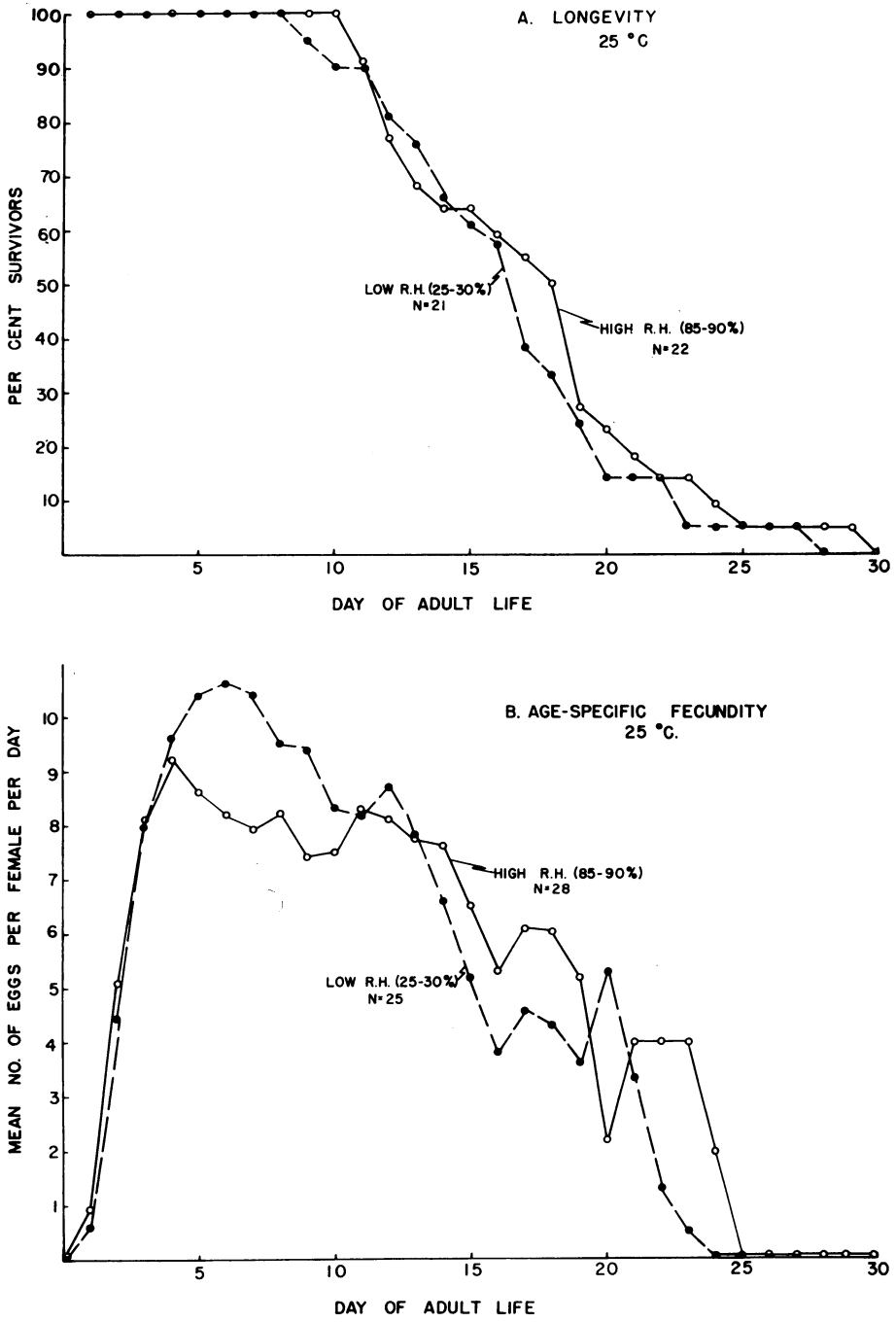

Fig. 18. Longevity and age-specific fecundity of adult *T. desertorum* females at 25°C (24.0 to 26.0°) and at low (closed circles) and high (open circles) humidity levels.

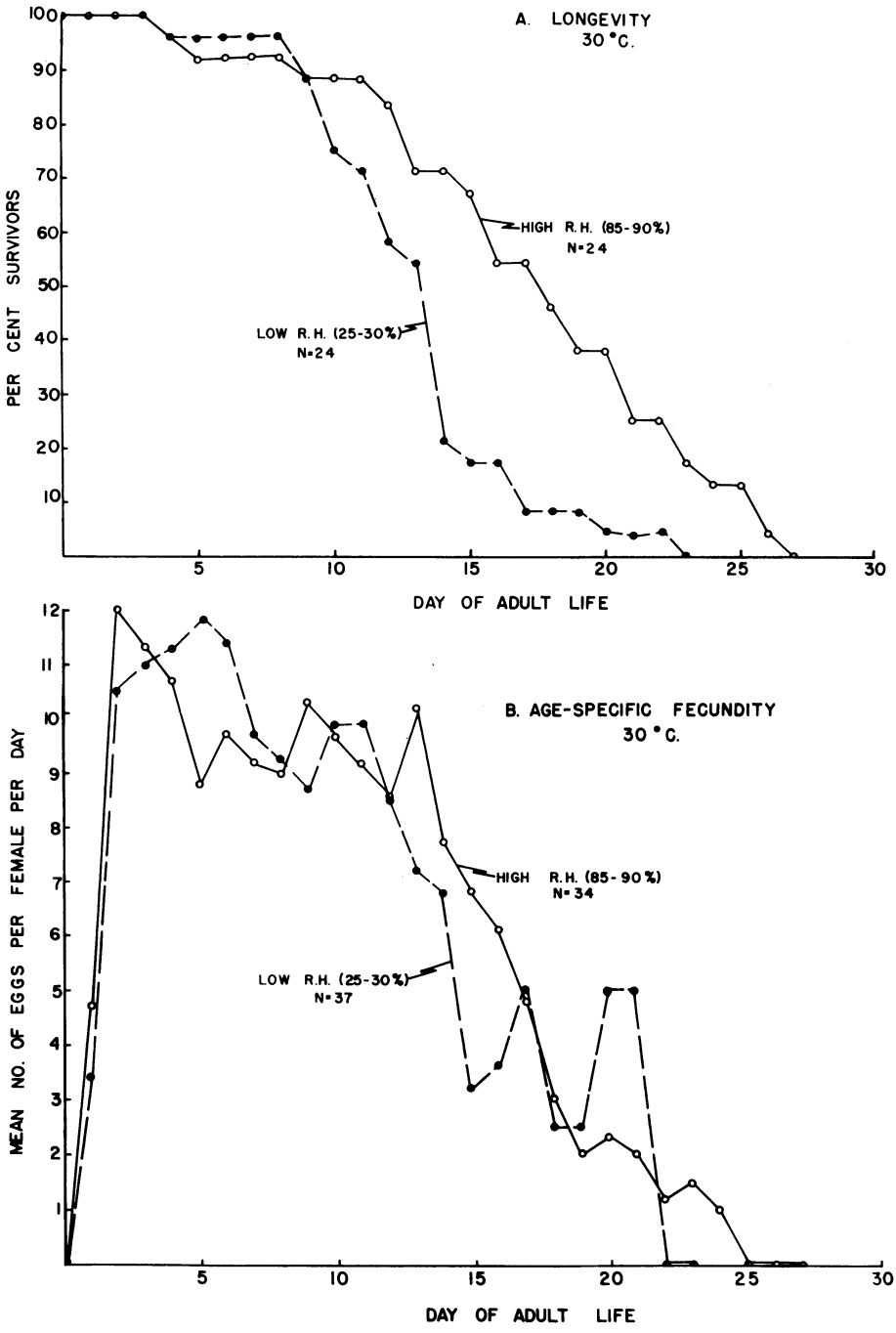

Fig. 19. Longevity and age-specific fecundity of adult *T. desertorum* females at 30°C (29.5 to 30.5°) and at low (closed circles) and high (open circles) humidity levels.

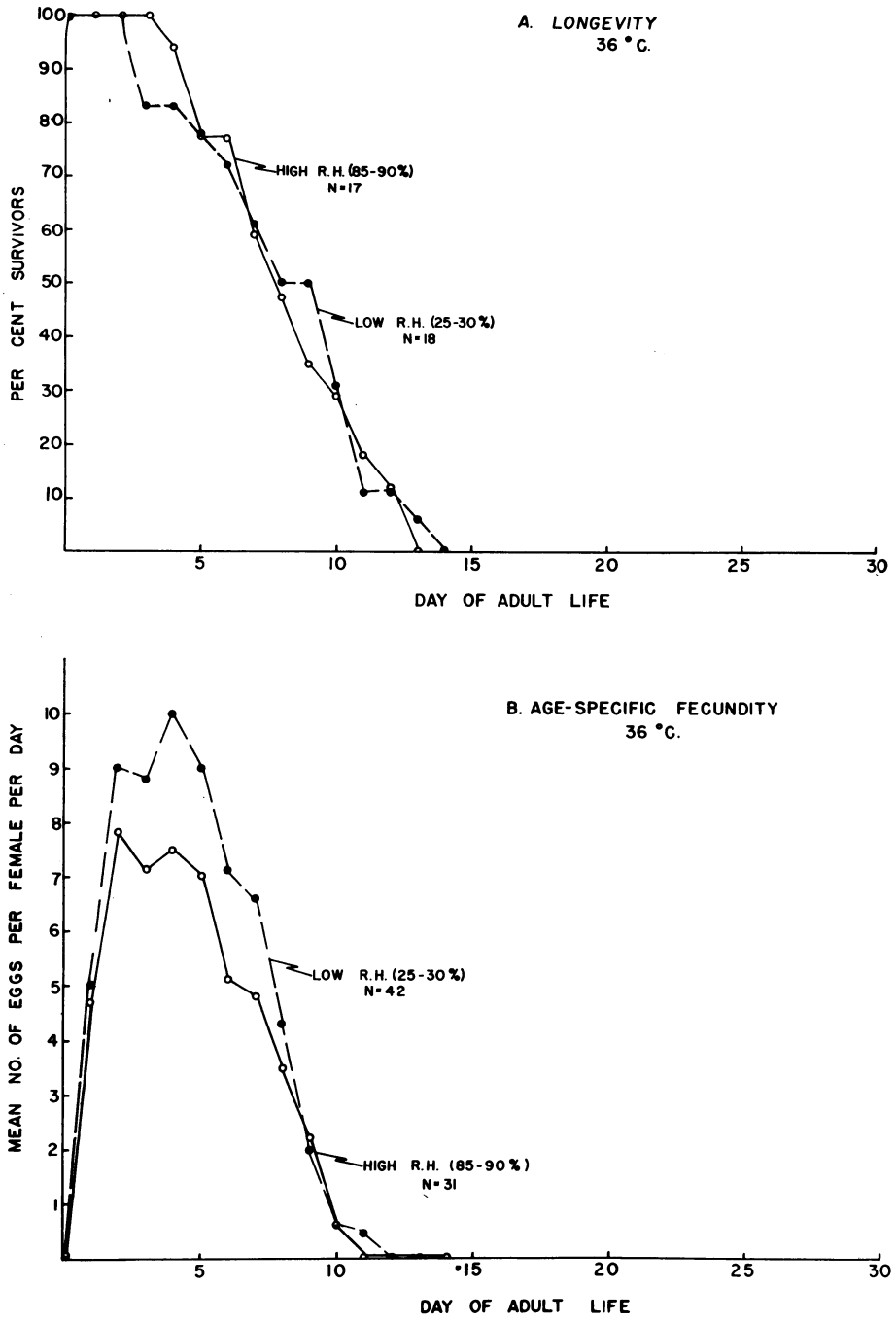

Fig. 20. Longevity and age-specific fecundity of adult *T. desertorum* females at 36° C (35.0 to 37.0°) and at low (closed circles) and high (open circles) relative humidities.

Fecundity. The number of eggs deposited daily was also observed for the females in the longevity trials. The total progeny per female at the various temperature and humidity conditions is given in table 13. The variability in oviposition rate is here added to the variability imposed by differences in longevity so that very broad ranges and high standard errors result; consequently the differences observed between humidity levels were insufficient to allow statistical separation. What differences were indicated, however, were a result of the combined effects of oviposition rate and longevity.

The age-specific fecundity—the mean number of eggs laid per female per

TABLE 13

TOTAL PROGENY OF *T. DESERTORUM* FEMALES AT DIFFERENT TEMPERATURE AND RELATIVE HUMIDITY LEVELS

Temp. °C	Low humidity (25–30%)			High humidity (85–90%)			t*
	Number mites	Total number eggs per female		Number mites	Total number eggs per female		
		Range	Mean ± SE_m		Range	Mean ± SE_m	
16	27	14–124	51.41±4.86	23	23–125	56.13±5.13	0.47
25	21	47–182	118.65±7.84	22	74–187	114.27±7.40	0.29
30	24	25–160	110.05±8.88	24	17–175	132.29±9.19	1.22
36	18	12–77	44.06±5.08	16	18–61	57.94±3.21	0.68

* t values calculated for differences between mean numbers of eggs per female at low and high humidities are not significant at the 5 per cent level.

day on any particular day—provides a clearer picture of oviposition rate, how it changes with age, and how it is affected by temperature and humidity. In calculating these figures it is also possible to utilize data on mites crushed or lost in the course of the experiments for the days in which data are available on them, thus increasing the accuracy of the estimate by utilization of a larger number of observations. Age-specific fecundities for the four temperatures and two humidities are given in the "m_x" columns of tables 14, 15, 16, and 17, and expressed graphically in figures 17B, 18B, 19B, and 20B.

The fecundity curves show the form typical of most insects and mites in which oviposition rate increases rapidly to reach a peak early in the adult life from which there is a gradual decline, the steepness depending on the temperature. A dip shortly after the peak, followed by a secondary peak, appears to be characteristic for *T. desertorum* at several of the conditions tested. The variability at the ends of the curves results from the fact that these portions are based on so few individuals. The results indicate an increase in the age-specific fecundity with an increase in temperature through 30°C, but a decrease at 36°C. No differences due to humidity are evident at 16°C. At the other three temperatures, however, a slightly lower oviposition rate, particularly during the peak period, appears to prevail for the higher humidity level.

TABLE 14

LONGEVITY (l_x), AGE-SPECIFIC FECUNDITY (m_x), AND NET REPRODUCTION RATE (R_0) OF FERTILIZED FEMALE *T. DESERTORUM* MITES AT 16° C (15.0–17.5) AND AT LOW AND HIGH RELATIVE HUMIDITIES

Adult age (days)	Low humidity (25–30%)*				High humidity (85–90%)†			
	Adult l_x	Adjusted l_x	m_x	l_xm_x	Adult l_x	Adjusted l_x	m_x	l_xm_x
1	1.00	0.85	0.0	0.00	1.00	0.96	0.0	0.00
2	1.00	0.85	0.2	0.17	1.00	0.96	0.2	0.19
3	1.00	0.85	0.7	0.60	1.00	0.96	0.5	0.48
4	1.00	0.85	1.1	0.94	1.00	0.96	1.2	1.15
5	1.00	0.85	1.6	1.36	1.00	0.96	1.3	1.25
6	1.00	0.85	2.2	1.87	1.00	0.96	1.9	1.82
7	1.00	0.85	2.2	1.87	1.00	0.96	2.0	1.92
8	1.00	0.85	2.6	2.21	1.00	0.96	2.4	2.30
9	1.00	0.85	2.7	2.30	1.00	0.96	2.4	2.30
10	1.00	0.85	3.0	2.55	1.00	0.96	3.3	3.17
11	1.00	0.85	3.4	2.89	1.00	0.96	3.2	3.07
12	1.00	0.85	3.7	3.15	1.00	0.96	3.5	3.36
13	0.96	0.82	3.3	2.71	1.00	0.96	3.6	3.46
14	0.93	0.79	3.5	2.77	0.96	0.92	3.3	3.04
15	0.89	0.76	3.6	2.74	0.91	0.87	3.4	2.96
16	0.81	0.69	3.0	2.07	0.87	0.84	3.6	3.02
17	0.81	0.69	3.2	2.21	0.83	0.79	3.0	2.37
18	0.67	0.57	2.9	1.65	0.74	0.71	2.9	2.06
19	0.56	0.47	3.0	1.41	0.65	0.62	2.7	1.67
20	0.42	0.36	2.8	1.01	0.52	0.50	3.1	1.55
21	0.37	0.32	2.8	0.90	0.52	0.50	2.3	1.15
22	0.33	0.28	2.9	0.81	0.39	0.37	1.5	0.56
23	0.30	0.25	3.1	0.78	0.39	0.37	2.2	0.81
24	0.26	0.22	2.1	0.46	0.39	0.37	2.6	0.96
25	0.26	0.22	2.9	0.64	0.39	0.37	2.0	0.74
26	0.26	0.22	2.0	0.44	0.35	0.33	2.3	0.76
27	0.22	0.19	2.3	0.44	0.30	0.29	2.1	0.61
28	0.22	0.19	2.0	0.38	0.26	0.25	2.1	0.53
29	0.22	0.19	2.0	0.38	0.26	0.25	1.6	0.40
30	0.19	0.16	2.4	0.38	0.22	0.21	2.0	0.42
31	0.19	0.16	1.6	0.26	0.22	0.21	1.6	0.34
32	0.19	0.16	2.2	0.35	0.22	0.21	2.1	0.44
33	0.19	0.16	1.2	0.19	0.22	0.21	1.5	0.32
34	0.19	0.16	1.2	0.19	0.22	0.21	1.5	0.32
35	0.19	0.16	1.6	0.26	0.22	0.21	1.5	0.32
36	0.15	0.13	1.5	0.20	0.22	0.21	1.2	0.25
37	0.11	0.09	1.0	0.09	0.17	0.17	1.2	0.20
38	0.11	0.09	1.0	0.09	0.17	0.17	1.0	0.17
39	0.11	0.09	1.0	0.09	0.17	0.17	1.6	0.27
40	0.07	0.06	1.5	0.09	0.17	0.17	1.0	0.17
41	0.07	0.06	1.0	0.06	0.17	0.17	1.0	0.17
42	0.07	0.06	0.5	0.03	0.17	0.17	1.3	0.22
43	0.04	0.03	1.0	0.03	0.13	0.12	2.3	0.28
44	0.04	0.03	1.0	0.03	0.13	0.12	2.0	0.24
45	0.04	0.03	0.0	0.00	0.13	0.12	1.7	0.20
46	0.00	0.00	0.0	0.00	0.13	0.12	1.3	0.16
47	....	....	....	....	0.13	0.12	2.3	0.28
48	....	....	....	....	0.13	0.12	1.7	0.20
49	....	....	....	....	0.13	0.12	1.3	0.16
50	....	....	....	....	0.13	0.12	0.3	0.04

(Continued)

TABLE 14—(*Concluded*)

Adult age (days)	Low humidity (25–30%)*				High humidity (85–90%)†			
	Adult l_x	Adjusted l_x	m_x	l_xm_x	Adult l_x	Adjusted l_x	m_x	l_xm_x
51	....	....	....	....	0.13	0.12	1.0	0.12
52	....	....	....	....	0.13	0.12	1.7	0.20
53	....	....	....	....	0.13	0.12	1.3	0.16
54	....	....	....	....	0.09	0.08	1.0	0.08
55	....	....	....	....	0.09	0.08	1.5	0.12
56	....	....	....	....	0.09	0.08	0.5	0.04
57	....	....	....	....	0.09	0.08	1.0	0.08
58	....	....	....	....	0.09	0.08	0.5	0.04
59	....	....	....	....	0.09	0.08	0.0	0.00
60	....	....	....	....	0.09	0.08	0.5	0.04
61	....	....	....	....	0.00	0.00	0.0	0.00
	R_0 = (Σlxmx) = 44.06				R_0 = (Σlxmx) = 53.71			

* l_x based on initial number of 27 mites; m_x based on initial number of 38 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.852.

† l_x based on initial number of 23 mites; m_x based on initial number of 33 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.960.

These differences are summarized and illustrated in figure 21. By dividing mean total progeny per female by mean total adult life, the mean number of eggs per female per day of adult life for each temperature and humidity is obtained. These results are in accordance with the data presented by Boudreaux (1958) who found that mites oviposited at a higher rate in a dry atmosphere than in a wet atmosphere and attributed this to their ability to ingest and utilize larger amounts of food in a dry atmosphere through the elimination of body moisture by evaporation from the cuticle. His findings that mites also lived longer under dry conditions were not supported by the above longevity data, however. This discrepancy will be discussed in more detail in a later section.

Net Reproduction Rate. The results as given above indicate a generally higher immature mortality, shorter adult longevity, and slightly higher fecundity for a low humidity of 25 to 30 per cent as opposed to a high humidity of 85 to 90 per cent. The combined effect of these differences on the reproduction of a species can be evaluated by the calculation of a *net reproduction rate* for each of the conditions listed. The method of calculating this statistic, usually designated as R_0, is given by Andrewartha and Birch (1954) who define it as the multiplication per generation. The R_0 is an estimate of the number of times a single female is able to reproduce itself under conditions of unlimited food supply and protection from natural enemies at any particular combination of physical conditions. The tabulation of these results and the calculation of the R_0 figures for the various temperature and humidity combinations are given in tables 14, 15, 16, and 17. Since the adult longevity (l_x) is based on females observed only during the adult life, the added factor of immature mortality must be incorporated to arrive at a true l_x figure which will reflect the probability of any egg to attain a given adult age. Immature survival factors were taken from the

TABLE 15

LONGEVITY (l_x), AGE-SPECIFIC FECUNDITY (m_x), AND NET REPRODUCTION RATE (R_0) OF FERTILIZED FEMALE *T. DESERTORUM* MITES AT 25°C (24.0–26.0) AND AT LOW AND HIGH RELATIVE HUMIDITIES

Adult age (days)	Low humidity (25–30%)*				High humidity (85–90%)†			
	Adult l_x	Adjusted l_x	m_x	l_xm_x	Adult l_x	Adjusted l_x	m_x	l_xm_x
1	1.00	0.89	0.6	0.53	1.00	0.98	0.9	0.88
2	1.00	0.89	4.4	3.92	1.00	0.98	5.1	5.00
3	1.00	0.89	8.0	7.12	1.00	0.98	8.1	7.94
4	1.00	0.89	9.6	8.54	1.00	0.98	9.2	9.02
5	1.00	0.89	10.4	9.26	1.00	0.98	8.6	8.43
6	1.00	0.89	10.6	9.43	1.00	0.98	8.2	8.04
7	1.00	0.89	10.4	9.26	1.00	0.98	7.9	7.74
8	1.00	0.89	9.5	8.46	1.00	0.98	8.2	8.04
9	0.95	0.84	9.4	7.90	1.00	0.98	7.4	7.25
10	0.90	0.80	8.3	6.64	1.00	0.98	7.5	7.35
11	0.90	0.80	8.2	6.56	0.91	0.89	8.3	7.39
12	0.81	0.72	8.7	6.26	0.77	0.75	8.1	6.89
13	0.76	0.67	7.8	5.23	0.68	0.66	7.7	5.08
14	0.71	0.63	6.6	4.16	0.64	0.63	7.6	4.79
15	0.67	0.59	5.2	3.07	0.64	0.63	6.5	4.10
16	0.57	0.51	3.8	1.94	0.59	0.58	5.3	3.07
17	0.38	0.34	4.6	1.56	0.55	0.54	6.1	3.29
18	0.33	0.29	4.3	1.25	0.50	0.49	6.0	2.94
19	0.24	0.21	3.6	0.76	0.27	0.26	5.2	1.35
20	0.14	0.12	5.3	0.74	0.23	0.22	2.2	0.48
21	0.14	0.12	3.3	0.40	0.18	0.18	4.0	0.72
22	0.14	0.12	1.3	0.16	0.14	0.14	4.0	0.56
23	0.05	0.04	0.5	0.02	0.14	0.14	4.0	0.56
24	0.05	0.04	0.0	0.00	0.09	0.09	2.0	0.18
25	0.05	0.04	0.0	0.00	0.05	0.05	0.0	0.00
26	0.05	0.04	0.0	0.00	0.05	0.05	0.0	0.00
27	0.05	0.04	0.0	0.00	0.05	0.05	0.0	0.00
28	0.00	0.00	0.0	0.00	0.05	0.05	0.0	0.00
29	....	....	....	....	0.05	0.05	0.0	0.00
30	....	....	....	....	0.00	0.00	0.0	0.00
	R_0 = (Σlxmx) = 103.17				R_0 = (Σlxmx) = 111.09			

* l_x based on initial number of 21 mites; m_x based on initial number of 20 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.887.

† l_x based on initial number of 22 mites; m_x based on initial number of 28 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.977.

survival data given in table 11. These figures were multiplied by the adult l_x figures to obtain an "adjusted l_x." A true m_x figure should represent the number of female offspring per female per day. Since the sex ratio was not accurately determined for the various conditions and ages, this aspect is not incorporated into the data and the total offspring per day is given in the mx columns. This results in R_0 values which are higher, probably by about 25 per cent, than the true value, but should not affect comparisons made between the various temperatures and humidities unless these conditions significantly affect the sex ratio.

Multiplication of the m_x by the adjusted l_x figures and the summation of these products for the total number of days resulted in the R_0 figures given. These net reproduction rates are plotted against temperature for the

TABLE 16

LONGEVITY (l_x), AGE-SPECIFIC FECUNDITY (m_x), AND NET REPRODUCTION RATE (R_0) OF FERTILIZED FEMALE *T. DESERTORUM* MITES AT 30°C (29.5–30.5) AND AT LOW AND HIGH RELATIVE HUMIDITIES

Adult age (days)	Low humidity (25–30%)*				High humidity (85–90%)†			
	Adult l_x	Adjusted l_x	m_x	l_xm_x	Adult l_x	Adjusted l_x	m_x	l_xm_x
1	1.00	0.91	3.4	3.09	1.00	0.97	4.7	4.57
2	1.00	0.91	10.5	9.56	1.00	0.97	12.0	11.64
3	1.00	0.91	11.0	10.01	1.00	0.97	11.3	10.96
4	0.96	0.88	11.3	9.94	0.96	0.93	10.7	9.95
5	0.96	0.88	11.8	10.38	0.92	0.89	8.8	7.83
6	0.96	0.88	11.4	10.03	0.92	0.89	9.7	8.63
7	0.96	0.88	9.7	8.54	0.92	0.89	9.2	8.19
8	0.96	0.88	9.3	8.18	0.92	0.89	9.0	8.54
9	0.88	0.80	8.7	6.96	0.88	0.85	10.3	8.76
10	0.75	0.68	9.9	6.73	0.88	0.85	9.7	8.25
11	0.71	0.65	9.9	6.44	0.88	0.85	9.2	7.82
12	0.58	0.53	8.5	4.51	0.83	0.80	8.6	6.88
13	0.54	0.49	7.2	3.53	0.71	0.69	10.2	7.04
14	0.21	0.19	6.8	1.29	0.71	0.69	7.7	5.31
15	0.17	0.16	3.2	0.51	0.67	0.65	6.8	4.42
16	0.17	0.16	3.6	0.58	0.54	0.52	6.1	3.17
17	0.08	0.07	5.0	0.35	0.54	0.52	4.8	2.50
18	0.08	0.07	2.5	0.18	0.46	0.44	3.0	1.32
19	0.08	0.07	2.5	0.18	0.38	0.37	2.0	0.74
20	0.04	0.04	5.0	0.20	0.38	0.37	2.3	0.85
21	0.04	0.04	5.0	0.20	0.25	0.24	2.0	0.48
22	0.04	0.04	0.0	0.00	0.25	0.24	1.2	0.29
23	0.00	0.00	0.0	0.00	0.17	0.16	1.5	0.24
24	....	....	....	....	0.13	0.13	1.0	0.13
25	....	....	....	....	0.13	0.13	0.0	0.00
26	....	....	....	....	0.04	0.04	0.0	0.00
27	....	....	....	....	0.00	0.00	0.0	0.00
	$R_0 = (\Sigma lxmx) = 101.39$				$R_0 = (\Sigma lxmx) = 128.51$			

* l_x based on initial number of 24 mites; m_x based on initial number of 37 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.913.

† l_x based on initial number of 24 mites; m_x based on initial number of 34 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.965.

two humidities in figure 22. These results show that under the particular conditions of preconditioning, handling, and food availability under which these trials were conducted, the temperature and humidity combination, of the eight combinations tested, most favorable for a high rate of reproduction per generation was 30°C and 85 to 90 per cent relative humidity. At the low humidity little difference was shown between the 25°C and 30°C temperatures. At all temperatures 85 to 90 per cent relative humidity was shown to be superior to 25 to 30 per cent, with the greatest spread due to humidity occurring at 30°C.

Boudreaux (1958), in studies of the effects of relative humidity on egg-laying, hatching, and survival of various species of *Tetranychus,* found that at variable temperatures between 75° and 95°F (23.9° to 35.0°C) *T. desertorum* females produced an average total of 40.6 eggs per mite during their lifetime at low humidities, ranging downward from 35 per cent to near

TABLE 17

LONGEVITY (l_x), AGE-SPECIFIC FECUNDITY (m_x), AND NET REPRODUCTION RATE (R_0)OF FERTILIZED FEMALE *T. DESERTORUM* MITES AT 36°C (35.0–37.0) AND AT LOW AND HIGH RELATIVE HUMIDITIES

Adult age (days)	Low humidity (25–30%)*				High humidity (85–90%)†			
	Adult l_x	Adjusted l_x	m_x	l_xm_x	Adult l_x	Adjusted l_x	m_x	l_xm_x
1	1.00	0.13	5.0	0.65	1.00	0.28	4.7	1.32
2	1.00	0.13	9.0	1.17	1.00	0.28	7.8	2.18
3	0.83	0.10	8.8	0.88	1.00	0.28	7.1	1.99
4	0.83	0.10	10.0	1.00	0.94	0.26	7.5	1.95
5	0.78	0.10	9.0	0.90	0.77	0.21	7.0	1.47
6	0.72	0.09	7.1	0.64	0.77	0.21	5.1	1.07
7	0.61	0.08	6.6	0.53	0.59	0.16	4.8	0.77
8	0.50	0.06	4.3	0.26	0.47	0.13	3.5	0.46
9	0.50	0.06	2.0	0.12	0.35	0.10	2.2	0.22
10	0.31	0.04	0.6	0.02	0.29	0.08	0.6	0.05
11	0.11	0.01	0.5	0.01	0.18	0.05	0.0	0.00
12	0.11	0.01	0.0	0.00	0.12	0.03	0.0	0.00
13	0.06	0.01	0.0	0.00	0.00	0.00	0.0	0.00
14	0.00	0.00	0.0	0.00	0.00	0.00	0.0	0.00
	$R_0 = (\Sigma lxmx) = 6.18$				$R_0 = (\Sigma lxmx) = 11.48$			

* l_x based on initial number of 18 mites; m_x based on initial number of 42 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.126.

† l_x based on initial number of 17 mites; m_x based on initial number of 31 mites. Adjusted l_x calculated by multiplying adult l_x by immature survival factor of 0.279.

zero, as opposed to an average total of 21.2 eggs per mite at high humidities ranging from 95 to 100 per cent. The mean temperature in his trials was probably nearest to the 30°C level tested above. This low humidity should be comparable with or lower than the low humidities reported above, and the high humidity used by Boudreaux was considerably higher than the high humidity used in these trials, since he used water in a closed system containing the test leaves. His results indicated only slightly more eggs laid per female per day at the low humidity level than at the very high humidity level (5.1 versus 4.7). The larger total progenies at the low humidity were, therefore, predominantly the result of a longer adult life under this condition—almost twice that at the very high humidity. He also reported a much higher nymphal mortality at the very high humidity. The daily fecundity difference due to humidity level was similar to that found in these studies as shown in figure 21. The reduced adult longevity by the very high humidity, however, is just the opposite from the results indicated in table 12. The low total numbers of eggs per mite reported by Boudreaux compared with the totals given for 30°C in table 13 suggest that the extremely high humidity tested by him may have been detrimental.

To determine whether a humidity near saturation would give different results from those obtained at the 85 to 90 per cent level, a series of longevity-fecundity observations were conducted at 30°C using water in the desiccators instead of the potassium nitrate solution. The results of these observations are compared with those obtained at the other two humidities

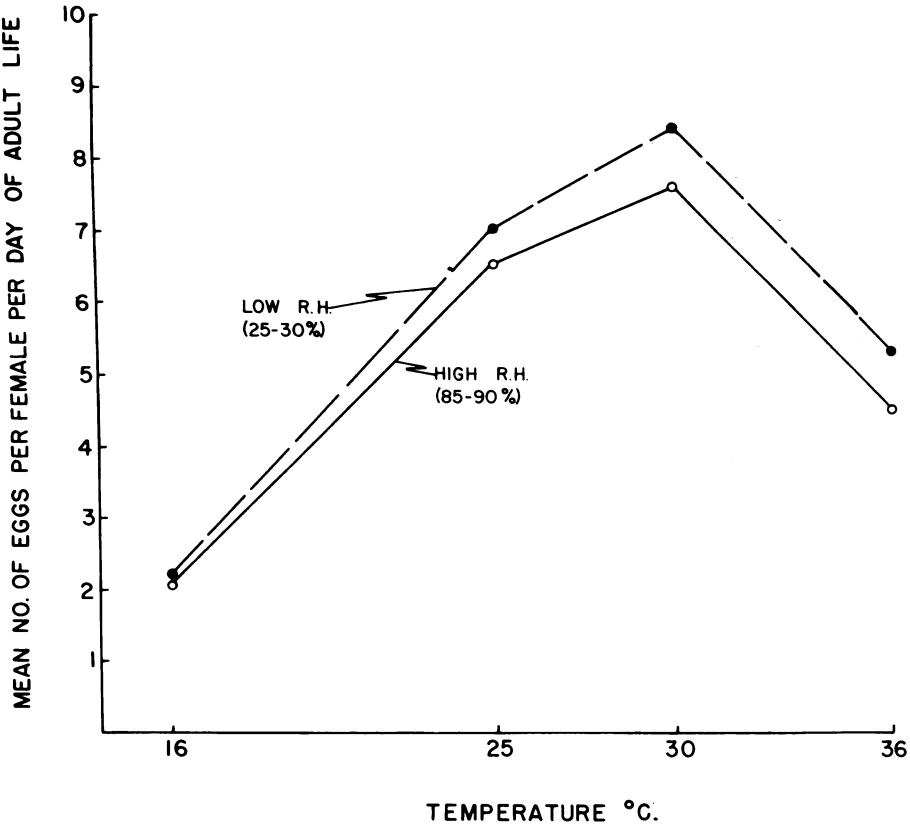

Fig. 21. Effect of temperature and relative humidity on mean daily fecundity of adult *T. desertorum* females.

TABLE 18

LONGEVITY AND FECUNDITY OF *T. DESERTORUM* AT 30°C (29.5–30.5) AND AT THREE RELATIVE HUMIDITY LEVELS

Property	Low humidity (25–30%)	High humidity (85–90%)	Very high humidity (95–100%)
Mean length of adult life (days)	13.17	17.42	13.22
Mean total number eggs per female	110.05	132.29	97.83
Mean number eggs per female per day	8.36	7.59	7.41

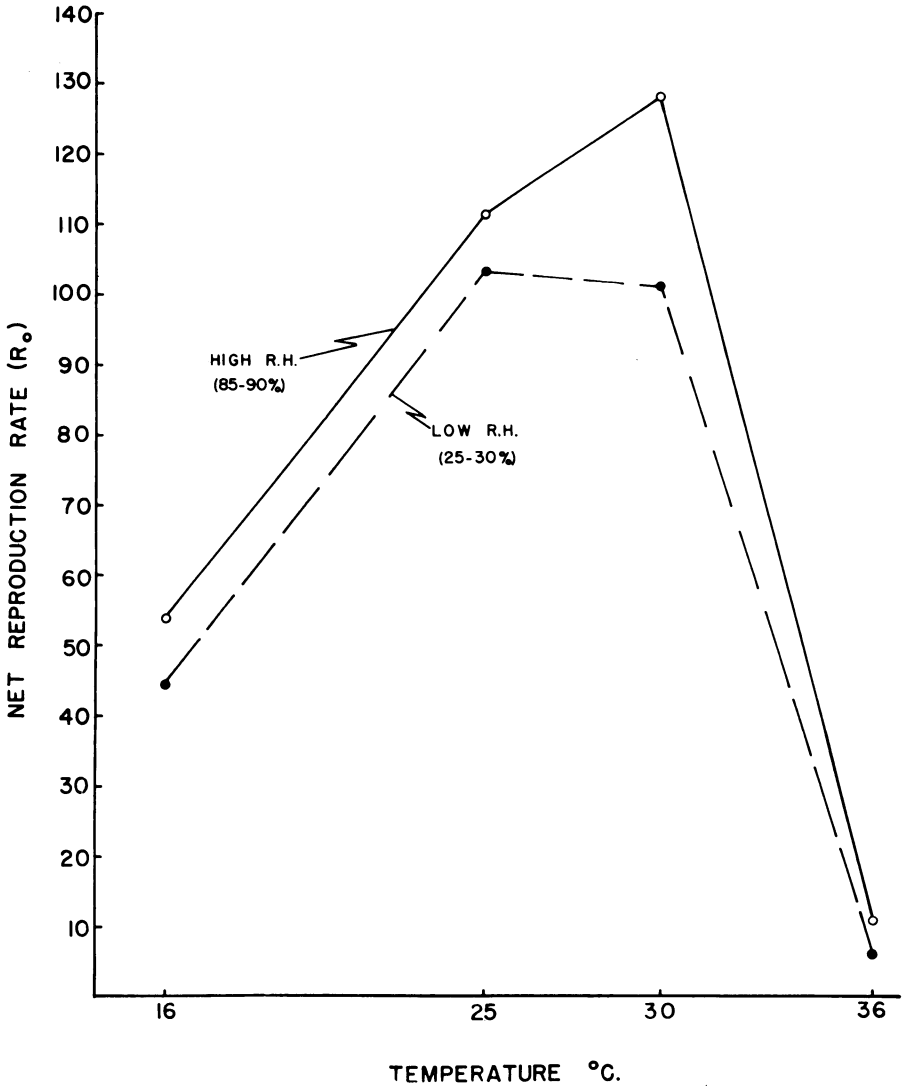

Fig. 22. Effect of temperature and relative humidity on the net reproduction rate of *T. desertorum.*

at this temperature in table 18. No immature mortality observations were made. However, even assuming the low immature mortality observed for the 85 to 90 per cent humidity, calculation of the net reproduction rate for the 95 to 100 per cent humidity level resulted in a R_0 of 94.83. This figure is lower than that calculated for either of the other two humidities tested at this temperature, and would have been even less if a greater immature mortality, as indicated by Boudreaux, had been used. The R_0 values for the three humidity levels are plotted in figure 23. These results tend to

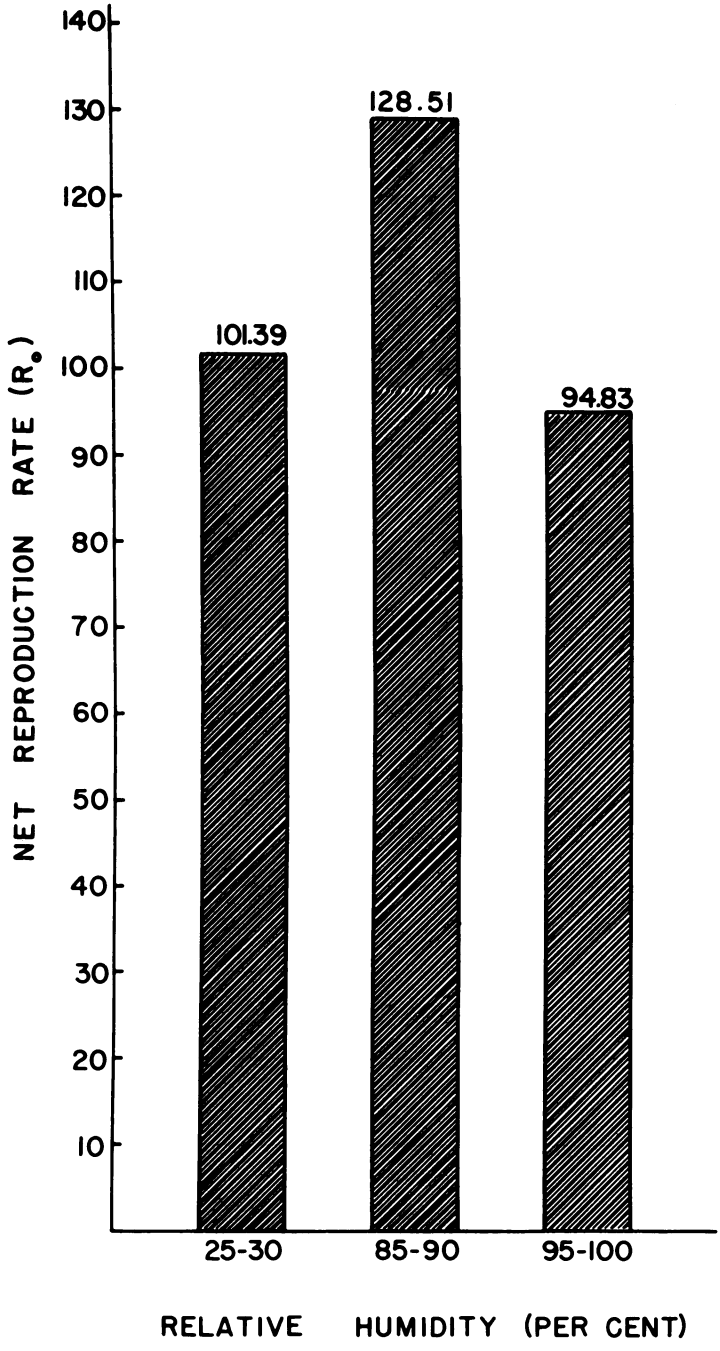

Fig. 23. Net reproduction rates of *T. desertorum* mites at 30° C (29.5 to 30.5) at various humidity levels.

confirm the suggestion that the apparent contradictions between the results reported in these studies and the reports of other investigators can at least partially be explained on the basis of different humidity levels.

Rate of Development. Another important factor in considering the relative favorability or unfavorability of various conditions is the effect these conditions have on the rate of development. This factor is important because it determines the length of time required to complete a generation and also because the length of time spent in various stages, especially the egg stage, may have an important bearing on exposure to predation.

The duration of the various immature stages was determined for *T. desertorium* at 16°C, 25°C, 30°C, and 36°C under low (25 to 30 per cent) and high (85 to 90 per cent) relative humidity conditions. Eggs laid by females in the longevity-fecundity trials during the second to fourth days of oviposition were separated and observed in the manner described for the variable temperature studies above. The durations of the immature stages at the various conditions are given in table 19. These are the combined values obtained for both females and males. The total developmental periods for each sex are given in table 20.

Because of difficulties in confining the mites to the cells at 36°C and because of the high mortality at this temperature, the information other than duration of the egg state is incomplete. The other three temperatures tested,

TABLE 19

DURATION OF IMMATURE STAGES OF *T. DESERTORUM* AT DIFFERENT TEMPERATURE AND RELATIVE HUMIDITY LEVELS

Temp. °C	Stage	Low humidity (25–30%)			High humidity (85–90%)			*t*†
		Number mites	Duration (days)*		Number mites	Duration (days)*		
			Range	Mean ± SE_m		Range	Mean ± SE_m	
16	Egg	82	11–14	12.37±0.16	87	11–14	12.21±0.08	0.64
	Larva	58	4–7	4.95±0.10	60	3–6	4.70±0.10	1.25
	Protonymph	43	3–5	4.00±0.05	58	3–6	4.10±0.08	0.77
	Deutonymph	41	4–7	5.54±0.09	24	4–6	4.92±0.12	2.95‡
	Total§	41	25–29	26.70±0.16	24	24–27	25.41±0.14	4.63‡
25	Egg	121	4.5–6.0	4.99±0.03	95	4.0–4.5	4.29±0.03	11.67‡
	Larva	92	1.5–2.5	1.95±0.02	75	1.5–2.0	1.75±0.03	4.00‡
	Protonymph	88	1.0–2.0	1.61±0.03	74	1.0–2.5	1.57±0.04	0.57
	Deutonymph	83	1.5–3.0	2.02±0.04	68	1.5–3.5	2.20±0.06	1.63
	Total§	82	9.5–12.0	10.52±0.07	68	9.0–12.5	9.82±0.09	4.38‡
30	Egg	89	2.5–3.5	3.21±0.03	131	2.5–3.0	2.86±0.02	7.00‡
	Larva	50	1.0–2.0	1.45±0.03	113	1.0–2.0	1.22±0.02	4.60‡
	Protonymph	49	0.5–1.5	1.09±0.03	110	0.5–1.5	1.11±0.02	0.40
	Deutonymph	49	1.0–2.0	1.61±0.04	105	1.0–3.0	1.67±0.04	0.75
	Total§	49	7.0–8.0	7.37±0.05	105	6.0–8.5	6.90±0.05	4.70‡
36	Egg	19	2.5–3.5	2.82±0.07	90	2.0–3.5	2.69±0.03	1.18

* Both sexes.
† *t* values calculated for differences between mean development times at low and high humidity.
‡ Statistical separation at the 0.01 level of significance.
§ Egg to adult.

TABLE 20

DURATION OF TOTAL IMMATURE DEVELOPMENT (EGG TO ADULT) OF *T. DESERTORUM* AT DIFFERENT TEMPERATURE AND RELATIVE HUMIDITY LEVELS

Temp. °C	Sex	Low humidity (25–30%)			High humidity (85–90%)			t*
		Number mites	Duration (days)		Number	Duration (days)		
			Range	Mean ± SE_m		Range	Mean ± SE_m	
16	Male	5	25–29	27.00±0.71	8	24–26	24.87±0.23	2.19†
	Female	36	25–29	26.67±0.16	24	24–27	25.69±0.18	2.83†
25	Male	39	10.0–11.5	10.46±0.08	15	9.0–10.0	9.33±0.08	5.95†
	Female	43	9.5–12.0	10.57±0.14	53	9.0–12.5	9.95±0.11	2.95†
30	Male	5	7.0–7.5	7.10±0.12	9	6.0–7.0	6.33±0.12	3.21†
	Female	44	7.0–8.0	7.40±0.06	96	6.0–8.5	6.95±0.05	4.09†
36	Male	2	6.0–6.5	6.25±0.25	1	6.5	6.50±0.00	0.76
	Female	3	8.0–9.0	8.50±0.29	5	7.5–9.5	8.70±0.41	0.37

* t values calculated for differences between mean development times at low and high humidities.
† Statistical separation at the 0.01 level of significance.

however, all showed highly significant decreases in total developmental time at high compared with low humidity. At 16°C most of this effect can be attributed to the shorter duration of the deutonymph stage. At 25°C and 30°C the major effect of humidity on rate of development appeared to be in the egg stage and a lesser, though significant, difference in the larval stage.

The rates of development for the various temperature and humidity combinations, as determined by multiplying the reciprocal of the duration in days by 100, are illustrated for the egg stage in figure 24 and for the total periods of immature development for females in figure 25. These show an increase in rate of development with increased temperature as is the rule for poikilothermous animals within the favorable temperature range. The 36°C temperature appears to be outside the favorable range, as evidenced by the decreased rates of development for the total immature period at this temperature. This decrease is mainly due to an increase in the duration of the deutonymph stage of females. The rate of development curves again indicate the general favorability of high as opposed to low relative humidities. These differences due to humidity level are most pronounced in the egg stage.

A number of eggs were also incubated at an intermediate humidity of 45 per cent at 30°C to determine whether or not a gradient was present in the effect of humidity on the duration of the egg stage. Observations made on 54 eggs indicated a mean incubation period (± SE_m) of 2.97 ± 0.02. The incubation periods for the three humidity levels at 30°C are plotted in figure 26. These results demonstrate a slight gradation of faster development with higher relative humidity.

The durations of the preoviposition periods at the various temperatures and at the two humidity levels are given in table 21. The duration of this

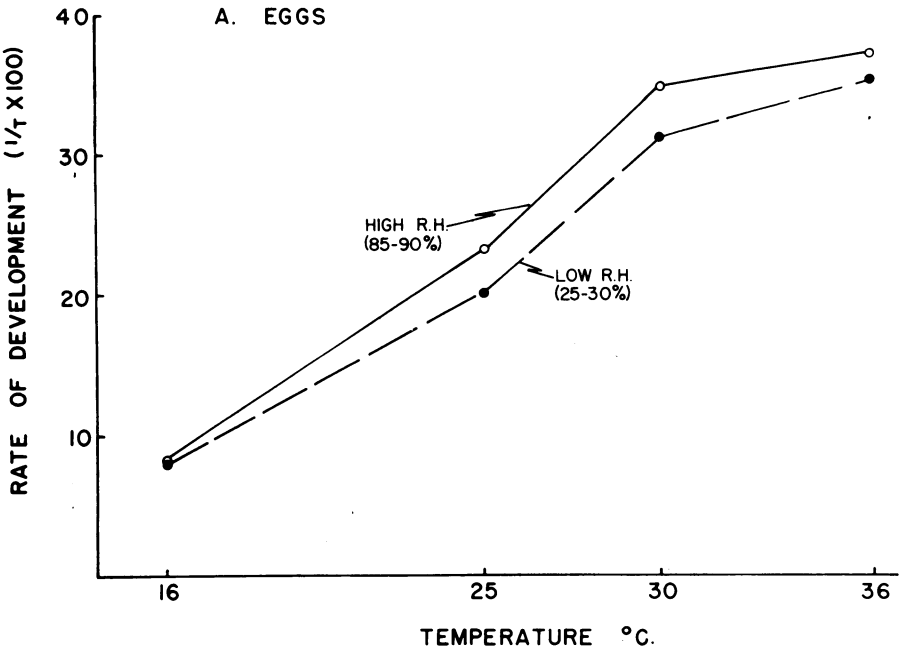

Fig. 24. Effect of temperature and relative humidity on the rate of development of *T. desertorum* eggs.

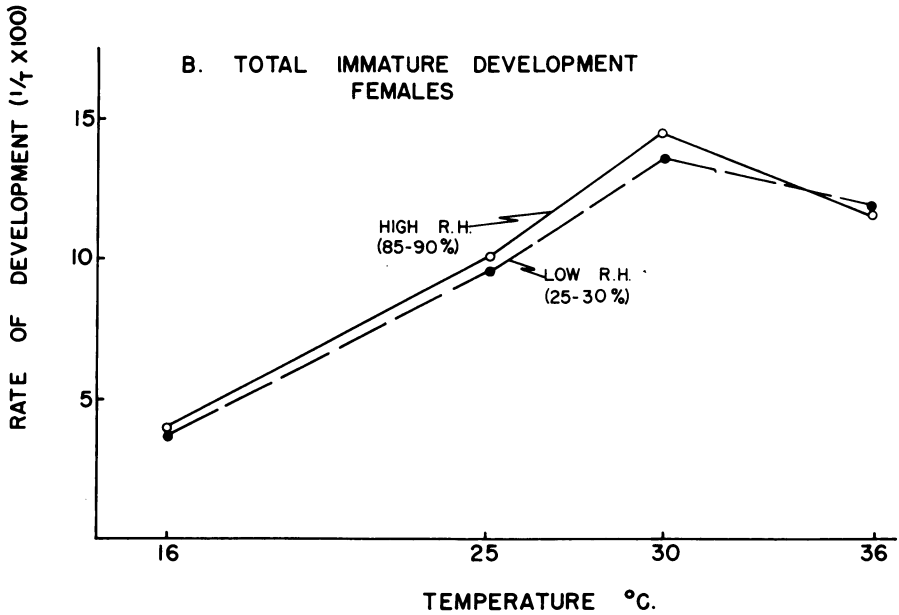

Fig. 25. Effect of temperature and humidity on the rate of development for the total developmental period (egg to adult) of *T. desertorum*.

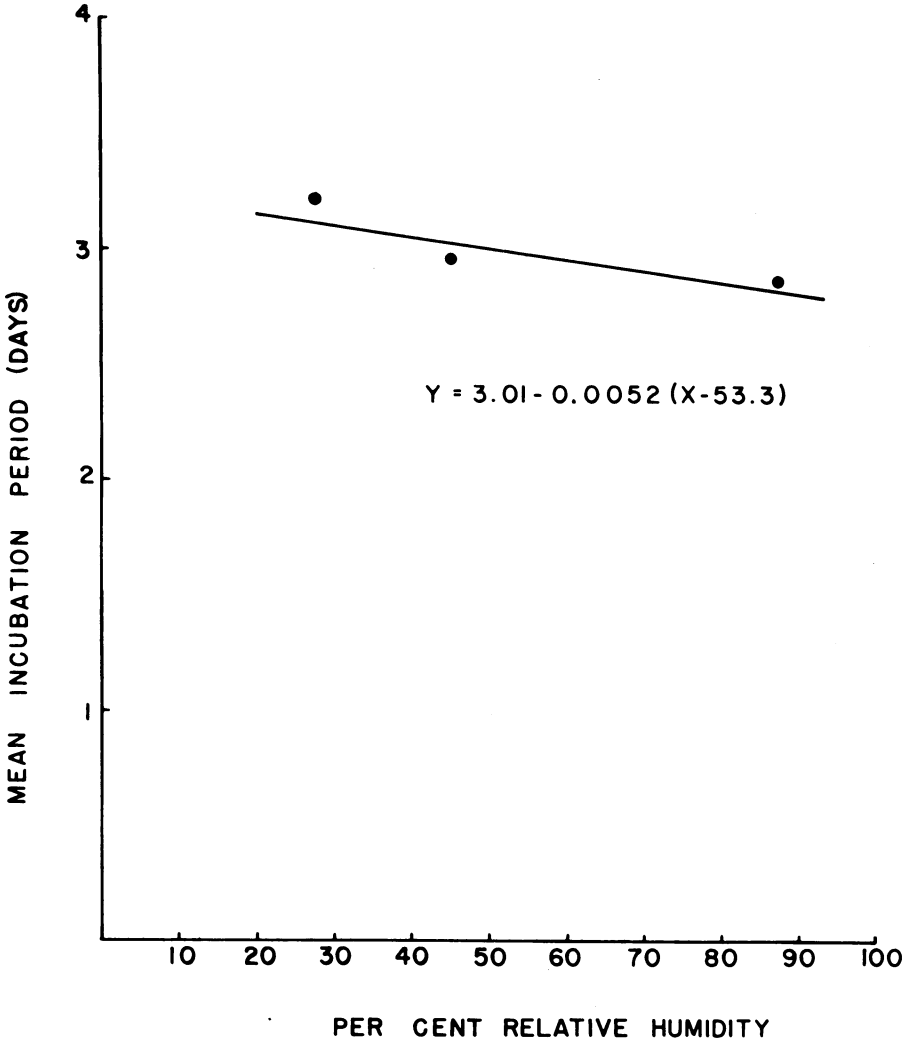

Fig. 26. Effect of relative humidity on incubation period of *T. desertorum* eggs at 30° C (29.5–30.5).

period was reduced by an increase in temperature. No significant difference due to relative humidity was observed.

Innate Capacity for Increase. The calculations of the reproduction rates for the various conditions as expressed by the R_0 figures shown above give merely the net multiplication per generation without regard to velocity, since the length of time required to complete a generation was not included in the calculations. Lotka (1925) incorporated the time factor for human populations in a function which he called "the intrinsic rate of natural increase." Birch (1948) applied this principal to insect studies. Andrewartha and Birch (1954) referred to "the innate capacity for increase" as the sta-

TABLE 21

PREOVIPOSITION PERIODS OF *T. DESERTORUM* FEMALES AT DIFFERENT TEMPERATURE AND RELATIVE HUMIDITY LEVELS

Temp. ° C	Low humidity (25–30%)			High humidity (85–90%)			t*
	Number mites	Duration (days)		Number mites	Duration (days)		
		Range	Mean ± SE_m		Range	Mean ± SE_m	
16	38	2.0–8.0	3.74±0.41	36	2.0–8.0	3.54±0.31	0.28
25	25	0.5–2.0	1.30±0.08	27	0.5–2.0	1.20±0.06	0.67
30	30	0.5–1.0	0.86±0.06	12	0.5–1.0	0.88±0.06	0.17
36	35	0.5–1.5	0.77±0.05	32	0.5–1.5	0.80±0.05	0.27

* t values calculated for differences between mean preoviposition periods at low and high humidities are not significant at the 5 per cent level.

tistic estimating the parameter of the intrinsic rate of natural increase of the population. This innate capacity for increase (r_m) represents the maximum rate of increase of a population of stable age distribution under any set of conditions in which food and space are unlimited and natural enemies are excluded. The above investigators gave the formula $(r_m = \log_e R_0)/T$ in which the T is the mean length of a generation. Since T can be accurately estimated only when r_m is known, the equation $\int_0^\infty e^{-rx} l_x m_x d_x = 1$ was also given. An approximation derived from this equation is $\Sigma e^{-rx} l_x m_x \rightarrow 1$ (Birch, 1948). By means of trial and error substitution into this equation an estimate of r_m can be made.

Using the latter formula, the $l_x m_x$ and adult age data from tables 14–17, and the total female developmental periods given in table 20, the innate capacities for increase (r_m) were calculated for the various temperature and humidity combinations. The results of these calculations are given in table 22. The pivotal age, x, used in the calculations was determined for each age by adding the total female developmental time to the adult age minus 0.5 day.

Using these estimates of the reproductive potential of *T. desertorum* as the criterion for favorability, the most favorable temperature of those tested was shown to be 30°C. A slight tendency was also indicated for the r_m at

TABLE 22

INNATE CAPACITIES FOR INCREASE OF *T. DESERTORUM* AT DIFFERENT TEMPERATURE AND RELATIVE HUMIDITY LEVELS

Temp. ° C	r_m	
	Low humidity (25–30%)	High humidity (85–90%)
16	0.10	0.10
25	0.28	0.29
30	0.40	0.42
36	0.15	0.21

high humidity to be more than that at low humidity. The humidity differences were not as marked as those indicated by the R_0 figures. This would appear to be surprising in that the generally faster rates of immature development established for high humidity should be additive to the higher rates of reproduction indicated by the R_0 values. One explanation for the smaller degree of separation lies in the fact that the r_m figures are logarithmic expressions. Also it must be recognized that the higher R_0 figures for the higher humidities were to a great extent the results of greater longevities. The effect of this factor in some instances was sufficient to counteract the slightly shorter time spent in immature development at the high humidity, resulting in slight increases in the T values. It is also to be noted from the formula $(r_m = \log_e R_0)/T$ that the time factor is placed arithmetically in relation to a logarithmic expression of the net reproduction rate. The consequent exaggeration of the time element, strongly influenced by adult longevity, would tend to diminish some of the greater differences due to humidity observed in the R_0 considerations when calculating r_m values.

Comparison with Tetranychus telarius. The results of laboratory studies with *T. desertorum* indicated, in general, that this species is favored by moderately high humidity. This would seem a plausible explanation for the fact that it is not an important pest of cotton in arid central California. Such an explanation would have little meaning, however, if a species, such as *T. telarius,* which is a serious cotton pest in this region, demonstrated the same relationship.

Studies on the humidity relationships of *T. telarius* by Andres (1957) showed this species to be favored by a low humidity. At 75°F (23.9°C) he calculated R_0 values of 150.35 at 45 per cent relative humidity, and 122.51 at near 100 per cent relative humidity. At 95°F (35°C) he demonstrated a R_0 of 69.99 at 45 per cent and 47.75 at 100 per cent relative humidity. As shown in the comparison with Boudreaux's (1958) investigations, a near 100 per cent relative humidity is not comparable to the 85 to 90 per cent level used in these studies. Other differences in methods between Andres' study and this precluded the direct comparison of his results with the *T. desertorum* figures so that observations with *T. telarius* using identical methods and temperatures as were used in the *T. desertorum* studies were considered essential. Since 30°C is comparable to the mean temperature commonly encountered under summer field conditions, and this temperature produced the greatest differences due to relative humidity level for *T. desertorum,* longevity, fecundity, and developmental observations were made with *T. telarius* at this temperature. Because of the large differences in egg mortality between the two humidities at 36°C, observations were also made for egg survival at this high temperature. The *T. telarius* mites used in these trials were reared on cotton seedlings under the standardized conditions described earlier for *T. desertorum.* The source of these mites was a population of *T. telarius* mites existing as a contaminant on the lima bean *T. desertorum* stock cultures.

The results of developmental studies at 30°C are given in tables 23 and 24. These results show a significantly more rapid rate of development at the low humidity, mainly attributable to the faster rate in the protonymph stage.

TABLE 23

DURATION OF IMMATURE STAGES OF *T. TELARIUS* AT 30°C AT LOW AND HIGH RELATIVE HUMIDITY LEVELS

Stage	Low humidity (25–30%)			High humidity (85–90%)			t‡
	Number mites	Duration (days)*		Number mites	Duration (days)*		
		Range	Mean ± SE_m		Range	Mean ± SE_m	
Egg	168	2.5–3.5	2.68±0.02	134	2.0–3.5	2.62±0.02	1.50
Larva	59	0.5–2.0	1.19±0.04	53	1.0–2.0	1.24±0.04	0.63
Protonymph	49	1.0–1.5	1.10±0.03	43	1.0–3.0	1.43±0.06	3.30§
Deutonymph	38	1.0–4.0	1.52±0.10	33	1.0–3.5	1.84±0.07	1.88
Total†	38	5.5–9.0	6.45±0.11	33	5.5–9.0	7.09±0.17	2.21¶

* Both sexes.
† Egg to adult.
‡ t values calculated for differences between mean durations for high and low humidities.
§ Statistical separation at 0.01 level of significance.
¶ Statistical separation at 0.05 level of significance.

TABLE 24

IMMATURE MORTALITY OF *T. TELARIUS* AT 30°C AT LOW AND HIGH RELATIVE HUMIDITY LEVELS

Stage	Low humidity (25–30%)			High humidity (85–90%)		
	Number mites	Number dead	Mortality (per cent)	Number mites	Number dead	Mortality (per cent)
Egg	182	14	7.7	147	13	8.8
Larva	61	2	3.3	57	4	7.0
Protonymph	49	0	0.0	44	1	2.3
Deutonymph	38	0	0.0	33	1	2.9
Total (accumulative)			10.7			19.6

The results (table 24) also indicate a generally lower rate of immature mortality at the low humidity.

The adult longevity and age-specific fecundity of *T. telarius* are illustrated in figure 27. They show slightly less longevity but considerably higher fecundity at the low humidity. This information, together with the immature mortality data, was compiled to calculate net reproduction rates in the manner described for *T. desertorum* above, resulting in R_0 values of 70.09 for the low humidity and 47.09 for the high humidity. Incorporating the rates of development, the innate capacities for increase were also calculated by the method described above, resulting in r_m figures of 0.42 for the low humidity compared with 0.36 for the high humidity.

The effects of relative humidity levels on rate of development, immature mortality, net reproduction rate, and innate capacity for increase for *T. telarius* are summarized in table 25 in comparison with the results obtained for the same functions with *T. desertorum* under the same conditions. For each of these properties the effect of humidity level on *T. desertorum* was reversed with *T. telarius*. Whereas high humidity was apparently most favor-

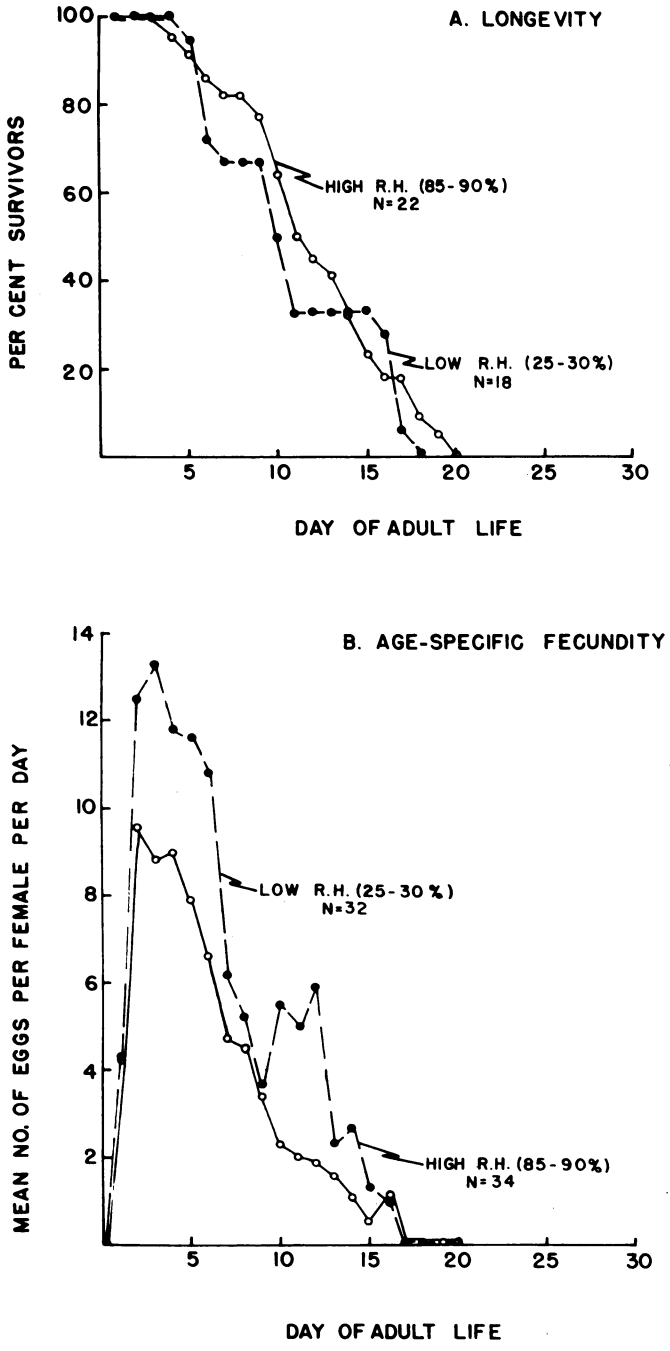

Fig. 27. Longevity and age-specific fecundity of adult *T. telarius* females at 30° C (29.5 to 30.5) and at low (closed circles) and high (open circles) humidity levels.

able in regard to each of these aspects for *T. desertorum, T. telarius* was favored by low humidity in each case. A comparison of the r_m figures indicates an advantage in the capacity for rapid population growth of *T. telarius* over *T. desertorum* at low humidity and of *T. desertorum* over *T. telarius* at high humidity. In the absence of other limiting factors, and assuming competition between these two species for broadly overlapping niche requirements, these results would indicate the ascendancy of *T. telarius* under arid, and of *T. desertorum* under humid conditions.

A high temperature of 36°C was demonstrated to be very detrimental to *T. desertorum* eggs, particularly at the low humidity; hence similar tests were conducted using *T. telarius* eggs to determine their tolerance to these conditions. A comparison of the results of these trials with those obtained with *T. desertorum* is given in table 26. These results indicate little difference in egg mortality at 36°C due to humidity level with *T. telarius,* but the differences observed were in the opposite direction from those observed with *T. desertorum. T. telarius* eggs showed a much greater tolerance to the hot and dry combination than did *T. desertorum* eggs.

TABLE 25

A COMPARISON OF THE RATE OF DEVELOPMENT, IMMATURE MORTALITY, NET REPRODUCTION RATE (R_0), AND INNATE CAPACITY FOR INCREASE (r_m) OF *T. DESERTORUM* AND *T. TELARIUS* AT 30°C AND AT LOW AND HIGH RELATIVE HUMIDITY LEVELS

Function	Low humidity (25–30%)		High humidity (85–90%)	
	T. desertorum	*T. telarius*	*T. desertorum*	*T. telarius*
Duration of immature dev. (days)*	7.40	6.64	6.95	7.48
Immature mortality (per cent)	8.7	10.7	3.7	19.6
R_0	101.39	70.76	128.51	47.09
r_m	0.40	0.46	0.42	0.36

* Egg to adult, females.

TABLE 26

EGG MORTALITY OF *T. DESERTORUM* AND *T. TELARIUS* AT 36°C (35.0 TO 37.0) AT LOW AND HIGH RELATIVE HUMIDITY LEVELS

Species	Per cent mortality	
	Low humidity (25–30%)	High humidity (85–90%)
T. desertorum	83.2	39.5
T. telarius	40.4	48.4

DISCUSSION

Having obtained the above data under the artificial conditions imposed by laboratory studies, it is necessary for these data to be ecologically meaningful, to relate them to the field conditions.

The field observations that *T. desertorum* is largely limited in its distribution to those regions in which winter monthly mean temperatures exceed 40°F are supported by the laboratory data indicating that little or no development takes place and some lethal effect is experienced at the somewhat higher temperature of 50°F (10°C).

The investigations with *T. desertorum* in Paraguay and California under conditions of variable temperature, with similar means recorded for the two regions, demonstrated a considerably shorter duration of the egg stage in Paraguay than in California, while no significant difference was evident between the two regions for the developmental rate of the other stages. Data presented for *T. desertorum* in Texas by Iglinsky and Rainwater (1954) showed the duration of the egg stage there to be similar to or less than that found in Paraguay. These differences suggest the possibility that, even though the mites in these regions are apparently morphologically indistinguishable, lack of economic severity in California may be correlated with intrinsic physiological differences, one manifestation of which is a slower incubation rate. The data reported by Iglinsky and Rainwater (1954) as well as those obtained in these investigations showed the egg stage to be the stage most sensitive to temperature and humidity differences. Since the data used in comparing the populations of the three areas were obtained under conditions of variable temperature and possibly different humidities, they cannot be accurately compared with each other. Consequently the suggestion of intrinsic physiological differences between the populations was not definitely confirmed or denied.

The hypothesis attributing lack of economic severity of *T. desertorum* in central California to the aridity of this region is supported by the data showing a higher rate of reproduction and faster rate of development at high, as compared with low, relative humidity. This view is further strengthened by the data showing *T. telarius,* a serious mite pest in central California, to have a lower rate of reproduction and a slower rate of development at high, as compared with low, relative humidity.

The humidity relationships of *T. desertorum* indicate that it is not well adapted to the arid conditions of central California but has been selected in a region of higher humidity. This indication plus the observation that its major summer host in California is an introduced species suggest that this mite is not native to California.

In relating this humidity information to the field conditions, it is very important to consider the microenvironment of the mites. Because of transpiration from the leaves it is a common assumption that there is layering of water vapor near the leaf surfaces resulting in a gradient in humidity such that a high humidity is present in the region next to the leaf, where the mites live, even when ambient humidity is low. However, observations with humidity indicator paper at or near the surface of leaves, both in the

cells used in these studies and on plants in the greenhouse, demonstrated that the relative humidity in the region in which mites live differs only slightly from that in the air around the leaves. Nonetheless, the humidity of the air surrounding the leaves is influenced by the plant cover. The water vapor transpired from the plants and evaporated from the soil in a cotton field results in relative humidities which are higher than those recorded in standard weather instrument shelters. The degree of this difference would be dependent on the amount of air movement, the distance above the ground surface, and the density of the plant cover. Nevertheless, a dependent relationship between the plant humidity and the weather instrument shelter humidity exists to the extent that the humidity at the leaf surface on a cotton plant in a region of high humidity would be higher than that in a region of low humidity. It is concluded, therefore, that the relative humidity range (25 to 90 per cent) used in these trials is comparable to humidities which could be experienced in the microenvironment of the mites under field conditions and that the conclusions reached from the laboratory humidity studies can largely be applied in the interpretation of field observations.

The confirmation of the hypothesis correlating economic distribution of *T. desertorum* with moisture relationships by no means indicates that other factors may not also be involved. Many unanswered questions remain in this complex problem which suggest other lines of investigation. The fact that within the total distribution of *T. desertorum* many areas exist with temperatures and humidities apparently suitable for *T. desertorum* in which it is not found as a pest clearly indicates that temperature and humidity are not the only important factors in the consideration of the economic distribution of this species. The fact that this mite can develop very dense populations on horseweed in California, in spite of aridity, and yet not spread to adjacent crops, and the observations that it appears on this weed most generally when it is not immediately adjacent to a cultivated crop also raise unanswered questions. The possibilities of differential insecticide or acaricide applications and of physiological races favored by different hosts have been suggested but were considered unlikely answers. It is possible that the horseweed plant may offer better protection from enemies or a more humid microenvironment in that its leaves are closely spaced (see figure 2B).

Certainly the factors of predation, dispersal, and competition must play important roles in the complex problem of the causal factors in economic severity. The factor of interspecific competition would appear to be a particularly interesting avenue for further investigations. The rapid decline of greenhouse cultures of *T. desertorum* in the presence of *T. telarius* coupled with the observations that intraspecific competition greatly affects longevity and fecundity, suggest that the presence of a closely related mite species increases the rate at which a leaf or plant becomes unsuitable for efficient reproduction and development and that conditions favoring one species more than the other cause that species to gain the ascendancy and gradually eliminate the other species. The results indicating a higher innate capacity for increase for *T. telarius* than *T. desertorum* at low and the reverse situation at high relative humidities suggest the desirability of interspecific competition experiments at different humidity levels.

SUMMARY

The desert spider mite, *Tetranychus desertorum* Banks, has been reported from California to North Carolina along the southern portion of the United States. Its distribution also includes Mexico, Peru, Paraguay, Argentina, and Australia. In Paraguay and several of the cotton belt states it has been reported as a major mite pest of cotton, while in California it exists mainly as spotty infestations on weeds, becoming a pest on cultivated crops only rarely and in isolated localities. The dominant summer hosts are horseweed, *Erigeron canadensis* Linnaeus, in California and cotton in the southern states. The major natural enemies are phytoseiid mites, predaceous thrips, anthocorid bugs, and ladybird beetles.

A comparison of climate and distribution of this species indicated that *T. desertorum* is limited in its northerly distribution by winter monthly mean temperatures of approximately 40°F and is an important pest only in areas where normal spring and summer rainfall exceeds 1 inch per month.

Life-history studies at variable temperatures approximating those experienced under summer field conditions indicated that these mites pass through the immature developmental period (egg to adult) in about 9½ days in California. Paraguay and Texas populations apparently complete their immature development about a day sooner; however, interpretation of these data is difficult because they were obtained under variable temperature conditions of comparable means but possibly dissimilar total heat.

Females developing on heavily infested plants displayed marked reductions in longevity and fecundity. The sex ratio of eggs deposited by fertilized females was found to change with the age of the females. These studies also showed that unfertilized females have a lower fecundity and greater longevity than fertilized females.

Studies at 10°C indicated that this temperature is near the threshold temperature for development and produces some lethal effects, especially at low humidity.

Studies at low (25 to 30 per cent) and high (85 to 90 per cent) relative humidity levels at 16°, 25°, 30°, and 36°C indicated that, of these eight combinations, a temperature of 30°C and high relative humidity were optimum for a high rate of reproduction and a rapid rate of development. At all of the temperatures tested, high humidity resulted in greater longevity, lower fecundity, lesser immature mortality, and a faster rate of immature development compared with low humidity. The combined effects of these factors were summarized in calculation of net reproduction rates (R_0) and innate capacities for increase (r_m). The R_0 values and, to a lesser extent, the r_m values were generally higher for the high humidity level.

Similar trials with *Tetranychus telarius* Linnaeus at 30°C and low and high humidities indicated a shorter longevity, lower fecundity, greater immature mortality, a slower rate of immature development, and lower R_0 and r_m values for high as compared with low humidity.

These results provide a partial explanation for the economic distribution of *T. desertorum*. They suggest that this species is not an important pest in central California because of the summer aridity in this region.

ACKNOWLEDGMENTS

The writer wishes to express sincere gratitude to Dr. R. F. Smith, of the Department of Entomology and Parasitology, University of California, Berkeley, for his helpful guidance throughout the course of this study. Advice and assistance during the course of the laboratory studies and suggestions in preparation of the manuscript by Dr. W. W. Allen, Department of Entomology and Parasitology, and suggestions by Dr. John W. Oswald, Department of Plant Pathology, University of California, Berkeley, for improvement of the manuscript are also gratefully acknowledged.

An expression of thanks is also due the Allied Chemical Corporation, donors of a fellowship awarded the writer for the year 1958–59, and Maple Leaf Enterprises, Wasco, California, for financial assistance which helped make these studies possible. The assistance of Peter Westigard and Stanley Gaede, of the Department of Entomology and Parasitology, Berkeley, in making some of the observations and in growing the host plants is gratefully acknowledged. The help of Evelyn Nickel in the preparation of the figures is gratefully acknowledged.

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