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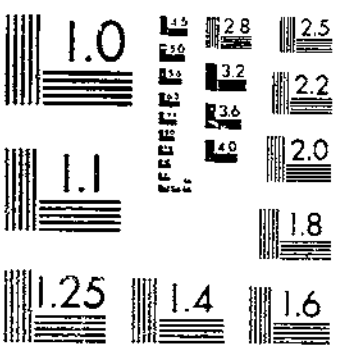

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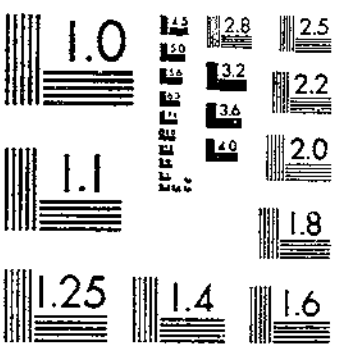

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Effect of Temperature and Photoperiod on the Biology of Blue Alfalfa Aphid, *Acyrthosiphon kondoi* Shinji

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Abstract

The developmental and reproductive biology of the blue alfalfa aphid, *Acyrthosiphon kondoi* Shinji, was studied under 15 temperature/photoperiod regimes. Five temperatures (10°, 15°, 20°, 25°, 30°C) and three photophases (8, 12, 16 h per 24 h) were utilized in controlled environmental chambers.

Temperature played the most significant role in the development and reproduction of the aphid. Optimum temperatures for development ranged from 20° to 25°, and the upper survival temperature ranged from 25° to 30°, depending upon the photoperiod. The lethal temperature was 30°. Higher survival and total fecundity occurred at low temperatures (10° to 15°) rather than at high temperatures (20° to 25°).

There were significant temperature by photoperiod interactions on the rates of nymphal development, fecundity, longevity, and generation time. The changes in these rates were most prevalent at low temperatures.

Shorter generation and doubling times, and a greater intrinsic rate of increase by *A. kondoi*, may account for the early dominance of this species over *A. pisum* in the spring in the U.S. alfalfa fields.

Keywords: Blue alfalfa aphid, *Acyrthosiphon kondoi* Shinji, alfalfa, biology, temperature effect, photoperiod effect.

Contents

June 1982

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By R.T. Kodet, M.W. Nielson, and R.O. Kuehl[1]

Introduction

The blue alfalfa aphid, *Acyrthosiphon kondoi* Shinji, commonly found throughout eastern and southwestern Asia on legume species of *Medicago*, *Trifolium*, and *Melilotus*, was introduced into the United States in 1974 (Sharma et al. *1975*).[2] From California, where it was first found, the aphid spread rapidly into Arizona, Nevada, and Utah (Nielson and Kodet *1975*, Cooperative Economic Insect Report *1975*). By 1978, it was reported in New Mexico, Kansas, Oregon, Oklahoma, Nebraska, Idaho, Texas, Washington, and Wyoming (Cooperative Plant Pest Report *1976, 1977, 1978*). Recently, the aphid was reported in Argentina (Luna *1977*), New Zealand (Aphidologist Newsletter *1977*), and Australia (Matheson and Baldwin *1978*).

The aphid is a serious pest of alfalfa, *Medicago sativa (L.)*, causing severe stunting and marked leaf chlorosis within 2 weeks after initial infestation (Nielson and Kodet *1975*). Recovery is slow and regrowth is so retarded that an additional 2 to 4 weeks are required before plants can resume normal growth. Many plants are killed after prolonged infestation. Damage caused by *A. kondoi* is much more severe than that caused by the pea aphid, *A. pisum* (Harris), a species closely related taxonomically and biologically.

The sudden appearance of the blue alfalfa aphid in widely separate regions of the world within a relatively short time is unprecedented in the annals of insect pandemics. Moreover, the establishment of the pest in the Northern and Southern Hemispheres is of biological and ecological significance; that is, these populations may possibly represent new biotypes, thus giving greater plasticity to the species heretofore unknown.

Biological and environmental factors that precipitate explosive outbreaks of insect populations are often peculiar to the species. Its pandemic activity cannot be explained by the little we know about the biology or the effect of environment on the biology of *A. kondoi*. Sexual forms are not known to exist, and experiments by Kodet and Nielson (*1980*) failed to produce such forms after subjecting the aphid to 15 temperature/photoperiod regimes. Temperature and photoperiod, however, did affect alary polymorphism. In general, apterae were predominantly produced at high temperatures (20° and 25°C) and at all photoperiods (8-, 12-, and 16-h photophases per 24 h); whereas, alatae were predominantly produced at low temperatures (10° and 15°) at these photoperiods (Kodet and Nielson *1980*).

A significant biological phenomenon was observed that was not induced by temperature or photoperiod but may be an inherent survival mechanism (Kodet and Nielson *1980*). The aphid switched from the production of one alary morph early in the reproductive period to the production of the opposite morph later in the reproductive period at all temperature/photoperiod regimes except 20°C/16 h when no switching occurred.

In this publication, we present data on the effects of temperature and photoperiod on the developmental and reproductive biology of the aphid under 15 temperature/photoperiod regimes. The information should serve as a predictive model for field populations so that the population dynamics of the species can be better understood. Where possible, the data are compared with those available on the pea aphid to show the relationship between these taxonomically close and ecologically associated aphid species.

Materials and Methods

This study was done at the USDA-ARS Forage Insects Research Laboratory in Tucson, Ariz., from September 1975 to June 1977. *Acyrthosiphon kondoi* was reared in four Percival E-54U environmental chambers in a factorial arrangement of five temperatures (10°, 15°, 20°, 25°, 30°C) and three photophases (8-, 12-, 16-h per 24 h). Temperatures were controlled to ±1.5°. Relative humidity ranged daily from 60 to 100 percent due to lamp heat during photophase. Chambers were divided into two levels by a wire rack. Data on reproductive biology (adults) were collected from the upper level; whereas, data on developmental biology (nymphs) were collected from the lower level. Light intensity averaged 2655.25 lux (range: 2257 to 3225 lux).

Host plants, *Melilotus officinalis* Lam., were propagated in the greenhouse from a single plant. Rooted cuttings were transferred to 14-cm-diameter plastic pots containing equal parts of earth, sand, and sphagnum peat moss. Plants were used when four lateral shoots had developed over 10 cm in length.

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[2]The year in italic, when it follows the author's name, refers to Literature Cited, p.10.

Aphids from greenhouse cultures were preconditioned for two generations to all temperature/photoperiod treatments in the chambers prior to data collection. Individual aphids were confined in 7.5-cm-long No. 36 dialyzer tubing. The tubing enclosed lateral shoots of the host plant and was stoppered with foam plugs.

In the experimental design, each of four aphid cages per plant was considered an observation and each of five plants per treatment was considered a replication. Consequently, there were four observations in each of five replications for each treatment. Data on reproductive and developmental biology were replicated four times at 10°C/12 h due to nymphal mortality and two and four times at 10°/12 h and 25°/8 h, respectively, due to adult mortality.

The data for developmental and reproductive biology were subjected to various statistical analyses that best elucidated the relationship between environmental factors and the biology of the aphid.

Four specific parameters — generation time, net reproductive rate, doubling time, and intrinsic rate of increase — were computed from age-specific schedules of births and deaths. These describe the dynamics of the species under specific environmental conditions and are theoretical values that may only be applicable to laboratory situations.

The generation time (T), that is, the mean time from birth of parents to birth of offspring, was calculated from the equation $T = \Sigma x l_x m_x / \Sigma l_x m_x$, where l_x is the probability of a female being alive at age x and m_x is the mean number of offspring produced in a unit of time of a female aged x.

The net reproductive rate (R_o), that is, the multiplication per generation or the ratio of total female births in two successive generations, was estimated by the formula $Ro = \Sigma l_x m_x$.

The number of days required for the population to double in number, that is, doubling time, was estimated by the formula $t = 0.69315/r_m$.

The intrinsic rate of increase (r_m), that is, the infinitesimal rate of increase of a population of stable age distribution, was estimated from the formula $r_m = \log_e(N_t/N_o)$, where N_o is the number of animals in time zero and N_t is the number of animals in time t. The relationship of these statistics and their respective parameters are discussed in Andrewartha and Birch (*1954*).

Results and Discussion

Developmental Biology

The analyses of variance for data on the effects of temperature and photoperiod with respect to development of *Acyrthosiphon kondoi* are shown in table 1.

Table 1—Mean squares for data on the effect of temperature, photoperiod, and the temperature by photoperiod interacton on the developmental biology of *Acyrthosiphon kondoi*

Variance source	d.f.	Mean squares: Stadia I	Stadia II	Stadia III	Stadia IV	Nymphal stage
Temperature	3	[1]108.5	[1]152.8	[1]152.1	[1]342.0	[1]2813.5
Photoperiod	2	[1]2.7	[1]6.5	[1]3.8	[1]15.2	[1]97.6
Temperature by photoperiod	6	[1]2.7	[1]6.7	[1]9.5	[1]17.6	[1]124.4
Error	47	.8	.6	.4	.5	1.9

[1]F test of mean square, statistically significant at the 0.05-percent level of probability.

Temperature, photoperiod, and their interaction had significant effects on development of all stadia and the entire nymphal stage. Temperature was the dominating factor as indicated by the larger mean square values. Photoperiod and the temperature/photoperiod interaction exerted a relatively minor influence on the developmental biology.

Stadia. The observed mean duration of each stadium shown in table 2 was analyzed to determine the

Table 2.—Mean duration (days) of each stadium[1] of *Acyrthosiphon kondoi* at different constant temperatures and photoperiods

Temperature (C°)	Mean No. days indicated photophase (hours): 8	12	16	Mean
Stadium I				
10	5.90	4.27	5.12	5.08
15	2.73	2.05	2.82	2.47
20	1.68	1.69	1.39	1.58
25	1.54	1.83	1.60	1.67
Mean	2.67	2.31	2.74	
Stadium II				
10	6.40	3.91	6.12	5.55
15	2.60	2.05	3.09	2.49
20	1.79	1.92	1.33	1.66
25	1.23	1.28	1.27	1.26
Mean	2.68	2.13	2.97	
Stadium III				
10	7.20	4.18	5.82	5.71
15	2.73	2.31	3.55	2.76
20	1.79	2.15	1.44	1.76
25	1.39	1.72	1.27	1.48
Mean	2.90	2.44	3.00	
Stadium IV				
10	10.30	5.73	8.29	8.08
15	4.53	3.26	4.55	4.00
20	2.00	2.85	2.11	2.26
25	2.15	2.00	1.73	1.96
Mean	4.16	3.25	4.18	

[1]2 nymphs required 1 day as a 5th stadium at 25°/12 h before complete nymphal development.

responses due to temperature and to clarify the nature of the interaction between temperature and photoperiod. An orthogonal polynomial regression was estimated to describe the response to temperature for each stadium and nymphal stage. Results shown in table 3 indicate that linear and quadratic effects were significant for all developmental stages, with occasional significant cubic effects. As a result of the small magnitude of cubic deviation, only the quadratic model was used to describe the responses.

Table 3.—Analysis of variance for the temperature regression (orthogonal polynomials) of nymphal data of *Acyrthosiphon kondoi*

		Mean Squares				
Source	d.f.	Nymphal stage	Stadium I	Stadium II	Stadium III	Stadium IV
		8-h photophase				
Temperature:						
Linear	1	[1]3108.88	[1]108.45	[1]142.07	[1]179.37	[1]401.26
Quadratic	1	[1]858.43	[1]29.87	[1]32.79	[1]52.11	[1]118.56
Cubic	1	[1]44.76	1.18	[1]5.99	[1]7.12	.24
Error	16	2.88	1.34	.57	.63	.49
		12-h photophase				
Temperature:						
Linear	1	[1]706.07	[1]30.33	[1]38.81	[1]32.95	[1]82.71
Quadratic	1	[1]170.90	[1]20.95	[1]5.92	[1]8.08	[1]10.37
Cubic	1	[1]49.39	[1]1.41	[1]3.53	[1]2.97	4.67
Error	15	.82	.30	.10	.26	.39
		16-h photophase				
Temperature:						
Linear	1	[1]3699.37	[1]123.35	[1]226.53	[1]206.75	[1]411.54
Quadratic	1	[1]472.21	[1]24.76	[1]33.67	[1]18.56	[1]44.13
Cubic	1	[1]9.38	.41	.12	[1]2.11	.38
Error	16	2.08	.70	1.10	.37	.64

[1]F test of mean square, significant at 5-percent level of probability.

The general response to temperature was typical: Each stadium required more time at low temperature and less time at high temperature to complete development (fig. 1). Photoperiod had no effect on development at high temperatures, but there was a significant photoperiod effect at low temperature. The response to temperature was less pronounced at 12 h than at 8 or 16 h.

The optimum temperature for development of stadia I-IV was between 20° and 25°C (table 4). In general, the nymphs required three to four times as long to develop at 10° than they did at 25° (table 2). The developmental period under an 8-h photophase was nearly twice that under one of 12 h, indicating that short photophases retarded development at a low temperature. The upper temperature for survival fell between 25° and 30°, when 30° proved to be lethal to all stadia. Moreover, two nymphs passed through five stadia at 25°/12 h, which further indicated that the normal biology had been disrupted and the upper survival temperature was being approached. Kenten *(1955)* found that 30° was also lethal to *A. pisum*.

Table 4.—Temperatures for minimum developmental time of nymphal stages of *Acyrthosiphon kondoi* at 3 photoperiods

Stage	Photophase	Temperature	Mean duration
	Hours	°C	*Days*
Stadium I	8	22.18	1.36
	12	20.75	1.47
	16	22.27	1.38
Stadium II	8	22.54	1.17
	12	24.13	1.38
	16	23.01	1.13
Stadium III	8	22.03	1.18
	12	22.76	1.75
	16	25.01	1.17
Stadium IV	8	22.05	1.67
	12	24.67	2.12
	15	24.06	1.67
Nymphal stage	8	22.17	5.38
	12	22.75	6.92
	16	23.55	5.46

The temperatures required for minimum developmental time for *A. kondoi* at three photoperiods were obtained from the regression equation (fig. 1) and are given in table 4. These data predict more precisely the optimum temperature for minimum developmental time of the stadia. Optimum temperature varied from 20.7° to 25.0°C for all stadia at all photophases. Slightly higher temperatures (22.2° to 25.01°) were required for optimum development at 12 h than at 8 h or 16 h. The minimum optimum period was 1.13 days for the second stadium at 16 h/23.01°.

Nymphal stage. Results of the analyses of variance for the temperature regression of the data on the nymphal stage are shown in table 3. Significant linear, quadratic, and cubic effects were obtained for all photoperiods. Inasmuch as the cubic effect was small, the quadratic model was used to describe the responses (fig. 2). The response of the total nymphal period was similar to the response of each stadium, that is, time of development was slower at low than at high temperatures at all photoperiods. Again, photoperiod had no effect on total nymphal developmental period at higher temperatures, but there was a significant effect at low temperatures.

The optimum developmental time of the nymphal stage based on predicted values was 5.87 days at a 25°C/16 h photophase (table 5); however, the minimum predicted developmental time was 5.38 days at 8 h, which occurred at 22.1° (table 4). Precise temperature for minimum development time ranged between 22.1° and 23.5°.

Data on development of *Acyrthosiphon kondoi* are compared with those obtained by Kilian and Nielson *(1971)* and Siddiqui et al. *(1973)* for *A. pisum* (table 5). The developmental time was generally similar for the two aphid species at the respective temperatures and photophases, although *A. kondoi* developed slightly more

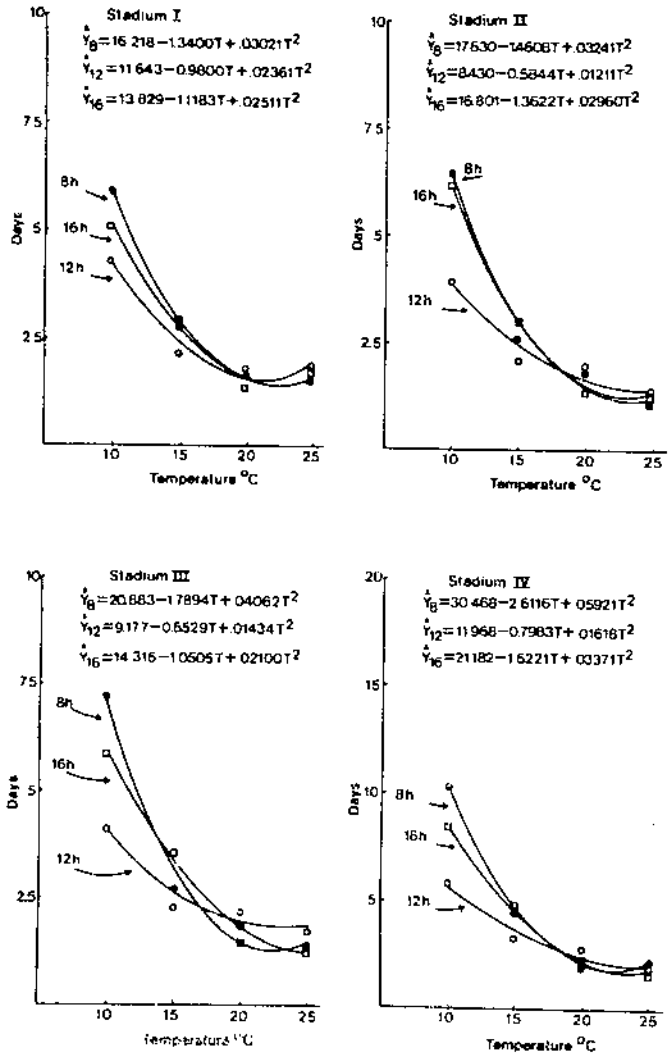

Figure 1.—Relationship between developmental time of nymphal stadia of *Acyrthosiphon kondoi* and temperature at three photoperiods.

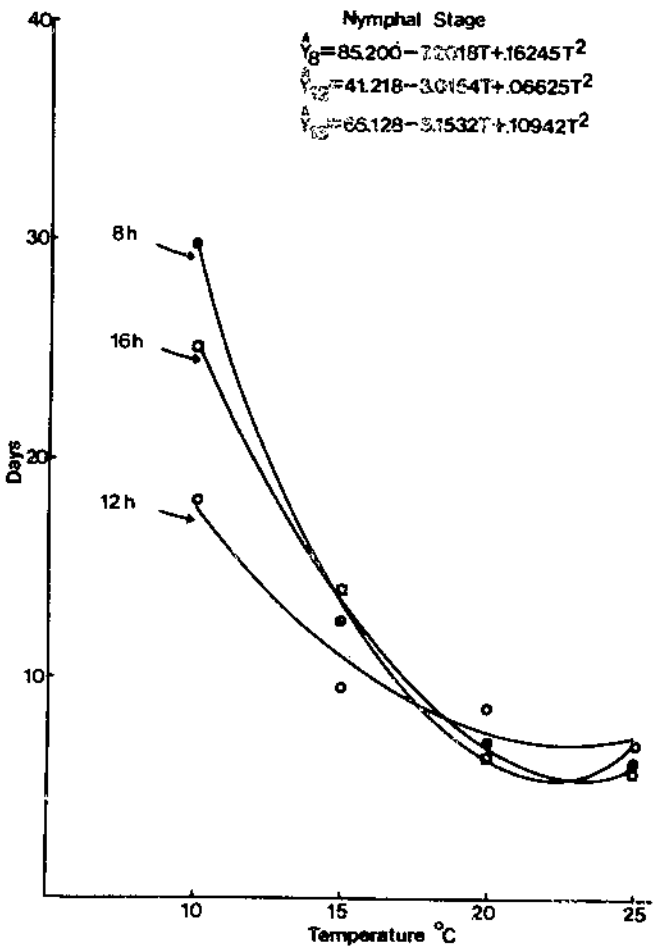

Figure 2.—Relationship between developmental time of nymphal stage of *Acyrthosiphon kondoi* and temperature at three photoperiods.

rapidly at higher temperatures at 16 h; however, the difference may not be statistically significant. Since *A. kondoi* does appear in alfalfa fields earlier in the spring than *A. pisum*, development may be faster in *A. kondoi* when photoperiod (12 h) interacts with low temperature (15°C). Unfortunately, data at the 12-h photophase are lacking for *A. pisum* to support this hypothesis.

Nymphal survivorship. The percent nymphal survival of *A. kondoi* at the various temperature and photoperiod regimes is shown on table 6. Survival was highest at 20°C and at 12 h. Survival was lowest at 10°/8h. Chi-square tests for the effects of temperature and photoperiod on nymphal survival were conducted according to the procedures outlined by Goodman *(1970)*. The results of the analysis (table 7) showed that survival was not affected by temperature and photoperiod interaction, but these factors by themselves produced different survival rates of the nymphs.

Table 5.—Mean duration (days) of nymphal stage of *Acyrthosiphon kondoi* and *A. pisum* at different constant temperatures and photoperiods

Temperature (°C)	Mean No. days of nymphal period in indicated photophase (hours)					
	A. kondoi				*A. pisum*	
	8	12	16	Mean	[1]16	[2]24
10	29.80	18.09	25.35	24.42	—	—
15	12.60	9.68	14.00	11.71	12.2	11.3
20	7.26	8.62	6.28	7.26	8.4	8.5
25	6.31	6.83	5.87	6.37	6.8	6.6
Mean	12.40	10.13	12.89			

[1]Siddiqui et al. *1973*.
[2]Killian and Nielson *1971*.

Table 6.—Percent nymphal survival of *Acyrthosiphon kondoi* at 4 temperatures and 3 photoperiods

Temperature (°C)	Percent survival at indicated photophase (hours) 8	12	16	Mean
10	77	100	77	83
15	88	95	69	85
20	95	100	100	98
25	65	100	94	85
Mean	81	98	85	

Table 7.—Chi-square analysis of nymphal survival of *Acyrthosiphon kondoi*

Hypothesis	Chi square	d.f.	Probability
Survival × temperature	10.5070	3	0.015
Survival × photoperiod	14.1523	2	.0008
Survival × temperature × photoperiod	9.4056	6	.152

Reproductive Biology

The analyses of variance for data on the effects of temperature and photoperiod on the reproductive biology of *A. kondoi* are shown in table 8. The effects of temperature, photoperiod, and their interactions were significant for much of the reproductive biology. Photoperiod did not significantly affect postparturition, total adult period, or fecundity. Temperature had the greatest effect with minor effects from photoperiod and the temperature/photoperiod interactions.

Adult parturition phases. A regression analysis was performed on the parturition phases and adult period data (table 9) and on fecundity (table 10) to more accurately characterize the effects of temperature and temperature/photoperiod interactions on the reproductive biology. Regression of days on temperature for each biological parameter was estimated separately for 8-, 12- and 16-h photophases. The results are shown in table 11 (parturition and total adult periods) and table 12 (fecundity). The quadratic response to temperature was considered that best model to describe most of the reproductive phases. Significant deviations from the quadratic model are discussed below to account for the interactions between temperature and photoperiod. In general, the length of the reproductive phases decreased as temperature increased. The most rapid adult phases occurred between 20° and 25°C (fig. 3).

Deviations from the typical quadratic model were evident at 12- and 16-h photophases during the preparturition period (fig. 3). A strictly linear effect was exhibited at 16 h as the time of development continued to decline up to

Table 9.—The mean duration of the preparturition, parturition, postparturition, and adult period of *Acyrthosiphon kondoi* at different constant temperatures and photoperiods

Temperature (°C)	Mean duration (days) at indicated photophase (hours) 8	12	16	Mean
	Preparturition period			
10	3.06	3.13	2.88	3.00
15	2.21	1.95	1.71	1.98
20	.81	.89	1.28	1.00
25	1.36	2.50	1.06	1.67
Mean	1.89	1.94	1.73	
	Parturition period			
10	40.94	53.75	49.29	46.90
15	25.21	20.37	22.36	22.67
20	7.75	8.79	11.53	9.34
25	6.21	10.33	10.59	9.25
Mean	20.69	18.28	23.26	
	Postparturition period			
10	13.31	24.13	15.59	16.37
15	11.79	4.21	4.93	7.17
20	.38	1.37	2.33	1.40
25	1.71	4.33	2.06	2.80
Mean	7.19	5.89	6.23	
	Adult period			
10	57.31	88.50	67.76	67.73
15	39.26	27.05	29.00	32.04
20	8.94	11.05	14.94	11.74
25	9.29	17.17	13.71	13.71
Mean	29.78	27.20	31.21	

Table 8.—Mean squares for data on the effect of temperature, photoperiod, and the temperature times photoperiod interaction on the adult biology of *Acyrthosiphon kondoi*

Variance source	df	Mean squares: Preparturition period	Parturition period	Postparturition period	Adult period	Total fecundity	Daily fecundity
Temperature	3	[1]31.6	[1]13,873.5	[1]2,022.1	[1]29,732.4	[1]17,154.9	[1]31.8
Photoperiod	2	[1]2.4	[1]174.3	21.6	261.9	337.6	1.0
Temp × photo	6	[1]3.3	[1]202.7	[1]223.5	[1]1,177.6	[1]4,098.8	[1]5.6
Error	44	.7	41.7	40.6	105.4	945.4	2.1

[1]F test of mean square, significant at the 0.05-percent level of probability.

Table 10.—The mean fecundity per female and the mean fecundity per female per day of *Acyrthosiphon kondoi* at different constant temperatures and photoperiods

Temperature (°C)	Mean total fecundity per female at indicated photophase (hours)				Mean daily fecundity per female at indicated photophase (hours)			
	8	12	16	Mean	8	12	16	Mean
10	58.31	107.60	66.94	71.51	1.45	2.06	1.36	1.53
15	69.26	43.42	47.43	53.94	2.66	2.14	2.10	2.32
20	20.31	29.32	40.50	30.40	2.24	3.30	3.63	3.09
25	26.50	32.50	38.18	32.76	3.83	2.75	3.75	3.40
Mean	45.31	44.19	48.18		2.51	2.65	2.75	

Table 11.—Analyses of variance for the temperature regression (orthogonal polynomials) for parturition phases and total period of *Acyrthosiphon kondoi*

Source	d.f.	Mean squares			
		Preparturition	Parturition	Postparturition	Total adult
			8-h photophase		
Temperature:					
Linear	1	[1]34.23	[1]11,546	[1]1,708	[1]23,928
Quadratic	1	[1]6.97	[1]748	18	[1]1,164
Cubic	1	[1]5.29	[1]266	[1]438	[1]1,577
Error	15	.53	56	70	150
			12-h photophase		
Temperature:					
Linear	1	1.27	[1]8,728	[1]1,285	[1]20,815
Quadratic	1	[1]30.68	[1]4,201	[1]1,748	[1]15,530
Cubic	1	[1]5.69	67	112	[1]483
Error	13	.52	25	25	89
			16-h photophase		
Temperature:					
Linear	1	[1]30.15	[1]14,019	[1]1,630	[1]26,982
Quadratic	1	3.56	[1]2,779	[1]426	[1]5,661
Cubic	1	.21	25	26	112
Error	16	1.07	41	25	77

[1]F test of mean square, significant at 0.05-percent level of probability.

25°C; whereas at 12 h, the preparturition period actually increased when temperature advanced beyond 20°.

During the postparturition period, a cubic response occurred at 8 h when duration declined after 15°C. There was also a slightly greater response to temperatures at 12 h than at 8 or 16 h for all phases of the adult stage. These deviations accounted for much of the interaction between temperature and photoperiod.

Adult longevity. The longevity (total period) of adult *A. kondoi* was significantly reduced as temperature increased at all photoperiods (table 9). The life of adults ranged from 88.5 days at 10°C/12 h to 8.94 days at 20°/8 h. Although deviations from the quadratic model were significant at all photoperiods (table 12), a quadratic equation was used to describe the response to temperature (fig. 3). Longevity decreased very rapidly between 10° and 15° with little or no decrease between 20° and 25°, but the rate of decrease was greater at 12 h than at 8 h or 16 h.

Daily fecundity. Temperature had a significant effect on daily fecundity (table 8); however, there was a significant interaction between temperature and photoperiod. Regression analyses were performed on the data to determine the effect of temperature on daily fecundity for each of the photoperiods. The results of the analyses are shown in table 12. There was a general increase in daily fecundity as temperature increased, but the responses to temperature were considerably different at each of the photoperiods (fig. 4).

The 8- and 16-h photophases both showed a significant increase in daily fecundity from 10° to 25°C, but the 8-h photophase equation was cubic and the 16-h equation was linear with no significant deviation from linearity. The 8-h photophase showed a definite decline in fecundity between 15° and 20°. Although the observed daily fecundity for the 12-h photophase was higher at the higher temperatures, there was not a significant trend from the mean production of 2.56 individuals per day.

Table 12.—Analyses of variance for the temperature regression (orthogonal polynominals) for fecundity of *Acyrthosiphon kondoi*

Source	d.f.	Mean squares: Total fecundity	Mean squares: Daily fecundity
		8-h photophase	
Temperature:			
Linear	1	[1]16,952	[1]32.53
Quadratic	1	295	.26
Cubic	1	[1]11,310	[1]11.18
Error	15	1,073	1.52
		12-h photophase	
Temperature:			
Linear	1	[1]22,735	6.66
Quadratic	1	[1]15,177	2.25
Cubic	1	954	6.78
Error	13	1,062	2.47
		16-h photophase	
Temperature:			
Linear	1	[1]7,530	[1]63.54
Quadratic	1	1,174	2.02
Cubic	1	51	3.93
Error	16	731	2.27

[1]F test of mean square, significant at 0.05-percent level of probability.

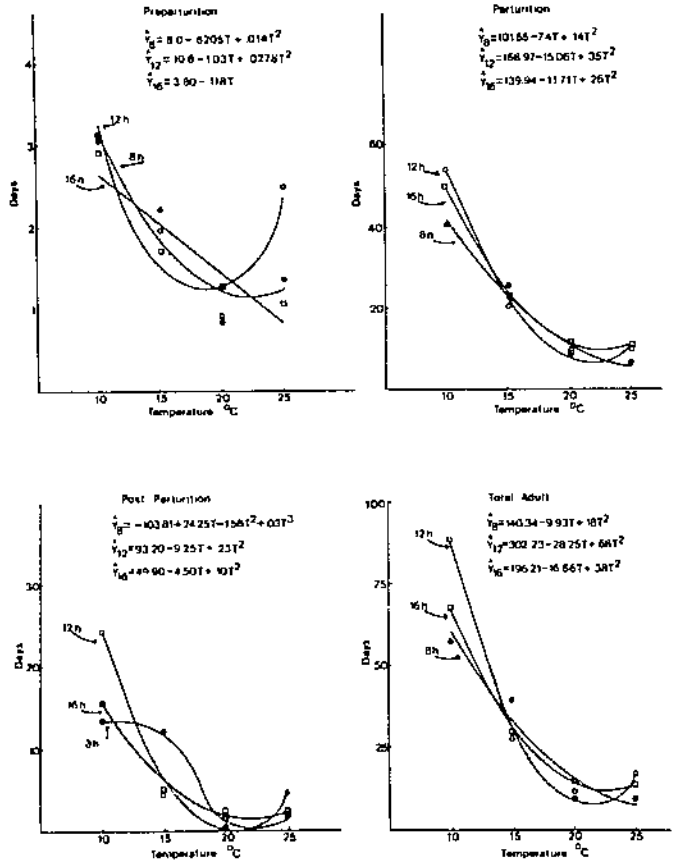

Figure 3.—Relationship between reproductive periods and adult longevity of *Acyrthosiphon kondoi* and temperature at three photoperiods.

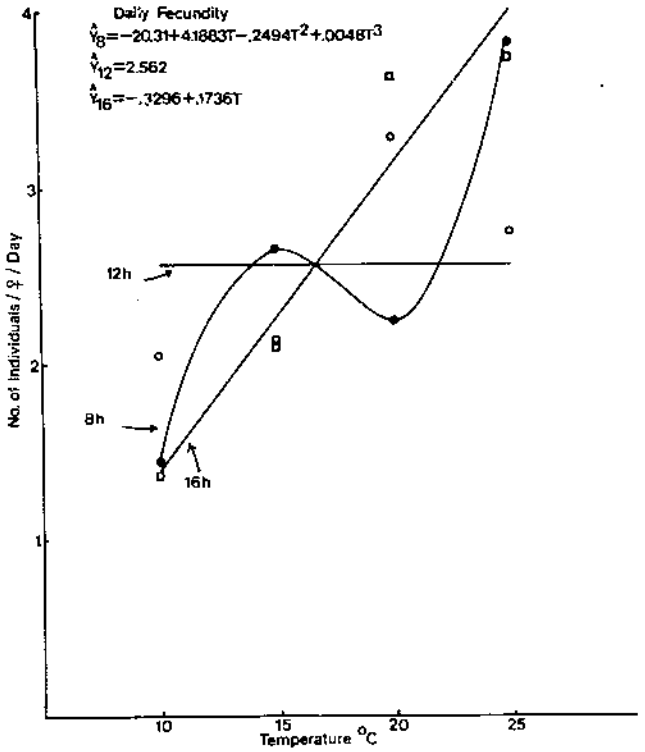

Figure 4.—Relationship between daily fecundity of *Acyrthosiphon kondoi* and temperature at three photoperiods.

Total fecundity. Temperature effects on total fecundity were highly significant as was the temperature/photoperiod interaction (table 8). Data on fecundity response to temperature were subsequently analyzed by orthogonal polynomial regression at each of the photophases to elucidate the nature of the interaction (table 12). Although the general trend was a decreasing fecundity with increasing temperature, there were notable differences among the three photophases (fig. 5). The fecundity response at the 8-h photophase was characterized by a significant cubic equation in temperature in which fecundity increased at the lower temperatures, declined decidedly after 15°C, and leveled off after 20°. The computed maximum and minimum fecundities within the experimental temperature range for the 8-h equation occurred at 12.7° and 22.6°, respectively.

At the 12-h photophase, the fecundity was very high at 10°C with a considerable decline up to 20° at which time the fecundity began to increase in a typical quadratic response. The computed minimum for the 12-h equation was 21°. At the 16-h photophase, fecundity gradually declined throughout the temperature range with no significant deviations from linearity. The estimated decline was 1.86 individuals per degree Centigrade increase.

Kenten *(1955)* reported that total fecundity of *Acyrthosiphon pisum* decreased as photophase increased at 20°C. At 15°, Sharma et al. *(1973)* found that the total fecundity of *A. pisum* increased with

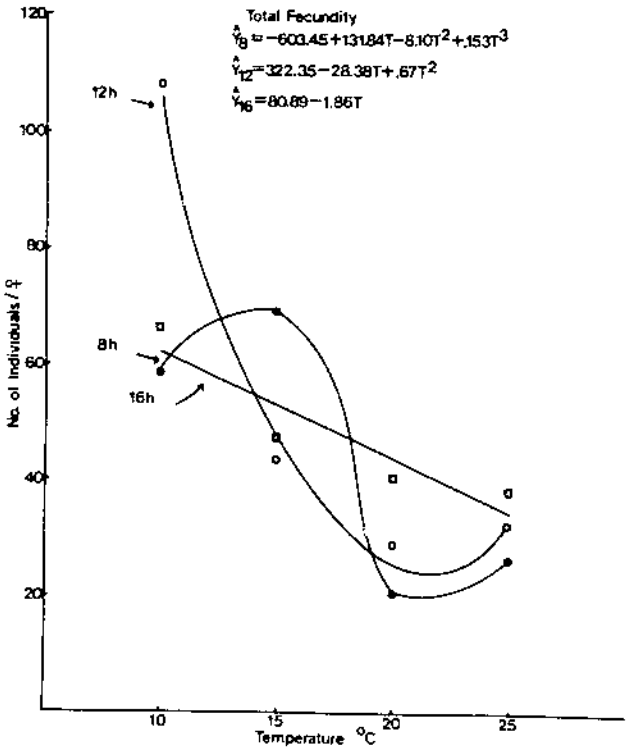

Figure 5.—Relationship between total fecundity of *Acyrthosiphon kondoi* and temperature at three photoperiods.

photophase. From these data, it is not clear whether *A. pisum* and *A. kondoi* are affected similarly by photoperiod.

Generation time. The generation time (T)—the mean period elapsing between the birth of a female and the birth of her first offspring of *A. kondoi*—is shown in table 13. The generation time decreased exponentially from 41.7 days at 10°C to 12.8 days at 20° but was shortest at 25° (11.9 days). The shorter generation time at higher temperatures was caused by increased developmental and fecundity rates and reduced preparturition periods at these temperatures. Temperatures in the range 10° to 20° were critical in controlling population growth of *A. kondoi* since a difference in the mean temperature of 1° or 2° would greatly increase or reduce the generation time of field populations. The occurrence of larger populations of *A. kondoi* than *A. pisum* in the late winter and early spring might be caused by *A. kondoi* having a slightly shorter generation time than that of *A. pisum*.

The generation time was shorter at the 12-h photophase (20.7 days) than at either the 8-h (22.6 days) or 16-h (22.1 days) photophases (table 13). This was the result of temperature/photoperiod interactions at 15°C/12 h and 10°/12 h photophases. Temperature and photoperiod also interacted to increase generation time at 20° and 25° at the 12-h photophase. Photoperiod had a greater effect on the length of the generation time at the lower temperatures (10° to 15°) than at the higher temperatures (20° to 25°).

Table 13.—The generation time[1] (days) of *Acyrthosiphon kondoi* at different constant temperatures and photoperiods

Temperature (°C)	Mean generation time (days) at indicated photophase (hours)			
	8	12	16	Mean
10	45.0	38.9	41.3	41.7
15	21.9	16.7	23.6	20.7
20	12.7	13.1	12.6	12.8
25	10.9	14.2	10.7	11.9
Mean	22.6	20.7	22.1	

[1]Period from birth of parent of first offspring.

Net reproductive rate. The net reproductive rate (R_0)—the ratio of the number of females produced in one generation to the number of females produced in the preceding generation—increased from 28.4 at 25° to 68.1 at 10°C (table 14). The rate was larger at the 12-h photophase (52.9) than at either the 8- or 16-h photophases (33.8 and 40.8, respectively) due to the temperature/photoperiod interaction at 10°/12 h, which increased the rate to 107.2. The temperature/photoperiod interaction strongly affected the net reproductive rate of *A. kondoi* at both high and low temperatures. The rate was generally increased as the result of longer adult parturition periods and greater mean total fecundity.

Doubling time. The doubling time (t) is defined as the period required for a population to double in number. The doubling time decreased from 7.1 days to 2.5 days as temperature increased from 10° to 25°C (table 15). *Acyrthosiphon kondoi* required 3.3 fewer days for their numbers to double at 15° than at 10°. The doubling time was 0.5 to 1.0 day shorter at the 12-h photophase than at the 16- and 8-h photophases. The temperature/photoperiod interaction caused the doubling time to be the longest at 10°/8 h (8.6 days) and shortest at the 25°/16 h photophase (2.1 days).

The doubling time was generally decreased as the result of rapid nymphal development, short parturition period, and high fecundity rates. Temperature was critical in controlling the increase in numbers of *A. kondoi* in the

Table 14.—The net reproductive rate[1] of *Acyrthosiphon kondoi* at different constant temperatures and photoperiods

Temperature (°C)	Net reproductive rate at indicated photophase (hours)			
	8	12	16	Mean
10	37.2	107.2	60.0	68.1
15	57.3	43.3	32.7	44.4
20	20.4	29.3	38.5	29.4
25	20.1	31.9	32.1	28.4
Mean	33.8	52.9	40.8	

[1]Ratio of number of daughters born in generation y + 1 to the number of daughters born in generation y.

Table 15.—The doubling time[1] of *Acyrthosiphon kondoi* at different constant temperatures and photoperiods

Temperature (°C)	Mean doubling time (days) at indicated photophase (hours)			
	8	12	16	Mean
10	8.6	5.8	7.0	7.1
15	3.8	3.1	4.7	3.8
20	2.9	2.7	2.4	2.7
25	2.5	2.8	2.1	2.5
Mean	4.5	3.6	4.1	

[1]Period required for population to double in number.

temperature range of 10° to 20°C. A small biological advantage of *A. kondoi* over *A. pisum* in this range, such as a smaller doubling time, could account for the observed predominance of *A. kondoi* over *A. pisum* in the early spring.

Intrinsic rate of increase. The intrinsic rate of increase (r_m) of *A. kondoi* (fig. 6) was greatest (0.32) at 25° C/16 h and smallest (0.08) at the 10°/8 h photophase. The rate increased as temperatures increased from 10° to 25°, and fell to zero because no survival occurred at 30° after one generation.

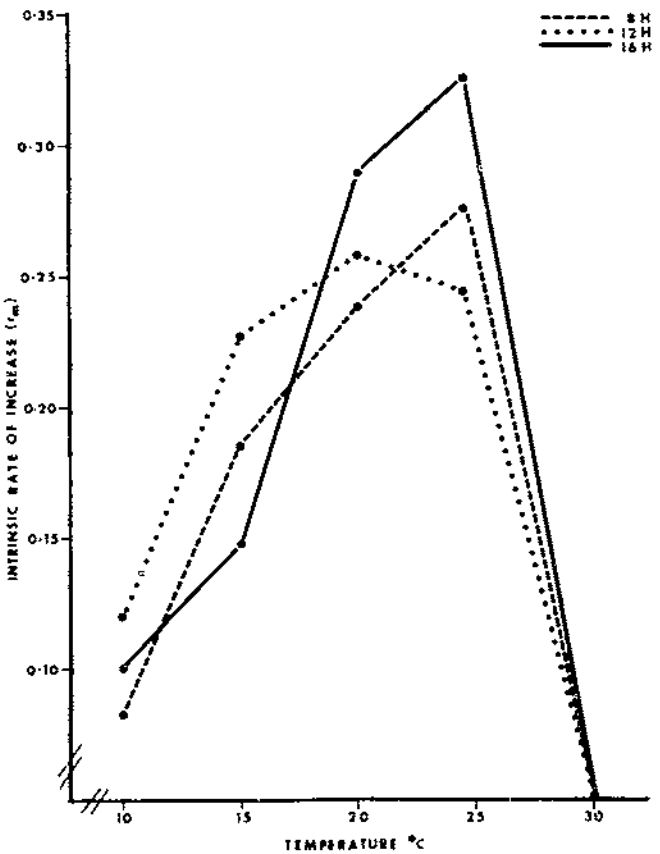

Figure 6.—Intrinsic rate of increase of *Acyrthosiphon kondoi* at three photoperiods.

The rate of increase was greatest at high temperatures when total fecundity per female and adult survival were greatest at low temperatures; however, the rate was not based only upon these parameters, but also upon the rate of nymphal development; the length of the preparturition, parturition, and postparturition periods; and the daily fecundity rate. The extremely rapid rates of nymphal development and daily fecundity, which occurred at high temperatures, overshadowed the greater survival and high total fecundity of *A. kondoi*, which occurred at low temperatures; thus, these parameters resulted in a greater rate of increase at higher temperatures. Lewontin *(1965)* showed that the developmental rate had 10 times greater effect on the rate of increase than a change in total fecundity or a change in survival.

Historically, *Acyrthosiphon kondoi* has been most numerous early in the growing season when temperatures were cool, and *A. pisum* has been most common later during warmer months. Therefore, the rate of increase of *A. kondoi* may be greater than that for *A. pisum* at lower temperatures, although other factors—such as disease, predation, and parasitism—may differentially affect these two *Acyrthosiphon* species.

Conclusions

Temperature exerted a major effect on the developmental biology of the blue alfalfa aphid. Photoperiod and the temperature/photoperiod interaction played a relatively minor role at high temperatures (20° to 25°C), but photoperiod influenced the rate of development at low temperatures (10° to 15°). Short photophases (8 to 12 h) retarded development. Optimum temperatures for minimum developmental time ranged between 20.7 and 25.0° at all photophases. The upper survival temperature fell between 25° and 30° when 30° proved to be lethal.

Temperature, photoperiod, and their interaction had significant effects on the reproductive biology of *A. kondoi.* Again, temperature was the major factor. Photoperiod did not significantly affect postparturition, adult longevity, or fecundity, but the temperature/photoperiod interaction produced differing response to temperature in preparturition and postparturition times.

Daily fecundity increased in response to increase in temperature but did so at different rates in response to photoperiod. At 12 h, there was no response to temperature. Total fecundity decreased as temperatures increased and at different rates depending upon the photoperiod. The rate of decrease in total fecundity was significantly greater at 12 h than at 8 or 16 h.

The higher rates of development and daily fecundity at high temperatures (20 to 25°C) and higher survival and higher total fecundity at low temperature (10 to 15°) may account for the earlier, predominant populations of *A. kondoi* over *A. pisum* in the spring in the United States. Moreover, the 12-h photophase that occurs in the spring and fall favored adult longevity and total fecundity. These factors may account for populations that are present in temperate regions of the Southern and Northern Hemispheres.

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