LIFE TABLE STUDIES ON APHIDS IN ALFALFA IN OKLAHOMA

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ALFALFA IN OKLAHOMA

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PREFACE

High costs of chemical controls and recent concerns over environmental contamination due to insecticidal applications, have indicated the need that pest management strategies be based on understanding of agroecosystems. The present studies were conducted to increase our understanding of the aphid pest complex in alfalfa in Oklahoma. Included in this research were 1) developing age-grading criteria for blue alfalfa aphid and spotted alfalfa aphid for use in life table studies, 2) determining spatial patterns of blue alfalfa aphid and pea aphid and developing sampling plans to estimate densities in the field with fixed levels of precision, and 3) developing time-specific life tables for blue alfalfa aphid to study the population dynamics of this species in Oklahoma. To enhance readibility and expedite preparation of journal articles, this manuscript was written in publication format. Thus each chapter is presented complete with introduction, materials and methods, results, discussion and references.

I wish to express my appreciation and gratitude to all the individuals who contributed to the successful completion of this research and educational endeavor.

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CHAPTER I

AGE-GRADING OF BLUE ALFALFA APHIDS AND SPOTTED ALFALFA APHIDS FOR LIFE TABLE STUDIES

Introduction

The time-specific life table approach of Hughes (1962) has been used extensively to analyze population data of several aphid species (Hughes 1963, Hamilton et al. 1983, Hutchison and Hogg 1986). To use this approach for studying the population dynamics of alfalfa aphids, reliable criteria for age-grading field populations are required. Hutchison and Hogg (1983) developed a criteria based on cornicle lengths for separating instars in field-collected pea aphids, Acyrthosiphon pisum (Harris), in alfalfa but no such information exists in the literature for the blue alfalfa aphid, Acyrthosiphon kondoi Shinji, or the spotted alfalfa aphid, Therioaphis maculata (Buckton).

In insects, major increments in the sizes of sclerotized structures are limited to periodic molts of the integument. Throughout each stadium, the size remains constant (Murdie 1969). This has led many researchers to use measurements of different morphological characters (morphometrics) for discriminating instars of many insect species (Daly 1985). In aphids, morphometrics have been used with varying degrees of success (Hutchison and Hogg 1983, Kirkland et al. 1981, Sana and Shultz 1967). Difficulties generally occur in separating instars of

field populations of aphids using one or a few characters because the ranges of measurements for body structures among successive instars frequently overlap (Otake 1958). Faced with similar problems of overlap in measurements of characters in closely related intraspecific groups, such as host races, researchers have successfully delineated these groups using multivariate statistical techniques (Kim et al. 1967, Sexsana and Rueda 1982, Alder and Kim 1985, Fargo et al. 1986). The objectives of this study were to develop classification criteria for age-grading field populations of blue alfalfa aphid and spotted alfalfa aphid using multivariate statistical techniques.

Materials and Methods

In the first phase of this study, aphids were reared in the laboratory and different morphological characters were measured on individuals of known ages (instars). On the basis of these measurements, parameter estimates of the characters for different instars were determined and classification criteria using multivariate statistical techniques, were developed. In the second phase, the classification criteria developed in the laboratory studies were validated on field populations of both species from different geographical locations in Oklahoma.

Blue Alfalfa Aphid (BAA)

Laboratory Studies

The progeny of two parental morphs (alate and apterous) were used in the laboratory studies. The adults were obtained from a greenhouse colony maintained at 22 $\pm$ 5°C and 75 $\pm$ 20% RH. Cohorts of first instars

were obtained from 48 adults of each morph which were caged individually for 24 hours in plastic funnels with a top diameter of 6 cm. Each funnel contained an alfalfa terminal with the stem submerged in plant nutrient solution in a water bottle. Three cohorts for each parental morph were reared. After 24 hours, all nymphs in excess of one/cage were removed along with the adults. The nymphs were reared individually in the funnels placed in a growth chamber maintained at 22 $\pm$ 1°C and 65 $\pm$ 10% RH. Nymphal development was checked daily and exuviae were removed after each molt.

In all the cohorts, development was followed through fourth instar. Ten nymphs of each instar were randomly removed from each cohort and preserved in 70% ethanol. Of the 56 fourth-instar nymphs reared in this study, 25% were alates. Although third and alate fourth instars could be distinguished by the presence of wing pads, the morphometric data for alate forms were recorded for comparison to apterous fourth instars. Morphological characters were measured using an ocular micrometer on a stereomicroscope. The characters measured were the antennal flagellar segments (I - IV), body length, cornicles, and tibial lengths on all legs. Size limits for these morphological characters were similar to those described by Murdie (1969).

In order to validate the laboratory results on morphometrics of BAA, the aphid populations were sampled from alfalfa fields in Payne, Garvin, Tillman, and Carter Counties during April, 1985. Additional validation samples were taken in Greer, Kiowa, Grant, Kay, Washita, Murray, and McClain Counties during March and April of 1986. Morphological characters were measured on more than 980 nymphs from these samples.

Statistical Analysis

In the field, the progenies of alate and apterous morphs of BAA may be present simultaneously and are virtually indistinguishable. However, this does not preclude the possibility that size measurements for different characters in the progeny may be influenced by the morph of the parents. Thus, classification criteria developed on the basis of measurements on nymphs obtained from only one parental morph may be of limited use for age-grading field populations. Therefore, laboratory data on size measurements of different characters for the progenies of both parental morphs (alate and apterous) were pooled for developing classification criteria.

Means, standard deviations, and ranges of measurements of morphological characters for both laboratory and field data were generated using a PROC MEANS procedure (SAS Institute Inc. 1985). The differences in the mean lengths of body structures among instars within each population (laboratory or field) or between laboratory reared vs. field populations within an instar were determined by analysis of variance adjusted for an unbalanced design by a general linear models procedure (SAS Institute Inc. 1985) and means were separated by Duncan's multiple range test (Duncan 1955).

Pimental (1979) suggested that the first step in comparing samples from several populations is to test the hypothesis that centroids of these populations are equal in multidimensional space. If the hypothesis of equality is rejected, the data could then be subjected to discriminant analysis. Therefore, multivariate analysis of variance was performed on the laboratory data using PROC GLM (Option:MANOVA) of SAS (SAS Institute Inc. 1985) to test the equality of centroids of instars.

The characters included in this analysis were linear measurements of first, second, and fourth flagellar segments, entire body, cornicles, fore-tibia, meso-tibia, and hind-tibia.

To select a subset of characters which best classifies the instars in multidimensional space and reduces the number of characters which must be measured for instar identification, the stepwise discriminant analysis was conducted on the laboratory data using PROC STEPDISC (option:stepwise) of SAS (SAS Institute Inc. 1985). The discriminatory power of each character, after its inclusion in the model, was determined by decrease in Wilk's lambda (SAS Institute Inc. 1985).

Discriminant analysis was further performed on laboratory, as well as, field data using characters selected by the stepwise discriminant procedure. In this analysis, the discriminant function was developed using laboratory data. Based on this function, each individual from the field populations was assigned to an instar from which it had the smallest generalized squared distance (SAS Institute Inc. 1985.).

An equivalent procedure to generalized squared distance for classifying field-collected aphids into instars is to calculate scores of each individual on the linear discriminant function of each instar. The score is calculated by multiplying the measurements of characters to the coefficients of the functions and adding them to the constant. The individual is classified to the instar for which the highest score is obtained (See Bennett and Bowers (1976), for detailed description of the procedure).

To further minimize the number of variables required for discriminant functions, an optimization procedure was carried out. In this procedure the variables were sequentially dropped from the

discriminant model and resulting misclassification of aphids by instar was checked. The model which included the minimum number of characters and resulted in missclassification of less than 1% of field populations was considered optimal.

Spotted Alfalfa Aphid (SAA)

The methods used for the SAA were essentially the same as described for BAA studies except that three replications for alate and two for apterous parental forms were included for laboratory studies. The morphological characters measured were the antennal flagellar segments (I - IV), body length, and the tibial lengths of all legs. As part of validating laboratory results, morphological characters were measured on 296 field-collected aphids from Grady and Kiowa Counties during April, 1986. The data for SAA were also analyzed using discriminant analyses but the optimization procedure as described for BAA was not conducted because missclassification of field collected nymphs exceeded 5% using the model which included all the variables selected by stepwise discriminant analysis.

Results

Morphometric data for laboratory cultured BAA are presented in table I. Mean lengths of second flagellar segments, fourth flagellar segments, body length, cornicles, foretibia, meso-tibia, and hind-tibia were significantly different ($P < 0.01$) among all successive instars. Significant differences ($P < 0.01$) were also found in mean lengths of first flagellar segments of first and second instars, as well as, third and fourth instars. There were three flagellar segments in first and

second instars and four in the third and fourth instars. Ranges of the measurements for all characters in laboratory populations are given in table II. No overlap in the measurements of cornicles was observed between first and second, second and third, or third and apterous fourth instars. Similarly, the measurements for first flagellar segment, fore-tibia, meso-tibia, and hind-tibia did not overlap between third and fourth instars.

Corresponding mean lengths of first, second, third, and fourth flagellar segments, body length, cornicles, fore-tibia, meso-tibia, and hind-tibia for the field populations of BAA are given in table III. Mean length of all the morphological characters of field population except cornicles were significantly greater ($P < 0.01$) than those of the laboratory population. In the field populations of BAA, none of the characters showed instar-specific ranges (Table IV). Although measurements of first flagellar segments, meso-tibia, and hind-tibia did not overlap between third and fourth instars, the absence of overlap disappeared if ranges of these characters for laboratory and field populations were examined simultaneously.

Multivariate analysis of variance (MANOVA) performed on laboratory data using first, second, third and fourth flagellar segments, body length, cornicles, fore-tibia, meso-tibia, and hind-tibia indicated that centroids of four instars were significantly different. The MANOVA statistics with significant probabilities were: Wilk's criterion, ($F = 191.78$, $DF = 24,653.2$, $P = 0.0$); Pillai's trace ($F = 83.93$, $DF = 24,681$, $P = 0.0$); and Hottelling-Lawley trace ($F=404.2$, $DF=24,671.0$, $P = 0.0$). These results suggested that data could be subjected to discriminant analysis.

TABLE I

LENGTHS (mm) OF SOME MORPHOLOGICAL CHARACTERS OF LABORATORY-CULTURED BLUE ALFALFA APHID

CHARACTERS	INSTARS I $\bar{x}$ (± S.D.)	n	II $\bar{x}$ (± S.D.)	n	III $\bar{x}$ (± S.D.)	n	IV-AP* $\bar{x}$ (± S.D.)	n	IV-AL** $\bar{x}$ (± S.D.)	n
FLAGELLAR SEGMENT - I	0.127 (.021)	62	0.243 (.030)	60	0.199 (.025)	60	0.381 (.035)	42	0.391 (.045)	14
FLAGELLAR SEGMENT -II	0.105 (.013)	62	0.163 (.023)	60	0.237 (.027)	60	0.372 (.036)	42	0.365 (.046)	14
FLAGELLAR SEGMENT -III	-		-		0.239 (.025)	60	0.343 (.030)	42	0.339 (.044)	14
FLAGELLAR SEGMENT -IV	0.362 (.040)	62	0.508 (.051)	60	0.640 (.073)	60	0.769 (.065)	42	0.794 (.092)	14
CORNICLES	0.111 (.016)	62	0.222 (.024)	60	0.364 (.033)	60	0.556 (.043)	42	0.543 (.053)	14
BODY LENGTH	0.738 (.079)	62	1.006 (.118)	60	1.298 (.212)	59	1.654 (.243)	42	1.702 (.251)	14
FORE-TIBIA	0.249 (.029)	62	0.366 (.034)	60	0.565 (.065)	60	0.842 (.065)	42	0.873 (.071)	14
MESO-TIBIA	0.255 (.026)	62	0.372 (.034)	60	0.575 (.057)	60	0.852 (.069)	42	0.884 (.072)	14
HIND-TIBIA	0.345 (.035)	62	0.517 (.050)	60	0.787 (.080)	60	1.187 (.099)	42	1.216 (.092)	14

* AP = Apterae

** AL = Alates

TABLE II

RANGES (mm) FOR LENGTHS OF SOME MORPHOLOGICAL CHARACTERS OF LABORATORY-CULTURED BLUE ALFALFA APHID

CHARACTERS	INSTARS				
	I	II	III	IV-AP*	IV-AL**
FLAGELLAR SEGMENTS					
I	0.099 - 0.165	0.165 - 0.297	0.132 - 0.242	0.297 - 0.429	0.297 - 0.462
II	0.099 - 0.132	0.132 - 0.198	0.165 - 0.297	0.264 - 0.462	0.264 - 0.462
III	-	-	0.165 - 0.297	0.297 - 0.429	0.231 - 0.396
IV	0.198 - 0.429	0.363 - 0.627	0.396 - 0.893	0.627 - 0.957	0.627 - 0.891
BODY LENGTH	0.594 - 0.957	0.726 - 1.254	0.891 - 1.709	1.155 - 2.110	1.257 - 2.160
CORNICLES	0.099 - 0.132	0.165 - 0.264	0.297 - 0.429	0.462 - 0.644	0.396 - 0.627
FORE-TIBIA	0.198 - 0.297	0.297 - 0.429	0.396 - 0.687	0.693 - 0.969	0.726 - 0.957
MESO-TIBIA	0.198 - 0.297	0.297 - 0.429	0.462 - 0.687	0.693 - 0.969	0.726 - 0.957
HIND-TIBIA	0.264 - 0.429	0.396 - 0.627	0.627 - 0.929	0.990 - 1.373	1.056 - 1.373

* AP = Apterae

** AL = Alates

TABLE III

LENGHTS (mm) OF SOME MORPHOLOGICAL CHARACTERS OF FIELD-COLLECTED BLUE ALFALFA APHID

CHARACTERS	INSTARS											
	I			II			III			IV-AP*			IV-AL**		
	$\bar{x}$	(± S.D.)	n	$\bar{x}$	(± S.D.)	n	$\bar{x}$	(± S.D.)	n	$\bar{x}$	(± S.D.)	n	$\bar{x}$	(± S.D.)	n
FLAGELLAR SEGMENT -I	0.140	(.017)	207	0.280	(.031)	239	0.244	(.023)	221	0.456	(.042)	91	0.473	(.036)	122
FLAGELLAR SEGMENT -II	0.117	(.016)	207	0.182	(.019)	239	0.273	(.028)	221	0.424	(.049)	91	0.440	(.037)	122
FLAGELLAR SEGMENT -III		-			-		0.284	(.026)	221	0.399	(.038)	91	0.421	(.032)	122
FLAGELLAR SEGMENT - TERMINAL	0.369	(.030)	207	0.510	(.046)	239	0.681	(.055)	217	0.834	(.078)	89	0.882	(.054)	121
BODY LENGTH	0.839	(.126)	194	1.097	(.173)	210	1.478	(.222)	193	2.026	(.295)	80	1.950	(.288)	119
CORNICLES	0.117	(.019)	207	0.226	(.025)	239	0.374	(.032)	221	0.568	(.052)	91	0.538	(.047)	122
FORE-TIBIA	0.266	(.023)	207	0.399	(.036)	239	0.626	(.052)	220	0.909	(.083)	91	0.973	(.061)	122
MESO-TIBIA	0.273	(.025)	207	0.405	(.035)	239	0.631	(.054)	220	0.914	(.084)	91	0.971	(.062)	122
HIND-TIBIA	0.371	(.031)	207	0.558	(.049)	239	0.866	(.068)	220	1.287	(.123)	88	1.337	(.088)	122

* AP = Apterae

** AL = Alates

TABLE IV

RANGES (mm) FOR LENGTHS OF SOME MORPHOLOGICAL CHARACTERS OF FIELD-COLLECTED BLUE ALFALFA APHID

CHARACTERS	INSTARS				
	I	II	III	IV-AP*	IV-AL**
FLAGELLAR SEGMENTS					
I	0.099 - 0.198	0.198 - 0.363	0.165 - 0.297	0.363 - 0.561	0.363 - 0.528
II	0.099 - 0.132	0.132 - 0.231	0.198 - 0.330	0.297 - 0.528	0.363 - 0.528
III	-	-	0.198 - 0.330	0.297 - 0.462	0.330 - 0.495
IV	0.297 - 0.429	0.264 - 0.594	0.429 - 0.792	0.528 - 0.990	0.726 - 0.990
BODY LENGTH	0.561 - 1.122	0.693 - 1.650	0.759 - 2.060	1.408 - 2.565	1.287 - 2.565
CORNICLES	0.066 - 0.198	0.165 - 0.297	0.231 - 0.429	0.363 - 0.660	0.396 - 0.627
FORE-TIBIA	0.231 - 0.330	0.330 - 0.495	0.462 - 0.726	0.726 - 1.089	0.825 - 1.156
MESO-TIBIA	0.231 - 0.330	0.330 - 0.495	0.462 - 0.726	0.759 - 1.122	0.825 - 1.156
HIND-TIBIA	0.297 - 0.462	0.366 - 0.660	0.693 - 0.990	1.089 - 1.584	1.122 - 1.508

* AP + Apterae

** AL = Alates

The stepwise procedure selected seven characters required for maximum discrimination between instars. Cornicle length was the single most important variable for which 96.5% of the total variation could be attributed to the instars, and thus was selected in the first step. The first flagellar segment was second to enter into the discriminant model. The sequence of all the characters as they were selected and associated statistics (Partial R^2, F values, Prob > F, Wilk's lambda and Prob < lambda) are given in table V. Although the F-tests were significant ($P < 0.05$) for all the characters selected by the stepwise procedure, the values for Wilk's lambda did not decrease substantially by adding new variables after the lengths of cornicles, first flagellar segments, fore-tibia and fourth flagellar segments were in the model.

Using variables selected by the stepwise procedure, discriminant analyses were further performed on the laboratory data to develop functions for separating instars in the field-collected aphids. Using these functions, all of the 226 second, 211 third and 202 fourth instar nymphs from the field populations were classified into their respective instars correctly. Misclassification occurred only between first and second instars where 2 of 218 first instars were placed with second instar (Table VI, model 1).

The results of an optimization procedure conducted to minimize the number of morphological characters required for age-grading in field populations are summarized in table VI. Model 1 describes the classification based on all the variables selected by the stepwise procedure. Elimination of hind-tibia (model 2); hind-tibia and second flagellar segments (model 3); hind-tibia, second flagellar segments, and body length (model 4); or hind-tibia, second flagellar segments, body

TABLE V

CHARACTERS REQUIRED TO CLASSIFY BLUE ALFALFA APHID BY INSTARS AS SELECTED IN A STEPWISE DISCRIMINANT ANALYSIS AND ASSOCIATED STATISTICS

STEP	VARIABLE SELECTED	PARTIAL R^2	F STATISTICS	PROB > F	WILK'S LAMBDA	PROB < LAMBDA
1	CORNICLE	0.9652	2144.932	0.0001	0.0348	0.0
2	FLAGELLAR SEGMENT -I	0.7749	264.998	0.0001	0.0078	0.0
3	FORE-TIBIA	0.4130	53.939	0.0001	0.0046	0.0
4	FLAGELLAR SEGMENT- IV	0.3456	40.311	0.0001	0.0030	0.0
5	BODY LENGTH	0.1024	8.673	0.0001	0.0027	0.0
6	FS - II	0.0797	6.557	0.0003	0.0025	0.0
7	HIND-TIBIA	0.0371	2.905	0.0351	0.0024	0.0

TABLE VI

PERCENT OF FIELD-COLLECTED BLUE ALFALFA APHIDS CLASSIFIED CORRECTLY BY INSTARS USING DISCRIMINANT FUNCTIONS BASED ON DIFFERENT CHARACTERS

ACTUAL INSTAR	MODEL*	CLASSIFIED TO INSTAR				
		I	II	III	IV	n
I	1	99.08	000.92	000.00	000.00	218
	2	99.08	000.92	000.00	000.00	218
	3	99.08	000.92	000.00	000.00	218
	4	99.13	000.87	000.00	000.00	231
	5	99.13	000.87	000.00	000.00	231
	6	99.57	000.43	000.00	000.00	231
II	1	00.00	100.00	000.00	000.00	226
	2	00.00	100.00	000.00	000.00	226
	3	00.00	100.00	000.00	000.00	226
	4	00.39	99.61	000.00	000.00	255
	5	00.00	100.00	000.00	000.00	255
	6	00.00	100.00	000.00	000.00	255
III	1	00.00	000.00	100.00	000.00	211
	2	00.00	000.00	100.00	000.00	211
	3	00.00	000.00	100.00	000.00	211
	4	00.00	000.00	100.00	000.00	238
	5	00.00	000.00	100.00	000.00	243
	6	00.00	1.64	98.36	000.00	244
IV	1	00.00	000.00	000.00	100.00	202
	2	00.00	000.00	000.00	100.00	204
	3	00.00	000.00	000.00	100.00	204
	4	00.00	000.00	000.00	100.00	217
	5	00.00	000.00	000.00	100.00	220
	6	00.00	0.90	000.00	99.10	220

* See text for description of models.

TABLE VII

LINEAR DISCRIMINANT FUNCTIONS BASED ON LENGTHS (mm) OF CORNICLES, FIRST FLAGELLAR SEGMENT AND FORE-TIBIA FOR CLASSIFYING BLUE ALFALFA APHID BY INSTARS

	APHID INSTARS			
VARIABLES	I	II	III	IV
CONSTANT	-13.0445	-39.8091	-88.9389	-189.4363
CORNICLE	23.2888	93.6861	293.3923	395.8748
FLAGELLAR SEGMENT - I	58.0250	194.6501	-177.7060	-46.5036
FORE-TIBIA	64.8406	31.5123	187.9054	209.5462

length, and fourth- flagellar segments (model 5) from the full model did not result in an increase in misclassification among instars exceeding 1%. However, when hind-tibia, second flagellar segments, body length, fourth-flagellar segments and fore-tibia (model 6) were dropped from model 1, 0.4% second instars were placed with first instars, 1.6% of third and 0.9% of fourth instars were also classified as second instars. Therefore, model 5 which included cornicle length, first flagellar segments, and fore-tibia was considered the optimum and was selected as a suitable criterion for separating instars of BAA. The linear discriminant functions for four instars based on the lengths of cornicles, first flagellar segments, and fore-tibia are presented in table VII. Using these functions, all of the second, third, and fourth instars and 99.1% of the first instars of field-collected BAA were correctly classified.

Spotted Alfalfa Aphid

Means, standard deviations, and sample sizes for first, second, third and fourth flagellar segments, body length, fore-tibia, meso-tibia and hind-tibia of laboratory-reared SAA nymphs are given in table VIII, and observed ranges of these characters are presented in Table IX. Numbers of flagellar segments in the antenna were two for the first, three for the second and four for the third and fourth instars. Mean lengths of all the characters were significantly ($P < 0.05$) different among instars. However, the measurements of each character showed overlap among successive instars.

Mean lengths of morphological characters of the field populations were greater than corresponding lengths of the laboratory population

TABLE VIII

LENGTHS (mm) OF SOME MORPHOLOGICAL CHARACTERS OF LABORATORY-CULTURED SPOTTED ALFALFA APHID

	INSTARS											
	I			II			III			IV-AP*		
CHARACTERS	$\bar{x}$	($\pm$ S.D.)	n	$\bar{x}$	($\pm$ S.D.)	n	$\bar{x}$	($\pm$ S.D.)	n	$\bar{x}$	($\pm$ S.D.)	n
FLAGELLAR SEGMENT - I	0.187	(.020)	62	0.207	(.017)	46	0.217	(.019)	46	0.359	(.033)	50
FLAGELLAR SEGMENT - II		-		0.108	(.015)	46	0.149	(.018)	46	0.232	(.027)	50
FLAGELLAR SEGMENT - III		-			-		0.154	(.020)	46	0.223	(.031)	50
FLAGELLAR SEGMENT - IV	0.135	(.010)	62	0.170	(.017)	46	0.215	(.021)	46	0.274	(.025)	50
BODY LENGTH	0.591	(.103)	62	0.801	(.081)	46	1.056	(.097)	46	1.354	(.184)	50
FORE-TIBIA	0.138	(.013)	62	0.189	(.020)	46	0.280	(.021)	46	0.407	(.036)	50
MESO-TIBIA	0.139	(.014)	62	0.189	(.017)	46	0.280	(.023)	46	0.407	(.035)	50
HIND-TIBIA	0.158	(.020)	62	0.215	(.019)	46	0.319	(.022)	46	0.471	(.037)	50

* AP = Apterae

TABLE IX

RANGES (mm) FOR LENGTHS OF SOME MORPHOLOGICAL CHARACTERS OF LABORATORY-CULTURED SPOTTED ALFALFA APHID

CHARACTERS	APHID INSTARS			
	I	II	III	IV-AP*
FLAGELLAR SEGMENTS				
I	0.165 - 0.231	0.165 - 0.231	0.165 - 0.264	0.297 - 0.462
II	-	0.099 - 0.132	0.132 - 0.198	0.165 - 0.264
III	-	-	0.132 - 0.198	0.165 - 0.264
IV	0.132 - 0.165	0.132 - 0.198	0.198 - 0.264	0.198 - 0.297
BODY LENGTH	0.396 - 0.827	0.660 - 0.990	0.759 - 1.254	0.990 - 1.759
FORE-TIBIA	0.132 - 0.165	0.165 - 0.231	0.264 - 0.330	0.330 - 0.495
MESO-TIBIA	0.132 - 0.165	0.165 - 0.237	0.264 - 0.363	0.330 - 0.495
HIND-TIBIA	0.132 - 0.264	0.198 - 0.264	0.264 - 0.363	0.396 - 0.528

* AP = Apterae

(Table X). The ranges of hind-tibial length in the field populations did not overlap among instars (Table XI). Similarly size ranges of fore-tibia and meso-tibia did not overlap among second and third or third and fourth instars indicating that these characters could be useful in discriminating field populations of SAA.

Multivariate analysis of variance performed on the laboratory data using first and fourth flagellar segments, body length, fore-tibia, meso-tibia, and hind-tibia indicated that centroids of four instars in multidimensional space are significantly different by Wilk's criterion ($F = 118.5$, $DF = 18,552.0$, $P = 0.0$), Pillai's trace ($F = 41.7$, $DF = 18,591.0$, $P = 0.0$), or Hotelling-Lawly trace ($F = 312.9$, $DF = 18,581.0$, $P = 0.0$). This suggested that the data could be subjected to discriminant analysis.

The stepwise discriminant procedure selected five variables which provided the best discrimination among the instars. Length of hind-tibia was the most important variable and was the first to enter the model followed by first flagellar segment. The variables in the sequence of their selection and associated statistics are presented in Table XII.

The linear discriminant functions for four instars generated by discriminant analysis of the laboratory data using the variables selected by stepwise procedure are given in Table XIII. When the classification was based on these functions, more than 98% of the first instar and 100% of the second, third, and fourth instars in laboratory studies were correctly classified. Validations of these models were conducted on 292 field-collected SAA which included 74 first, 71 second, 81 third, and 66 fourth instar nymphs. Using discriminant functions,

TABLE X

LENGTHS (mm) OF SOME MORPHOLOGICAL CHARACTERS OF FIELD-COLLECTED SPOTTED ALFALFA APHID

	APHID INSTARS				
	I	II	III	IV-AP*	IV-AL**
CHARACTERS	$\bar{X}$ (± S.D.) n	$\bar{X}$ (± S.D.) n	$\bar{X}$ (± S.D.) n	$\bar{X}$ (± S.D.) n	$\bar{X}$ (± S.D.) n
FLAGELLAR SEGMENT - I	0.224 (.018) 75	0.243 (.019) 72	0.244 (.021) 81	0.382 (.036) 24	0.403 (.031) 43
FLAGELLAR SEGMENT - II	-	0.133 (.007) 72	0.184 (.017) 81	0.264 (.026) 24	0.284 (.024) 43
FLAGELLAR SEGMENT - III	-	-	0.197 (.016) 81	0.263 (.025) 24	0.283 (.023) 43
FLAGELLAR SEGMENT - IV	0.154 (.016) 75	0.195 (.009) 72	0.249 (.017) 81	0.297 (.026) 24	0.306 (.022) 43
BODY LENGTH	0.711 (.065) 75	0.946 (.099) 71	1.308 (.165) 81	1.704 (.113) 24	1.699 (.230) 43
FORE-TIBIA	0.165 (.011) 76	0.235 (.015) 72	0.350 (.021) 81	0.481 (.029) 24	0.533 (.034) 43
MESO-TIBIA	0.162 (.010) 76	0.229 (.012) 72	0.336 (.021) 81	0.457 (.032) 24	0.486 (.036) 43
HIND-TIBIA	0.178 (.016) 76	0.258 (.015) 72	0.385 (.024) 81	0.532 (.033) 24	0.580 (.040) 43

* AP = Apterae

** AL = Alate

TABLE XI

RANGES (mm) FOR LENGTHS OF SOME MORPHOLOGICAL CHARACTERS OF FIELD-COLLECTED SPOTTED ALFALFA APHID

CHARACTERS	APHID INSTARS				
	I	II	III	IV-AP*	IV-AL**
FLAGELLAR SEGMENTS					
I	0.132 - 0.264	0.198 - 0.297	0.198 - 0.297	0.297 - 0.429	0.330 - 0.462
II	-	0.132 - 0.165	0.132 - 0.198	0.198 - 0.297	0.330 - 0.462
III	-	-	0.165 - 0.198	0.231 - 0.297	0.231 - 0.330
IV	0.132 - 0.198	0.165 - 0.198	0.231 - 0.297	0.231 - 0.330	0.231 - 0.363
BODY LENGTH	0.561 - 0.858	0.660 - 1.254	0.825 - 1.617	1.452 - 1.617	1.452 - 1.910
FORE-TIBIA	0.132 - 0.198	0.198 - 0.264	0.297 - 0.396	0.429 - 0.528	0.462 - 0.594
MESO-TIBIA	0.132 - 0.165	0.198 - 0.264	0.264 - 0.363	0.396 - 0.495	0.429 - 0.561
HIND-TIBIA	0.165 - 0.198	0.231 - 0.297	0.330 - 0.429	0.495 - 0.594	0.491 - 0.627

* AP = Apterae
** AL = Alate

TABLE XII

CHARACTERS REQUIRED TO CLASSIFY SPOTTED ALFALFA APHID BY INSTARS AS SELECTED IN A STEPWISE DISCRIMINANT ANALYSIS AND ASSOCIATED STATISTICS

STEP	VARIABLE SELECTED	PARTIAL R^2	F STATISTICS	PROB > F	WILK'S LAMBDA	PROB < LAMBDA
1	HIND-TIBIA	0.9589	1554.134	0.0001	0.0411	0.0
2	FLAGELLAR SEGMENT - I	0.6155	106.199	0.0001	0.0158	0.0
3	MESO-TIBIA	0.1458	11.268	0.0001	0.0135	0.0
4	BODY LENGTH	0.1138	8.432	0.0001	0.0120	0.0
5	FLAGELLAR SEGMENT -IV	0.0461	3.154	0.0257	0.0114	0.0

TABLE XIII

LINEAR DISCRIMINANT FUNCTIONS BASED ON MORPHOMETRIC CHARACTERS FOR CLASSIFYING SPOTTED ALFALFA APHID BY INSTARS

VARIABLES	APHID INSTARS			
	I	II	III	IV
CONSTANT	-43.1371	-63.1283	-108.6086	-220.1490
FLAGELLAR SEGMENT -I	245.8868	192.1988	30.9729	202.6454
FLAGELLAR SEGMENT -IV	228.2170	272.3914	300.8190	286.7514
BODY LENGTH	5.8537	13.0032	20.3352	11.5609
MESO-TIBIA	44.8192	88.0023	199.5288	298.6046
HIND-TIBIA	-2.3223	60.7420	215.5745	322.0279

90.0% of the first, 95.7% of the second, 96.3% of the third, and 100% of the fourth instars were correctly classified.

Discussion

In the time specific-life table approach of Hughes (1962), the estimates of mortality were obtained by comparing the age structure of the aphid populations over a specific time interval. Therefore, proper interpretations of mortality factors would become impossible if a reliable criterion for age-grading field populations is not available.

In the present study, classification criteria in the form of linear discriminant functions developed from the laboratory populations of BAA provided an accurate classification of all nymphal instars. The criteria have been validated on field- collected aphids from 10 different geographical locations of Oklahoma. Despite greater variation and larger sizes of aphids in the field populations, misclassification was only observed in the first instar where 0.9% of nymphs were classified as second instars. This suggested that these functions are accurate and could be used for age-grading field populations of BAA for life table studies. To use these criteria for classifying individuals from field populations, lengths of cornicles, first flagellar segments, and fore-tibia are required. The score is calculated on all the discriminant functions and the individual is classified to the instar for which the highest score is obtained.

For the SAA, the linear discriminant functions provided a classification criterion which correctly classified more than 95% of the second, third, and fourth instars from field populations. The misclassification rate was somewhat higher for SAA than for BAA. A comparatively larger overlap in the lenghts of different morphological

characters among successive instars was also observed for SAA which suggested that size in this aphid species might be affected more by the environmental conditions. This suggests that use of linear discriminant functions developed in these studies for separating instars in other populations must be approached with caution.

Previous studies with other aphid species have involved a 'key out' approach in which the classification of individuals by instars is based either on presence/absence of some qualitative characters or on measurements of some morphological characters falling within a specified range (Sana and Shultz 1967, Kirkland et al. 1981, Takahashi 1924). Generally, three problems are associated with using a 'key out' classification approach for life table studies including; 1) different combinations of characters are used to separate different instars which requires more time of a trained personnel, 2) errors in misclassification are not quantified, and 3) the ranges of measurements of morphological characters of the same instar may vary because size in aphids varies if reared at different temperatures or population densities (Murdie 1969), at different locations (Hutchison and Hogg 1983), or under different nutritional conditions (Dixon 1985).

In the present studies, discriminant analyses have been found suitable for developing classification criteria for age- grading BAA and SAA, which avoid the limitations mentioned above and are recommended for similar studies in other aphids.

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CHAPTER II

DISPERSION INDICES AND SAMPLING PLANS FOR THE BLUE ALFALFA APHID AND THE PEA APHID IN OKLAHOMA

Introduction

The blue alfalfa aphid (BAA), Acyrthosiphon kondoi Shinji, and the pea aphid (PAA), Acyrthosiphon pisum (Harris), are serious pests distributed throughout major alfalfa, Medicago sativa L., growing regions in the United States (Kodet et al. 1982). Both species are found in spring and early summer in Oklahoma (Berberet et al. 1983) and population densities frequently exceed the economic threshold levels determined by Stern et al. (1980) and Cuperus et al. (1982). Accuracy in estimation of population densities in the field is vital for studies of aphid biologies as well as decision-making regarding chemical controls. Time requirements for conducting sampling which provides a high degree of precision are dependent on the spatial patterns of the subject species among habitat units to be sampled (Elliott and Kieckhefer 1986). Spatial patterns of the same species may vary in different years (Ekbom 1985) and over the season in the same year (Trumble et al. 1983, Picket and Gilstrap 1986, Chandler and Gilstrap 1986).

A high degree of aggregation or "clumping" in the spatial pattern

increases greatly the difficulty in obtaining precise population density estimates.

Several analytical techniques are available for determining how the insects are distributed in their habitats. For species-specific spatial patterns, regression of mean crowding on the mean density as described by Iwao (1968, 1977) and Iwao and Kuno (1971) has been widely used for describing the spatial patterns of many arthropod species (Chandler and Gilstrap 1986, Christensen et al. 1977, Ekbom 1985, Gutierrez et al. 1980).

To verify that changes in spatial patterns of a species have occurred over time, Lloyd's Patchiness index (Lloyd 1967) is often utilized because it is not affected by random addition or removal of individuals from the population (Pielou 1977). It has been found useful in describing seasonal changes in spatial patterns of many aphid species (Baumgartener et al 1983, Gutierrez et al. 1980, Trumble 1982, Trumble et al. 1983).

Based on relative abundance of both species in California, Stern et al. (1980) and Gutierrez et al. (1980) reported that BAA has been competitively displacing spring populations of PAA. If these species show a significant degree of association or co-occurrence within sampling units, interactions could arise due to similarity of habitat requirements that may result in competitive displacement and affect spatial patterns of the species.

Several indices have also been proposed to describe the association of occurrence between two species. However, Cole's (1949) coefficient of association was proposed especially for ecological problems (Pielou 1977). Cole's coefficient is preferred because its values range from 0

in case of random occurrence to 1 where association is highest. Also, the changes in the probability of co-occurrence show a linear relationship with values of the index.

This research included studies on, 1) the variations in the spatial patterns of BAA and PAA in Oklahoma and, 2) the association of co-occurrence of these species. Based on the spatial patterns of the aphid species, sampling plans for estimation of population densities in the field with a fixed level of precision were developed.

Materials and Methods

Sampling Procedures

This investigation was conducted on two alfalfa (var:Buffalo) plots with dimensions 4.6 x 46 m and 7.6 x 46 m during 1985, which were designated as site I and site II, respectively. One plot (var: OK-08) was used during 1986 with dimensions of 20 x 35 m. Neither alfalfa variety had been bred for resistance to either BAA or PAA. The study sites were located at Stillwater, Oklahoma, during 1985 and at Chickasha during 1986. An experimental insecticide designated SN-72129 (Nor-Am Agricultural Products, Inc.) which had showed moderate activity against the alfalfa weevil, Hypera postica (Gyllenhal), but no aphicidal activity was applied in March or early April @ 1.65 Kg AI/ha to delay the onset of weevil damage.

During 1985, sampling began on 15 April at site I and 17 April on site II and terminated on 10 May when the aphids were no longer found. Due to mild winter weather in 1986, sampling was started on 23 February and terminated on 5 April. Sampling intervals were based on accumulated day degrees above a threshold of 3.5°C and each plot was sampled at

least twice per aphid generation time (ca. 140 C° days). Each site was divided into 10 equal subplots. A stratified random sampling plan was adopted using single stems as sampling units. Numbers of samples taken from each subplot varied according to the aphid population densities. Twelve stems were randomly sampled from each subplot (total=120/date) if the densities of aphids were less than 100/stem. Only six samples (total=60/date) were taken when the densities exceeded 100/stem.

Two aphid collection methods were used. Early in the season, when alfalfa was short (< 20 cm), stems were clipped from crowns with scissors while a small card was held beneath to catch the aphids which were dislodged. The stems along with the aphids were transported to the laboratory for counting in jars containing 50% alcohol. When the stem lengths exceeded 20 - 25 cm, aphids were collected by tapping the stems over a pan containing 50% alcohol. The stems were then checked carefully and the remaining aphids were removed with a camels hair brush and stored in alcohol. Aphid species were identified using method described by Kono (1977) at the time of counting.

Statistical Analysis

The spatial variation in aphid densities was analyzed for subplots within a site at each sampling date using a general linear model approach (SAS Institute Inc. 1985). Since no significant differences ($P > 0.05$) in numbers of BAA and PAA were found among the subplots on 20 of 22 sampling occasions, further analysis was conducted on data pooled for all subplots on each sampling date.

Since the quantitative estimates of spatial patterns are based on variance to mean density relationships, the magnitude of these estimates

is dependent on whether the basic unit of contagion used is an individual or a colony of several aphids. A regression technique (Iwao (1968, Iwao and Kuno 1971) was used to determine the basic unit of the distribution. This technique also provided estimates for species-specific aggregation patterns. The regression equation is of the form:

$$m^* = \alpha + \beta m \qquad (2.1)$$

where

m = mean density.

m*= mean crowding which is defined as mean number/individual of other individuals in a sampling unit and is calculated by:

$$m^* = m + ((s^2/m) - 1) \qquad (2.2)$$

where

s^2 = sample variance.

The intercept (α) indicates the basic unit of contagion of the distribution. If $\alpha = 0$, a single individual is the unit, whereas a colony forms the basic unit when $\alpha > 0$. Values less than 0 indicate repulsion among the individuals. The slope of the line (β) is designated as the density contagiousness coefficient and indicates the pattern of dispersion of the species population among the sampling units. The values of $\beta = 1$, $\beta > 1$ or $0 < \beta < 1$ indicate random, aggregated and regular spatial patterns, respectively. Temporal changes in dispersion of BAA and PAA were documented using Llyod's Patchiness

Index (LPI) (Llyod 1967). This index is calculated as the ratio of mean crowding (m*) to the mean (m):

$$LPI = m^*/m \qquad (2.3)$$

Values of LPI less than, equal to, or greater than 1 indicate regular, random and aggregated patterns, respectively.

The degree of association of BAA and PAA was determined for each sampling date by a Chi-squared (χ^2) test. This test takes the form:

$$\chi^2 = \frac{(ad - bc)^2 * N}{mnrs} \qquad (2.4)$$

where

a = Frequency of co-occurrence of both species in a sampling unit.

b = Frequency of sampling units with only PAA.

c = Frequency of sampling units with only BAA.

d = Frequency of sampling unit with no aphids.

N = Sample size.

m = a+b, n = c+d, r = a+c and s = b+d

Significant values for the χ^2 test suggest rejection of hypotheses of independence of occurrence of species in a sampling unit. The magnitude of association was measured using Cole's coefficient of association. For positive association, the Cole's coefficient is defined as:

$$C = \frac{ad - bc}{(a + b)*(b + d)} \qquad (2.5)$$

where a,b,c and d are as defined earlier.

The values of index range from +1 to -1, with +1 indicating

complete association whereas -1 meaning complete repulsion among the individuals of the two species. A value of 0 indicates that species select their host plants independently of each other.

In each population, the possible displacement of PAA as a result of increases in BAA densities occurring on the same stems was tested using a linear regression where BAA density was chosen as the independent variable and PAA density as the dependent variable.

Sample sizes required for estimation of mean density with fixed levels of precision, in terms of a confidence interval with half width equal to a stated percentage of the mean (Karandinos 1976), were calculated using the equation developed by Christensen et al. (1977) which takes the form:

$$n = (t^2/D^2)*(m*/m - 1 + 1/m) \qquad (2.6)$$

where

n = sample size.

t = student's t for the frequency with which a sample of size n will give an estimate of precision D or better.

D = half length of the confidence interval required as a percent of the mean.

m* and m as defined earlier.

Results

The spatial variation in mean densities of BAA was generally consistent throughout the season for all three sites. The differences among subplot means were not significant ($P > 0.05$) on 20 of 22 sampling

TABLE XIV

SIGNIFICANCE OF F-TESTS FOR DIFFERENCES IN POPULATION DENSITIES OF BLUE ALFALFA APHID AMONG SUBPLOTS FOR EACH SAMPLING OCCASION DURING 1985 AND 1986

YEAR	SITE	DATE	MEAN DENSITY	D.F.	PROB > F
1985	1	APRIL-17	3.66	9, 110	0.9519
1985	1	APRIL-23	34.47	9, 110	0.6160
1985	1	APRIL-25	54.16	9, 110	0.8670
1985	1	MAY-01	238.64	9, 49	0.1396
1985	1	MAY-03	277.22	9, 49	0.4112
1985	1	MAY-08	11.22	9, 50	0.1523
1985	1	MAY-10	0.85	9, 50	0.9654
1985	2	APRIL-15	3.70	9, 110	0.8139
1985	2	APRIL-17	3.31	9, 110	0.2990
1985	2	APRIL-24	32.88	9, 110	0.0069*
1985	2	APRIL-26	63.93	9, 110	0.1072
1985	2	MAY-01	218.47	9, 50	0.2768
1985	2	MAY-03	239.72	9, 50	0.0848
1985	2	MAY-08	4.73	9, 50	0.0003*
1985	2	MAY-10	0.08	9, 50	0.6158
1986	1	FEB-23	0.28	9, 110	0.4904
1986	1	MARCH-04	2.75	9, 110	0.2806
1986	1	MARCH-06	3.38	9, 110	0.6683
1986	1	MARCH-21	23.45	9, 110	0.5433
1986	1	MARCH-25	87.38	9, 50	0.8025
1986	1	APRIL-01	246.00	9, 50	0.5050
1986	1	APRIL-05	285.00	9, 50	0.1289

* F. values significant (P>0.05).

TABLE XV.

SIGNIFICANCE OF F-TESTS FOR DIFFERENCES IN POPULATION DENSITIES OF THE PEA APHID AMONG SUBPLOTS FOR EACH SAMPLING OCCASION DURING 1985 AND 1986

YEAR	SITE	DATE	MEAN DENSITY APHIDS/STEM	D.F.	PROB > F
1985	1	APRIL-17	0.35	9, 110	0.0015*
1985	1	APRIL-23	0.53	9, 110	0.0071*
1985	1	APRIL-25	0.59	9, 110	0.1685
1985	1	MAY-01	3.07	9, 49	0.0067*
1985	1	MAY-03	8.27	9, 49	0.2278
1985	1	MAY-08	5.68	9, 50	0.1981
1985	1	MAY-10	1.20	9, 50	0.2097
1985	2	APRIL-15	0.09	9, 110	0.0025*
1985	2	APRIL-17	0.03	9, 110	0.6372
1985	2	APRIL-24	0.62	9, 110	0.2186
1985	2	APRIL-26	0.91	9, 110	0.2421
1985	2	MAY-01	1.95	9, 50	0.8776
1985	2	MAY-03	4.13	9, 50	0.0506
1985	2	MAY-08	1.67	9, 50	0.0106*
1985	2	MAY-10	0.07	9, 50	0.7346
1986	1	FEB-23	1.64	9, 110	0.3223
1986	1	MARCH-04	5.45	9, 110	0.1991
1986	1	MARCH-06	9.03	9, 110	0.6824
1986	1	MARCH-21	38.46	9, 110	0.8852
1986	1	MARCH-25	90.28	9, 50	0.5044
1986	1	APRIL-01	172.28	9, 50	0.3949
1986	1	APRIL-05	200.13	9, 50	0.8499

* F. values significant (P>0.05).

dates (Table XIV). Similarly, no significant differences ($P > 0.05$) among subplot means for PAA were observed on 17 of 22 sampling dates (Table XV). Significant differences in aphid populations among subplots occurred primarily at low densities. Based on these results, data were pooled for all subplots by sampling date and analyses of spatial patterns were completed using single alfalfa stems as sampling units.

The intercept of Iwao's patchiness regression (α) for either species did not differ significantly ($P > 0.05$) from 0, indicating that the basic unit of contagion of the population was individual aphids. The slopes of the regression line (β) in all the populations for BAA were significantly ($P < 0.05$) greater than 1 (Table XVI) indicating an aggregated spatial pattern. Similarly, the slopes for PAA were significantly ($P < 0.05$) greater than 1 in 1985 site II and 1986 populations (Table XVI). A value not significantly greater than 1 ($F = 1.9$, $DF = 1,5$, $P > 0.23$) for the 1985 site I population of PAA was not interpreted as random dispersion because it resulted from high variability in the estimate (S.E.=0.30) and a relatively poor fit of the regression model ($R^2 = 0.82$). Discounting this instance, differences were not observed in the aggregation patterns of BAA and PAA for a particular year and site.

Changes in the spatial patterns of both species during the growing season were revealed by LPI. Two patterns of dispersion were observed for each species. Early in the season when densities were less than 10 aphids/stem, the LPI values ranged between 2.0 to 2.7. Values above this were not considered either because they were not significantly higher than 2.7 ($P > 0.05$) or they were based on extremely small densities. As the densities increased the LPI stabilized in the range

TABLE XVI

REGRESSION OF MEAN CROWDING (m*) TO MEAN DENSITY (m) FOR THE BLUE ALFALFA APHID AND THE PEA APHID

YEAR	SITE	EMS* d.f.	$\alpha \pm$ S.E	PROB > T H_0: $\alpha = 0$	$\beta \pm$ S.E	PROB > T H_0: $\beta = 1$	R^2
			BLUE ALFALFA APHID				
1985	1	5	3.83 ± 3.15	0.33	1.27 ± 0.025	0.0001	0.99
1985	2	6	-0.15 ± 3.40	0.97	1.50 ± 0.029	0.0001	0.99
1988	1	5	25.93 ± 16.6	0.18	1.34 ± 0.113	0.0299	0.96
			THE PEA APHID				
1985	1	5	1.33 ± 1.18	0.31	1.41 ± 0.30	0.2300	0.82
1985	2	6	0.17 ± 0.21	0.45	1.55 ± 0.12	0.0030	0.97
1986	1	5	11.37 ± 5.25	0.08	1.24 ± 0.05	0.0040	0.99

* Degrees of freedom for error mean squares.

Figure 1. Spatial patterns of three populations of blue alfalfa aphid. (Each data point represents a sampling date).

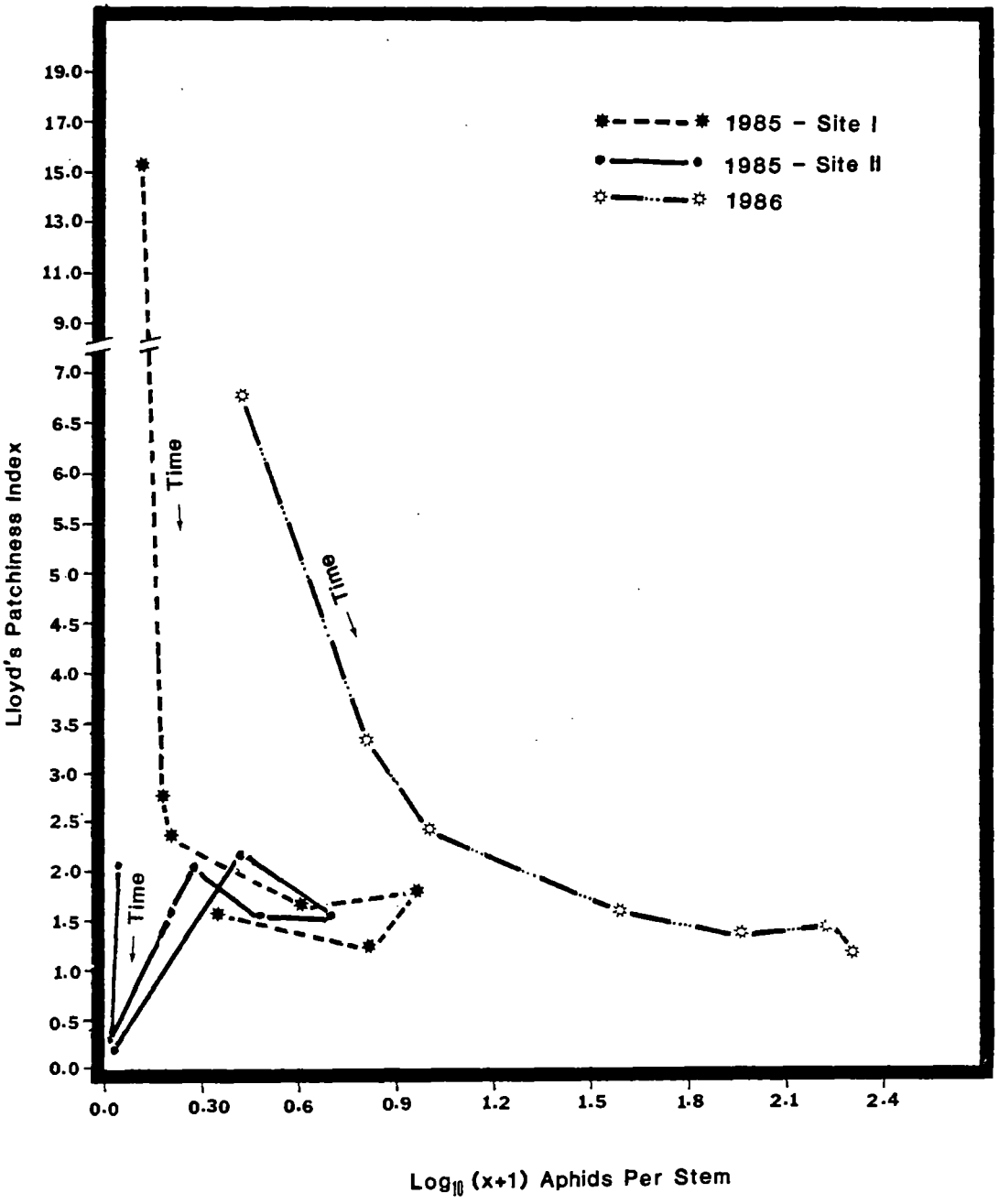
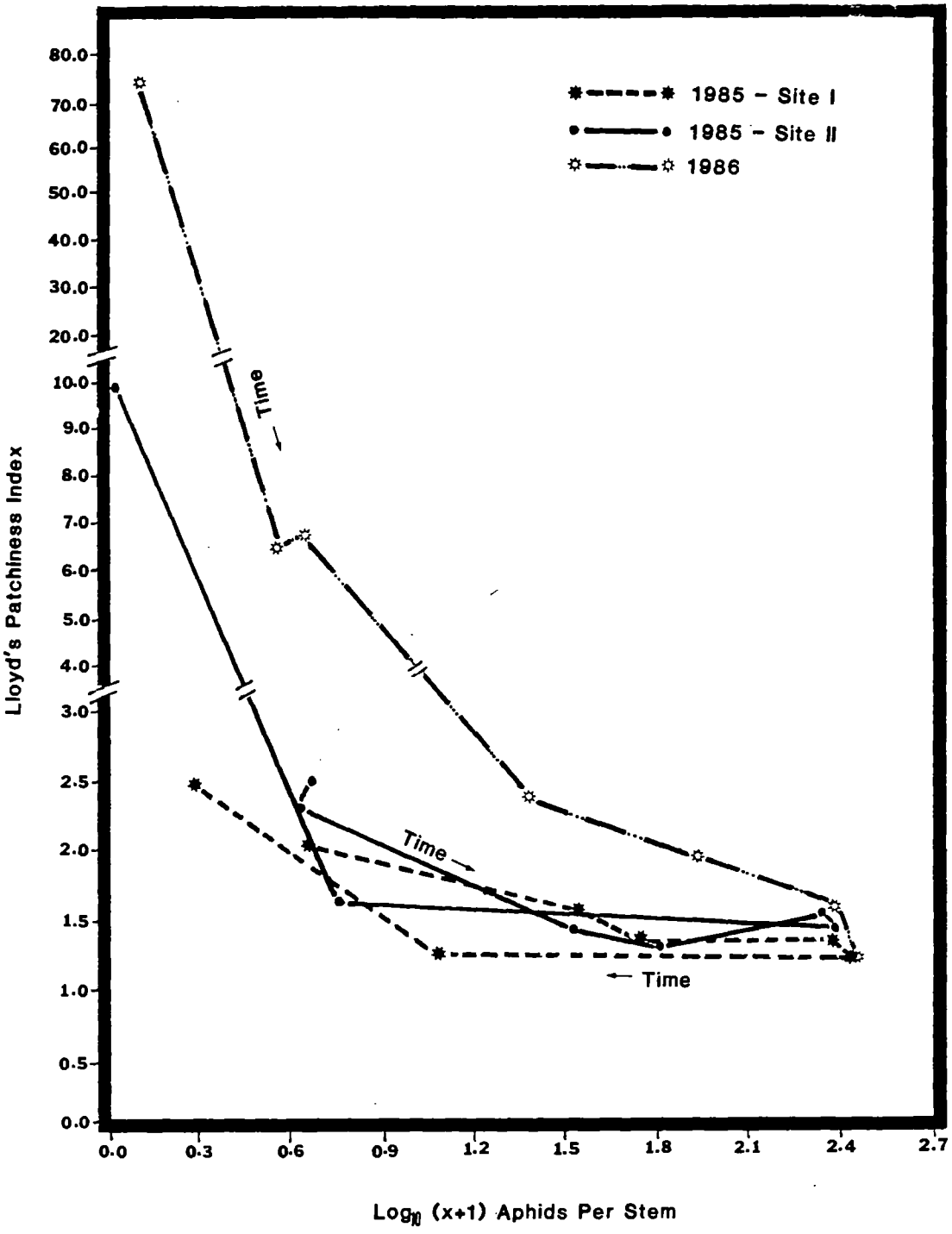

1985 - Site I
1985 - Site II
1986
Time
Time
Time
Lloyd's Patchiness Index
19.0
17.0
15.0
13.0
11.0
9.0
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.30
0.6
0.9
1.2
1.5
1.8
2.1
2.4
Log10 (x+1) Aphids Per Stem

Figure 2. Spatial patterns of three populations of the pea aphid (Each data point represents a sampling date).


1985 - Site I
1985 - Site II
1986
Time
Time
Time
Lloyd's Patchiness Index
Log10 (x+1) Aphids Per Stem
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.3
0.6
0.9
1.2
1.5
1.8
2.1
2.4
2.7

of 1.2 to 2.0 (Fig. 1-2). To document whether the changes in LPI values were independent of the mean density, a regression of LPI on mean density was performed. The results are summarized in Table XVII. The slopes for all the regression lines were not significantly ($P > 0.05$) different from 0 for both the species indicating that the values of the LPI observed in this study were not affected by the changes in mean density.

The BAA was the the most common species throughout the season at both sites during 1985 (Fig. 3, A-B). It accounted for more than 91% of the combined species population at site I and more than 97% at site II until 8 May when the population declined due to massive emigration of alates. During 1986, the infestation of aphids in the study area started earlier in the season due to mild winter temperatures. The increase in BAA density was slower than that for PAA initially with the result being that the PAA was the more common species until late March. When the optimal temperatures for development occurred in late March, the BAA densities increased rapidly and by 5 April it accounted for ca. 59% of the total aphid population (Fig. 3, C). Peak densities for both species were observed on 5 April after which the populations disappeared within 2-3 days, primarily due to the destruction of the alfalfa plants by the large numbers of aphids and alfalfa weevil larvae.

If Fig. 3 is viewed without considering population densities through the season for both species, an interpretation that BAA populations suppressed PAA during 1985 may result. However, comparison of mean population densities across sampling dates for both species (Table XIV and Table XV) show that trends in percentages observed in Fig. 3 may be misleading. Peak densities for both species were observed

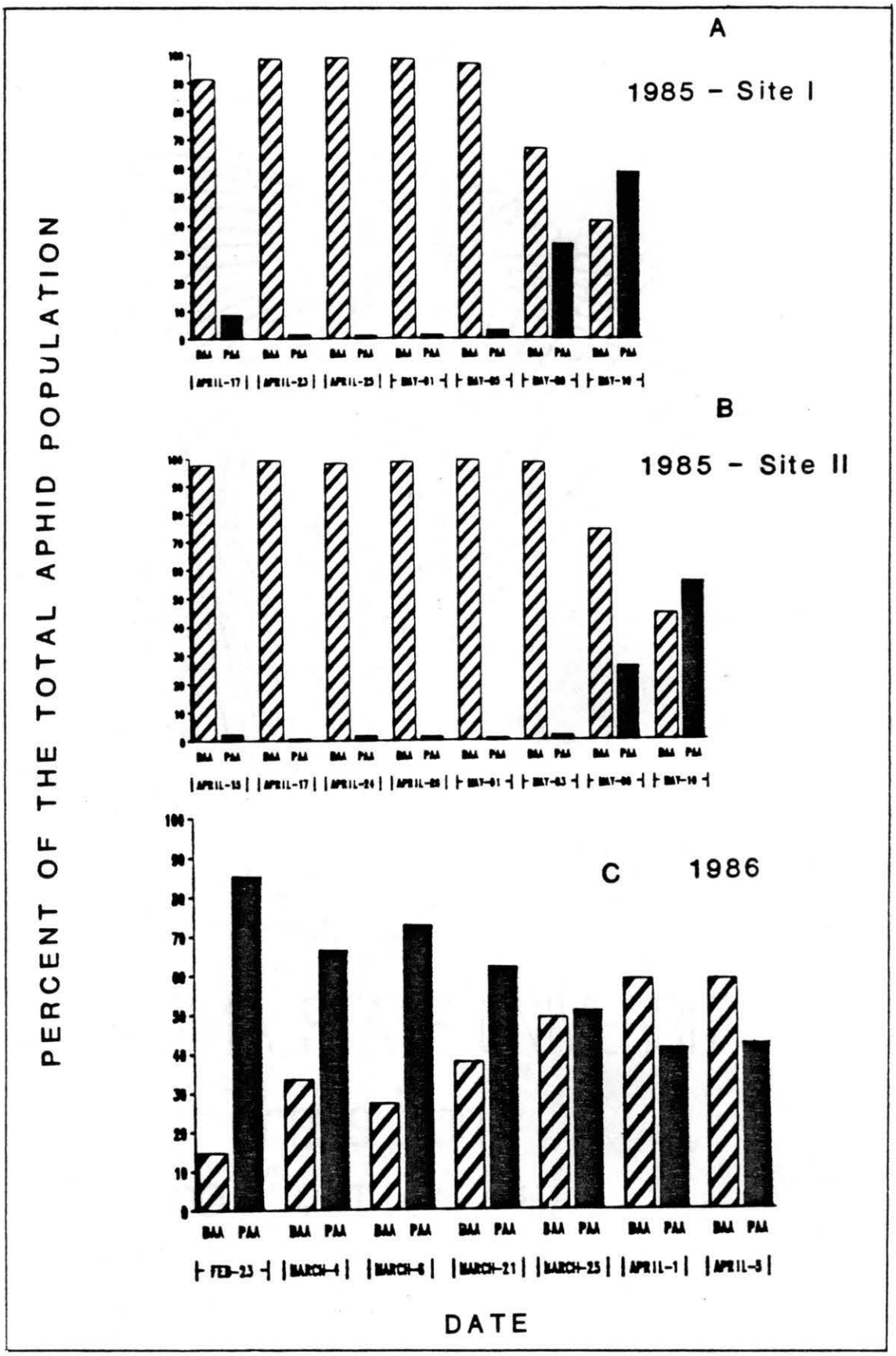
TABLE XVII

REGRESSION OF LLOYD'S PATCHINESS INDEX ON MEAN DENSITIES OF BLUE ALFALFA APHID AND PEA APHID

YEAR	SITE	*EMS d.f.	SLOPE ± S.E.	PROB > T H0: β = 0	R^2
			BLUE ALFALFA APHID		
1985	1	5	-0.0022 ± .0015	0.1857	0.32
1985	2	6	-0.0102 ± .0112	0.3965	0.12
1986	1	5	-0.0856 ± .0899	0.3847	0.15
POOLED	-	20	-0.0324 ± .0310	0.3079	0.05
			THE PEA APHID		
1985	1	5	-0.6674 ± .6779	0.3701	0.16
1985	2	6	0.1703 ± .2109	0.4503	0.10
1986	1	5	-0.0149 ± .0085	0.1393	0.38
POOLED	-	20	-0.0094 ± .0122	0.4510	0.03

*Degrees of freedom for Error Mean Squares.

Figure 3. Relative abundance of blue alfalfa aphid (BAA) and pea aphid (PAA) during 1985 (A-B) and 1986 (C).


A
1985 - Site I
B
1985 - Site II
C
1986
PERCENT OF THE TOTAL APHID POPULATION
DATE

on same sampling date (3 May in 1985 and 5 April in 1986) which would not be expected if competitive displacement had occurred. These results suggested that species percentages or seasonal mean densities may not lead to the proper conclusions regarding interactions between these species.

In order to more fully investigate the possibilities for competitive displacement of PAA by BAA, I have developed two possible mechanisms by which it could occur. In the first possibility, the best niches (stems) in the habitat may be occupied by BAA thus forcing PAA to select poorer quality stems with the result being slower growth of populations. This possibility assumes that all desirable niches (stems) are occupied by BAA as soon as they become available. For this to result in competitive displacement, a strong negative association of co-occurrence (meaning that if on a certain alfalfa stem BAA is found, PAA should be absent) would be observed in the field especially in early season infestations.

In the second possibility, competitive displacement may occur due to occupation of optimal niches by BAA on the same stems on which PAA was found. For example BAA generally feeds on the terminals which may affect the quality of food available to PAA feeding on lower parts of the stem. Another possibility could be that BAA may drive PAA to more exposed parts of the plants where natural mortality factors such as predators take a larger toll (Gutierrez et al. 1980). For either possibility to be operable, production of a high proportion of alates to permit emigration of PAA from stems where BAA predominates would be expected. As a result of the displacement or the tendency of PAA immigrants to avoid stems with BAA, the PAA densities relative to BAA

densities on stems should decrease. Thus, if densities of PAA are regressed on BAA densities on the same stems, a regression line with a negative slope should result. In addition, the magnitude of the negative slope should increase with each generation period as population densities of BAA increase over the season.

To analyze the potential for displacement resulting from the first possibility, that of PAA not selecting stems occupied by BAA, an analysis of co-occurrence was performed. In this analysis, the χ^2 values were significant ($P < 0.10$) for all the sampling dates except 1 May 1985 (site II), indicating that species were found together on stems more often than would be expected from independent occurrence (Table XVIII). Values of Cole's coefficient ranged between 0.52 to 1.00 indicating that association between two species was strong. Negative association was not observed on any date. On the sampling dates when the association of co-occurrence of these species was either complete (one species was always found associated with the other whereas the first may have occupied the niche independently) or absolute (both species always occurred in the sampling units together and neither occurred independently) the value of χ^2 and Cole's index were not estimated. The weakness in these tests was discussed by Pielou (1977).

For the second possibility, that relating to relative numbers of BAA and PAA on the same stems, several regressions of PAA on BAA were calculated to analyze relative densities within these habitat units. Population density of PAA at both sites during 1985 was very low (<8.5 aphids/stem) throughout the season and there was a huge difference in the densities of both species until 3 May. Low numbers of PAA may have been completely unrelated to the presence of BAA. However on 8 May the

TABLE XVIII

ASSOCIATION OF CO-OCCURRENCE OF BLUE ALFALFA APHID AND PEA APHID IN ALFALFA AS MEASURED BY COLE'S COEFFICIENT

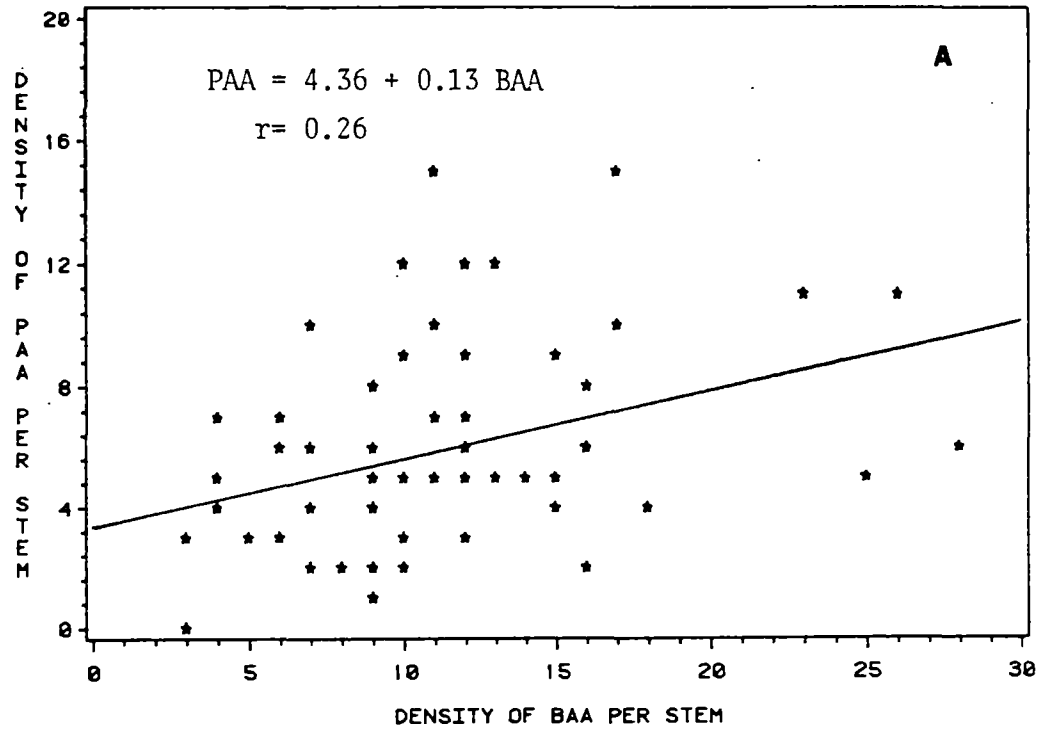
YEAR	SITE	DATE	n	χ^2	C + (S.E)
1985	1	17-APRIL	120	6.63**	0.83 ± (.10)
1985	1	23-APRIL	120	5.76**	1.00 ± (.17)
1985	1	25-APRIL	120	2.93*	1.00 ± (.58)
1985	1	01-MAY	59	NE	COMPLETE
1985	1	03-MAY	60	NE	COMPLETE
1985	1	08-MAY	60	60.00**	1.00 ± (.09)
1985	1	10-MAY	60	14.00**	0.70 ± (.13)
1985	2	15-APRIL	120	3.70*	0.62 ± (.15)
1985	2	17-APRIL	120	3.08*	1.00 ± (.57)
1985	2	24-APRIL	120	4.37**	0.64 ± (.31)
1985	2	26-APRIL	120	2.78*	1.00 ± (.60)
1985	2	01-MAY	60	2.19 NS	1.00 ± (.67)
1985	2	03-MAY	60	NE	COMPLETE
1985	2	08-MAY	60	20.95**	0.89 ± (.19)
1986	1	23-FEB	120	6.24**	0.52 ± (.26)
1986	1	04-MARCH	120	31.05**	1.00 ± (.18)
1986	1	06-MARCH	120	29.49**	1.00 ± (.18)
1986	1	21-MARCH	120	19.16**	1.00 ± (.23)
1986	1	25-MARCH	60	NE	COMPLETE[a]
1986	1	01-APRIL	60	NE	ABSOLUTE[a]
1986	1	05-APRIL	60	NE	ABSOLUTE[a]

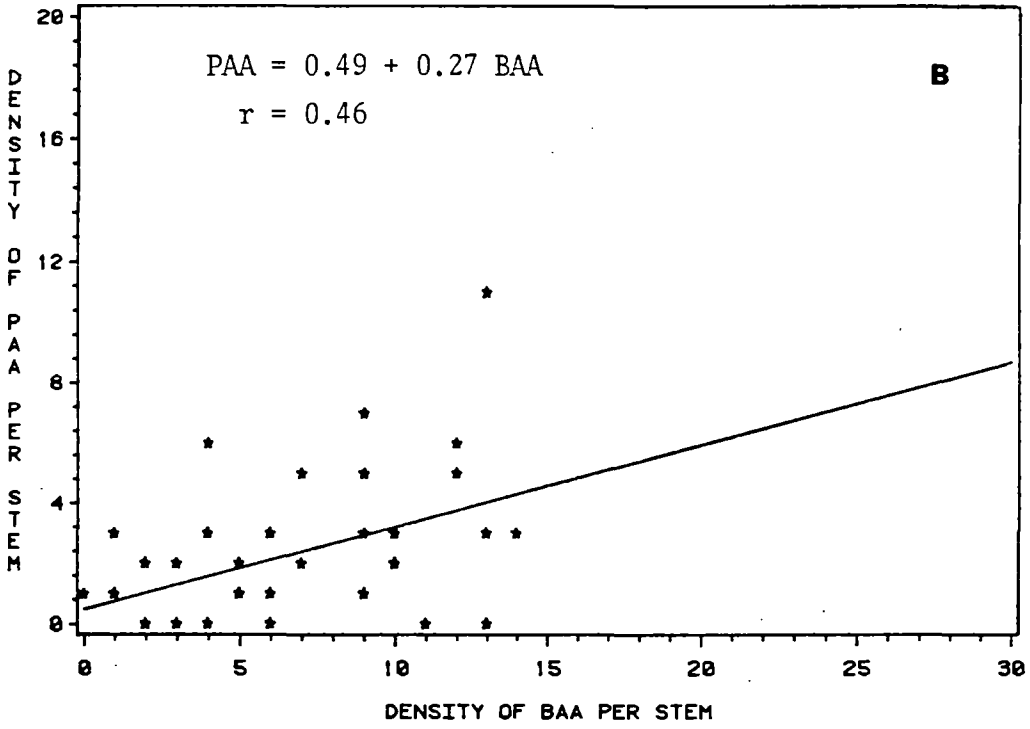
* χ^2 = (P <0.10)
** χ^2 = (P <0.05)
NE = Can not be estimated
[a] = See text for definitions

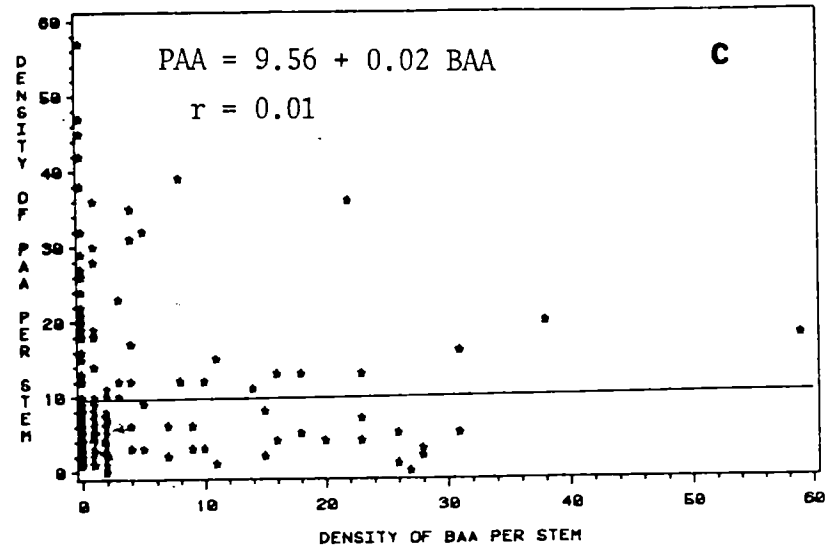
percentages of the aphid population comprised by BAA and PAA were similar and interactions of the species were expected to be more evident. Therefore, data for this date only were analyzed for both sites (Fig. 4, A-B). Regressions of PAA density on BAA density was significant at both sites ($F = 4.06$, $F = 1,57$, $P < 0.049$, and $F = 11.74$, $DF = 1,44$, $P < 0.001$, for sites I and II respectively) and slopes of the regression lines were significantly ($P < 0.05$) greater than 0 indicating that on the same stems PAA density (on the average) was not decreased by BAA.

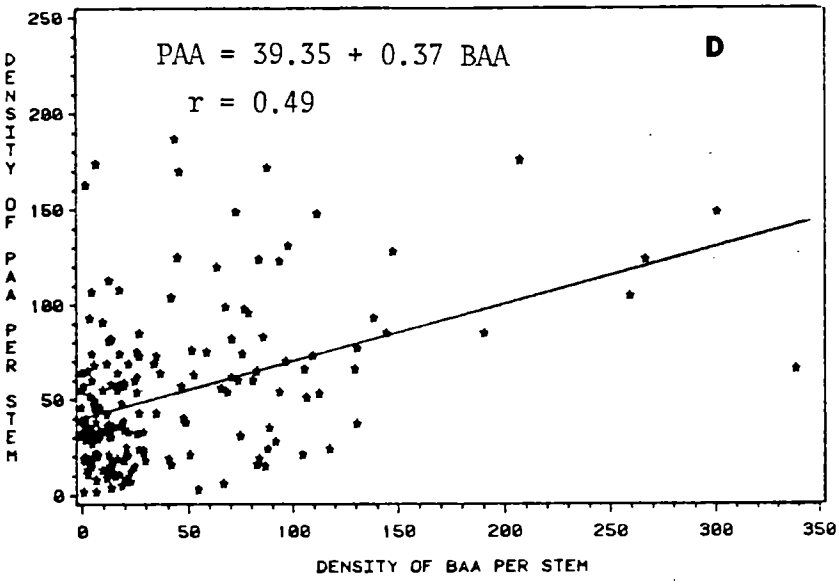
Higher population densities of PAA relative to BAA during 1986 permitted more extensive regression analyses than were possible in 1985. A separate regression was performed for each generation period of PAA based on occumulated day degrees for development (140C° days/generation) (Fig. 4, C-E). During the first generation period, which included samples from 23 February to 6 March, regression of PAA on BAA densities was not significant ($F = 0.03$, $DF = 1,199$, $P > 0.86$). However, during the second and third generation periods, regressions were significant ($F = 57.28$, $DF = 1,177$, $P < 0.0001$, and $F = 171.37$, $DF = 1,118$, $P < 0.0001$, respectively) indicating that PAA densities showed a strong tendency to increase on the stems occupied by increasing BAA populations. Confidence limits (95%) for the slopes of the regression lines for successive generation periods did not overlap indicating that the lines were not parallel. The increases in the slopes were positive over time. These results were opposite to what would be expected under the hypothesis of competitive displacement. Analysis of both possibilities for competitive displacement of PAA by BAA indicated that such displacement did not occur in our study.

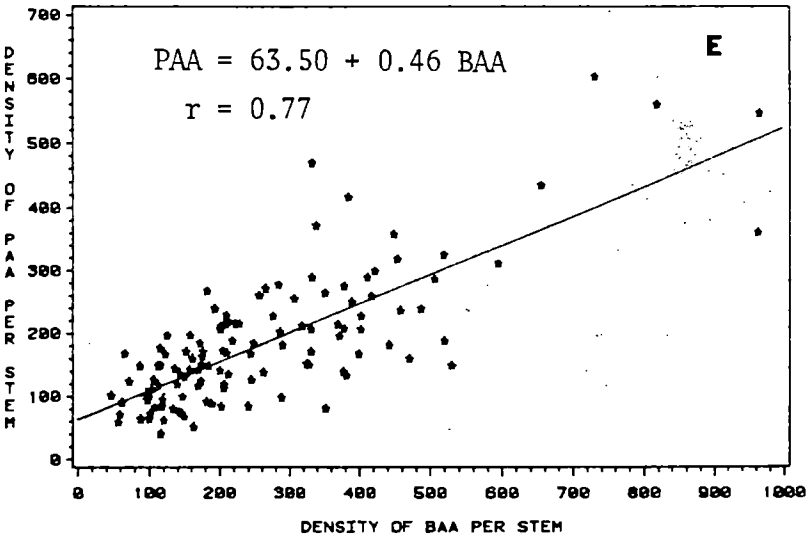
Figure 4. Regression of pea aphid densities on blue alfalfa aphid densities occurring on the same stems (A: 1985 - Site I, B: 1985 - Site II, C-E: 1986).


PAA = 4.36 + 0.13 BAA
r= 0.26
A
DENSITY OF PAA PER STEM
DENSITY OF BAA PER STEM
0
4
8
12
16
20
0
5
10
15
20
25
30


PAA = 0.49 + 0.27 BAA
r = 0.46
B
DENSITY OF PAA PER STEM
DENSITY OF BAA PER STEM
0
4
8
12
16
20
0
5
10
15
20
25
30


PAA = 9.56 + 0.02 BAA
r = 0.01
C
DENSITY OF PAA PER STEM
DENSITY OF BAA PER STEM
0
10
20
30
40
50
60


PAA = 39.35 + 0.37 BAA
r = 0.49
D
DENSITY OF PAA PER STEM
DENSITY OF BAA PER STEM
0
50
100
150
200
250
300
350


PAA = 63.50 + 0.46 BAA
r = 0.77
E
DENSITY OF PAA PER STEM
DENSITY OF BAA PER STEM
0
100
200
300
400
500
600
700
800
900
1000

Number of Samples Required

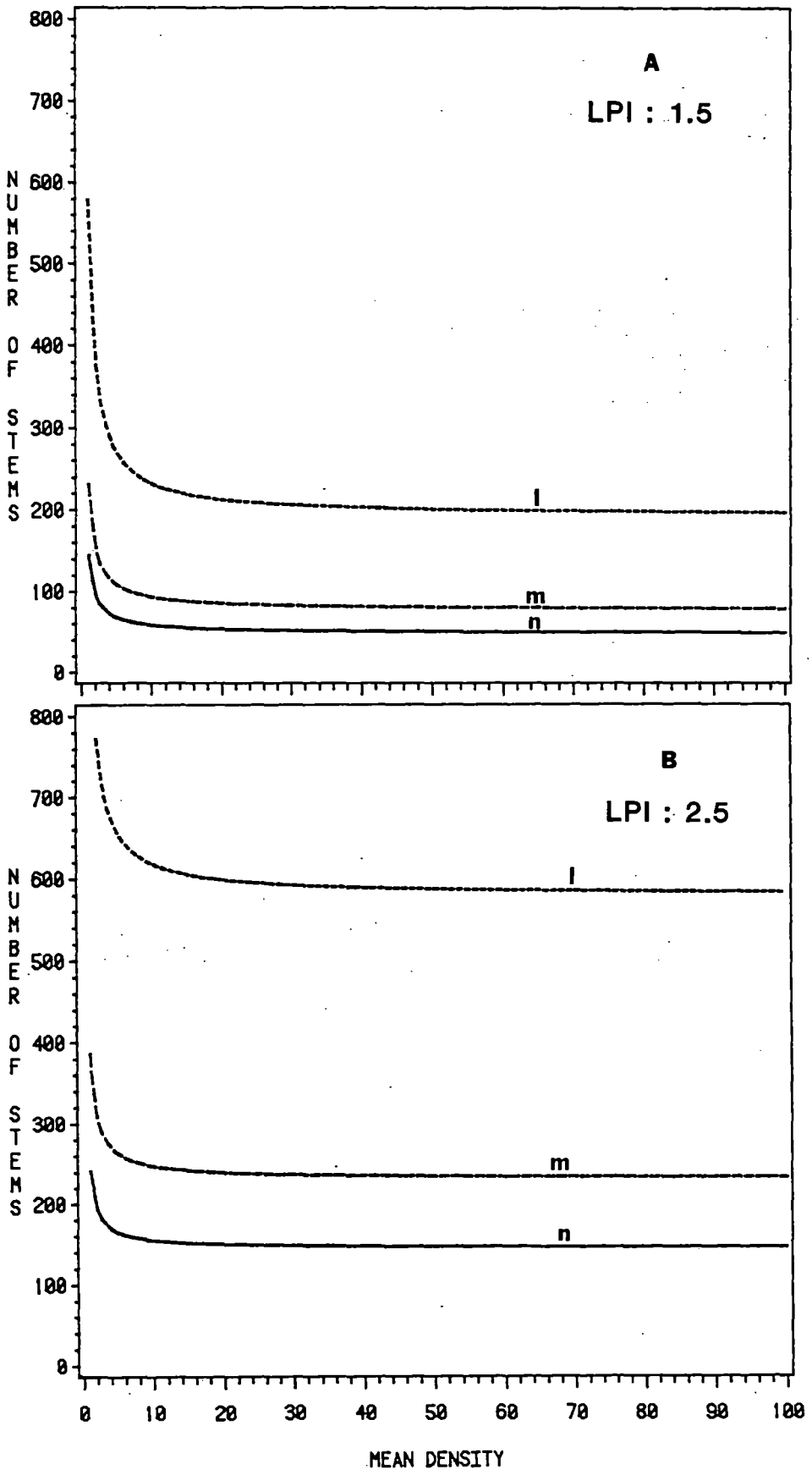
Since spatial patterns for both BAA and PAA were similar and there was not sufficient evidence supporting the hypothesis of competitive displacement of either species, a single sampling plan was considered suitable for estimating densities of both species. An LPI value of 2.5 was considered representative of early season increasing populations when densities were less than 10 aphids/stem. For later in the season when densities were greater than 10/stem a value of 1.5 was considered suitable for developing sampling plans.

The optimum sample sizes for two levels of LPI and three levels of precision, (in terms of the half length of confidence interval for some fraction of the mean, e.g. 10, 15 and 20% of the mean) are shown in Fig. 5 (A-B). Approximately 100 stems must be sampled to achieve a 15% precision level for both species in the range of densities which approximate economic threshold levels of these pests. However, more than 279 stems would be required to achieve the same level of precision if early season (<10 aphids/stem) populations are being sampled.

Discussion

Populations of both BAA and PAA conformed to aggregated spatial pattern in this study. However, the extent of aggregation decreased with increasing populations. Two patterns of aggregation were recognized for both species. Early in the season, when densities were less than 10 aphids/stem and populations were increasing, the LPI values fluctuated around 2.5. For populations where densities exceeded 10 aphids/stem, the LPI values stabilized around 1.5. Despite variations in the relative abundance of BAA and PAA in different populations, the

Figure 5. Numbers of samples required to estimate densities of blue alfalfa aphid and pea aphid in alfalfa with fixed precision of 0.1 (L), 0.15 (M), and 0.20 (N) defined as half the length of the confidence interval as a fraction of the mean with 95% confidence probability. A=Number of samples required using LPI value of 1.5. B=Number of samples required using LPI value of 2.5.


A
LPI : 1.5
B
LPI : 2.5
l
m
n
NUMBER OF STEMS
MEAN DENSITY
0
100
200
300
400
500
600
700
800
10
20
30
40
50
60
70
80
90

species exhibited similar spatial patterns. These observations were expected since, in these studies, the species had a high degree of association with each other in terms of co-occurrence. Spatial patterns for pea aphid observed in this study appeared to be less aggregated than reported by Gutierrez et al. (1980) and Baumgartner et al. (1983). However, similar patterns for this species were reported by Iwao and Kuno (1971). Similarly, BAA populations in California appear to be more aggregated than observed in our study. Differences in aggregation patterns of the same species from different locations or from different host plants have also been observed in cereal aphids (Elliot and Kieckhefer 1986). These observations suggest that sampling plans developed for other geographical locations should be used with caution.

Similar spatial patterns and high association of co-occurrence on stems between BAA and PAA provided the basis for developing a common sampling plan for both the species. Our sampling plan takes into account the changes in the spatial patterns of these aphid species which occur with varied population densities. Approximately 100 stem samples would be required to estimate densities which represent economic threshold (15-45 aphids/stem) of BAA and PAA with a precision resulting in the half width of a 95% being 15% of the mean. Our sampling technique should be useful for both intensive population studies as well as for decision making regarding chemical control. However, an initial rough estimate of population density would be required to select the appropriate plan.

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CHAPTER III

TIME-SPECIFIC LIFE TABLES FOR THE BLUE ALFALFA APHID IN OKLAHOMA

Introduction

Since its introduction into California in 1974 (Sharma et al.1975), the blue alfalfa aphid (BAA), Acyrthosiphon kondoi Shinji has been reported from all major alfalfa, Medicago sativa L., growing regions of the western United States (Kodet et al. 1982). In Oklahoma, it was first recorded in 1977 and has since been spread into 50 counties in this state (Berberet et al. 1983). High population densities of the aphid cause severe stunting, leaf curling and discoloration of leaves with resulting reductions in yield and quality of alfalfa forage (Rohita and Penman 1983a, Stern et al. 1980, Kain and Biggs 1980). There are several reports on developmental biology and population growth of BAA under laboratory conditions (Kodet and Nielson 1980, Rohita and Penman 1983b, Summers et al. 1984). Information on seasonal life history under field conditions is essential for developing sound pest management strategies for this pest.

Since the publication of time-specific life tables of cabbage aphid, Brevicoryne brassicae (L.) (Hughes 1963), this approach (with some modifications) has been widely used to study the population dynamics of several aphid species (Hamilton et al. 1982, Voegtlin and

Dahlsten 1982, Gilbert et al. 1976). Recently, Hutchison and Hogg (1986) developed time-specific life tables for the pea aphid (PAA), Acyrthosiphon pisum (Harris), in alfalfa, but such studies with the BAA have not been reported.

Although alfalfa is its principal host, the BAA can attack a wide range of leguminous hosts including members of the genera Astragalus, Lotus, Medicago, and Melilotus and may be a potential pest in food crops such as lentil, peas, and cowpeas (Ellsbury and Nielson 1980). The BAA prefers to feed on the tender and succulent parts of the alfalfa plants and clusters in colonies on the terminal growth. As the population levels increase, the aphids tend to congregate on tender shoots and beneath the older leaves (Stern et al. 1980). The aphid generally completes four instars before becoming an adult but occasionally a fifth nymphal instar may occur (Rohita and Penman 1983). The duration of the first three stadia as well as that of the fourth stadium in apterae measured in degree days is approximately equal. The average duration of the fourth stadium in alates is 1.4 times longer than the preceding three stadia (Summers et al. 1984). The lower and upper thresholds for development are 3.5 and 27.1°C, respectively. The maximum intrinsic rate of increase is realized at fairly low temperatures (10-18.3°C) and the aphid is capable of building to high densities in a short time period. (Summers et al. 1984, Kodet and Nielson 1982).

Sexual forms are not known to exist in this species (Kodet and Nielson 1980), and during the growing season only parthenogenetic females are present as apterae or alates. Alate production is maternally controlled and the same female can alternate from the production of one form early in the reproductive period to the other

form later. More alates are produced at 10 - 15°C whereas apterous forms are predominantly produced at higher temperatures (Kodet and Nielson 1980).

The objectives of this study were to develop time-specific life tables for BAA to improve understanding of population dynamics of this species in Oklahoma.

Materials and Methods

Sampling procedures

This research was conducted near Stillwater (Payne Co.) during 1985 and at Chickasha (Grady Co.) during 1986. The research area consisted of two plots (var: Buffalo) in 1985 which were designated site I and II, with dimensions of 4.6 x 46 m and 7.6 X 46 m, respectively. In 1986 one plot (var: OK-08) with dimensions of 20 X 35 m was used. To employ a stratified sampling plan, each plot was divided into ten equal subplots. An experimental insecticide designated SN-72129 (Nor-Am Agricultural Products, Inc.), which had shown a selective toxicity to alfalfa weevil, Hypera postica (Gyllenhal), without any effect on aphids was used @ 1.65 kg AI/ha at all study sites. During 1985, sampling began on 17 April at site I and 15 April at site II and terminated on 10 May at both sites. During 1986, sampling was started on 23 February and terminated on 5 April. Daily records of minimum and maximum temperatures and rainfall were obtained from weather stations maintained on the agricultural experiment stations where research was conducted and degree days were calculated by a cosine wave algorithm (Hartstack et al. 1976) using lower and upper thresholds of 3.5 and 27.1°C, respectively. The

sampling interval was based on degree-day accumulations for instar periods (one instar period = 35.1 C°days).

A twin sampling approach similar to that of Hamilton et al. (1982) was adopted. On each main sampling date, data on aphid population densities, stem heights, predator densities, parasitism and occurrence of pathogens were collected. On each corresponding twin sampling date, only the aphid densities were recorded. The time interval between successive main sampling dates was intended to be five instar periods ≈ one generation. The interval between main sampling and corresponding twin sampling dates was one instar period. Due to variable weather conditions, the interval between successive main samples was actually 3.3 instar periods (115.9 C° days) during 1985 and 4.1 instar periods (143.9 C° days) during 1986. The average time between main and twin sampling was 0.79 instar period (27.7 C° days) during 1985 and 0.99 instar period (34.7C° days) during 1986.

A stratified sampling plan was employed to obtain estimates of population densities. Single stems were used as sampling units and numbers of samples taken on each date varied according to aphid population densities. Twelve stems were randomly sampled from each subplot (120/date) if the aphid densities were less than 100/stem whereas six samples from each subplot (60/date) were taken if the density of aphids exceeded 100/stem. With these sample numbers, the standard errors were within 5 to 13% of the means for 17 of the 22 dates over the 2 years. Two methods were adopted for aphid sampling. Early in the season, when alfalfa was short (< 20 cm), stems were clipped from the crowns with scissors while a small card was held beneath to catch any aphids which were dislodged. Aphids and stems were transported to

the laboratory in glass jars containing 50% ethanol for counting and age-grading. When stem heights exceeded 20 cm, the aphids were collected by tapping the stems over a pan containing 50% ethanol. After tapping, stems were checked carefully and remaining aphids were removed with a camels hair brush. The contents of the pan were transferred to glass jars for storage until counting.

Pea aphids and spotted alfalfa aphids (SAA), Therioaphis maculata (Buckton) were removed from the samples and BAA were then classified by instars using measurements of cornicles, first flagellar segments on the antennae, and fore-tibia. Aphids in the fourth instar and adults were further classified as alate or apterae. For age-grading purposes, the stem samples within each subplot were combined after counting. If the number of aphids in a subplot exceeded 500, only 500 were age-graded.

Data for stem heights and predators were recorded at five locations in each subplot selected at random. At each location, stems were measured for plant heights and the total of 10 stems were searched for predators and aphid mummies. Predators were classified by families as Coccinellidae, Chrysopidae, Syrphidae and others. For an additional estimate of parasitism, 200 third and fourth instars were collected at random on each date of a main sample. One half of these aphids were dissected to detect larvae of parasites while the remainder were reared on excised alfalfa stems for 4-5 days at 22 $\pm$ 3°C for parasite emergence.

Framework of Analysis

Hughes (1963) method as modified by Hutchison and Hogg (1986) was

used for developing life tables for BAA. By this method, a stable instar distribution (SID) characteristic of the species is calculated from the recruitment and survival data observed under the laboratory conditions. Comparisons of the age structures observed in the field populations are then made to the empirically determined SID. If the age structures in the field populations approach the SID, Hughes (1963) potential rate of increase is replaced with the intrinsic rate of increase (r^m) (originally described as rate of growth of a stable population Birch (1948)).

The SID for BAA was calculated from age-specific fecundity and survival data (18.3°C) published by Summers et al. (1984). Calculations were completed by the method of Birch (1948). The SID consisted of 44.4% first, 25.3% second, 14.4% third, 8.2% fourth instars and 7.8% adults. The intrinsic rate of increase (r^m) was calculated as 0.565/ instar period.

To facilitate comparisons of observed rates of increase in the population to the potential rates, the densities were transformed to $\log_e (X + 1)$ to linearize the exponential growth patterns. Thus, the slope of the line becomes the observed rate of increase. The potential population density for each sampling date was projected from the observed density at the previous sampling date using an exponential model of population growth:

$$LOG_e N_{(p+1)} = LOG_e N_{(p)} + r^m \cdot t \qquad (3.1)$$

where

r^m = Intrinsic rate of increase (0.565).

t = Time interval (in instar periods).

N(p) = Population density at time p.

N(p+t)= Projected density after time interval t.

Life tables for two successive sampling dates were constructed by projecting the observed density at time p to the time p+t using r^m as the potential rate of growth. Projected total density and age structure was then compared to the observed density and age structure at the next sampling occasion (p+t). The data are presented in tabular form to give more resolution of the age structures, but the information contained in these is similar to time-specific life tables presented graphically by Hughes (1971).

The first three instars and apterous fourth (IV - APT) instar of BAA require 35.1 C° days to complete development whereas it takes 49.8 C° days for alate fourth instars (IV - ALT) to become adults (Summers et al. 1984). The degree day requirement of the first three instars (35.1 C° days) was designated as one instar period. Thus after one instar period, all aphids at a particular life stage were assumed to have molted to the next stage. The proportion of alate fourth instars molting to alate adults was calculated by Hughes (1963) modified model (Hutchison and Hogg 1986), as follows:

$$\text{Proportions molting} = \frac{e^{-C1.rm} - e^{-C2.rm}}{1 - e^{C2.rm}} \qquad (3.2)$$

where

r^m = Intrinsic rate of increase (0.565).

C2 = Developmental time for alate fourth instar relative to preceding instars (1.4).

C1 = C2 - 1

When projections were for less than one instar period, the ages of the individuals in a particular instar were assumed to be uniformly distributed. Thus, the proportion of indviduals molting to next stage was equal to the time interval. If the life table was constructed for 0.8 instar periods, 80% of the individuals of a particular instar were projected to have molted to the next stage.

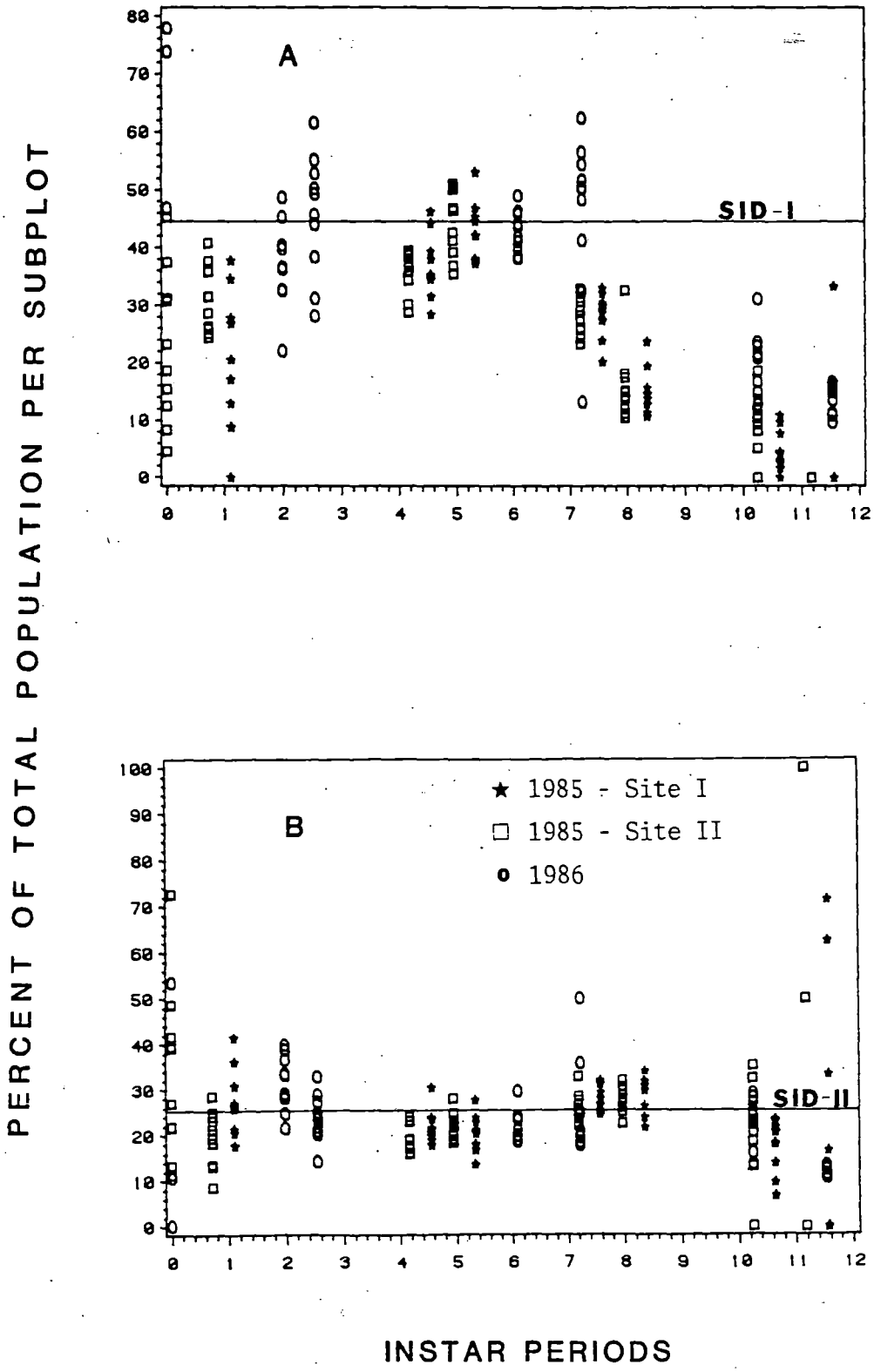
If the projections were for less than 1.3 instar periods, the proportion of third instars molting to IV - ALT or IV - APT were determined by the ratio of IV - ALT to IV - APT observed at time p. However, if the time interval exceeded 1.3 instar periods, ratio of IV-ALT to IV-APT was corrected at each time step by adding a value equal to the slope of the line fitted to the ratios observed at time p and p+t.

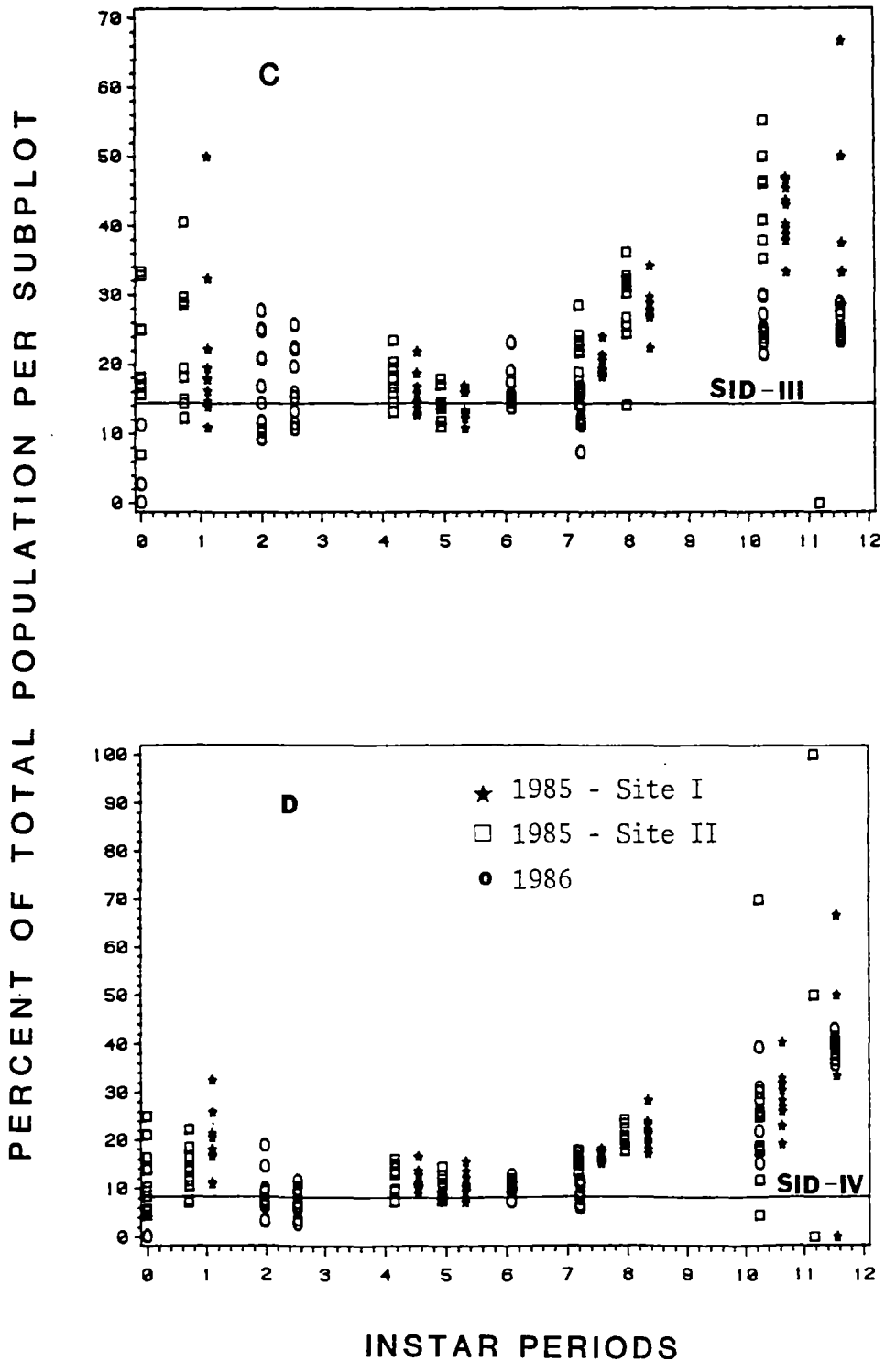
For cases where time elapsed between two sampling occasions was more than one instar period, projections were made for each instar period elapsed and values for mortality or alate ratios were incorporated for each period complete.

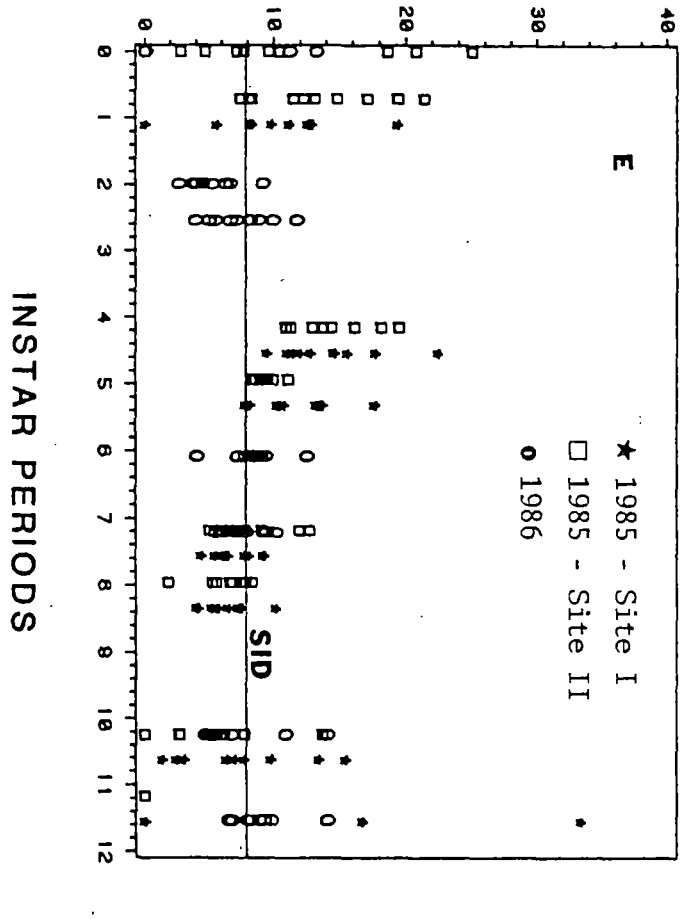
Results

The age structures of three populations of BAA studied during 1985-86, with reference to the stable age distribution, (SID) are presented in Fig. 6 (A - E). The proportions of second instar nymphs (Fig. 6,B) and adults (Fig. 6,E) in the populations were close ($\pm$ 5%) to

Figure 6. Numbers of first (A), second (B), third (C) and fourth (D) instars and adults (E) as percentage of the total population on each sampling date on a subplot basis, for three populations (1985 site I, 1985 site II and 1986). (The solid line in the figure represents stable age distribution values for each instar).


A
SID-I
B
SID-II
★ 1985 - Site I
□ 1985 - Site II
o 1986
PERCENT OF TOTAL POPULATION PER SUBPLOT
INSTAR PERIODS


C
SID-III
D
★ 1985 - Site I
□ 1985 - Site II
o 1986
SID-IV
PERCENT OF TOTAL POPULATION PER SUBPLOT
INSTAR PERIODS

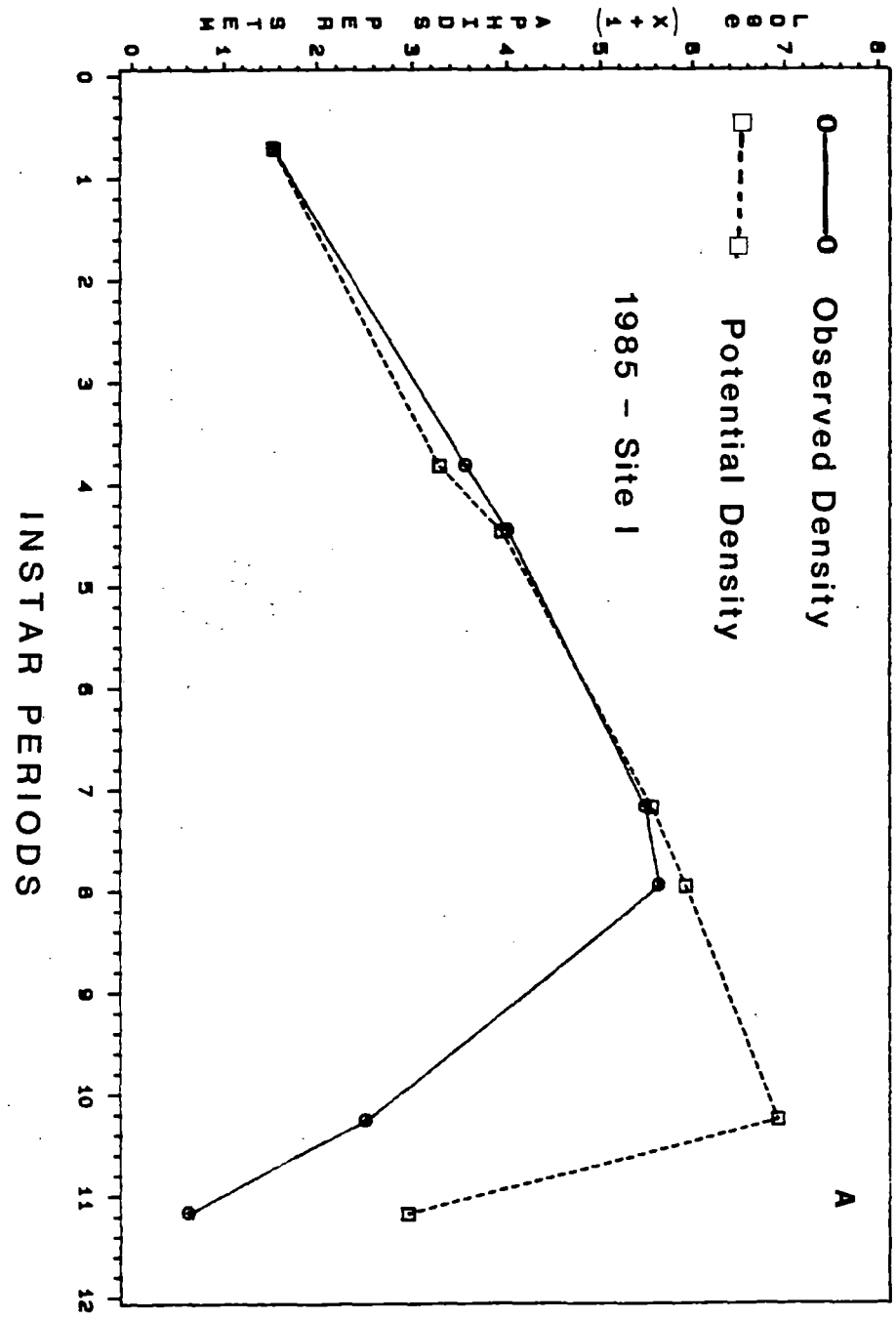

PERCENT OF TOTAL POPULATION PER SUBPLOT
INSTAR PERIODS
0
10
20
30
40
0
1
2
3
4
5
6
7
8
9
10
11
12
E
SID
★ 1985 - Site I
□ 1985 - Site II
o 1986

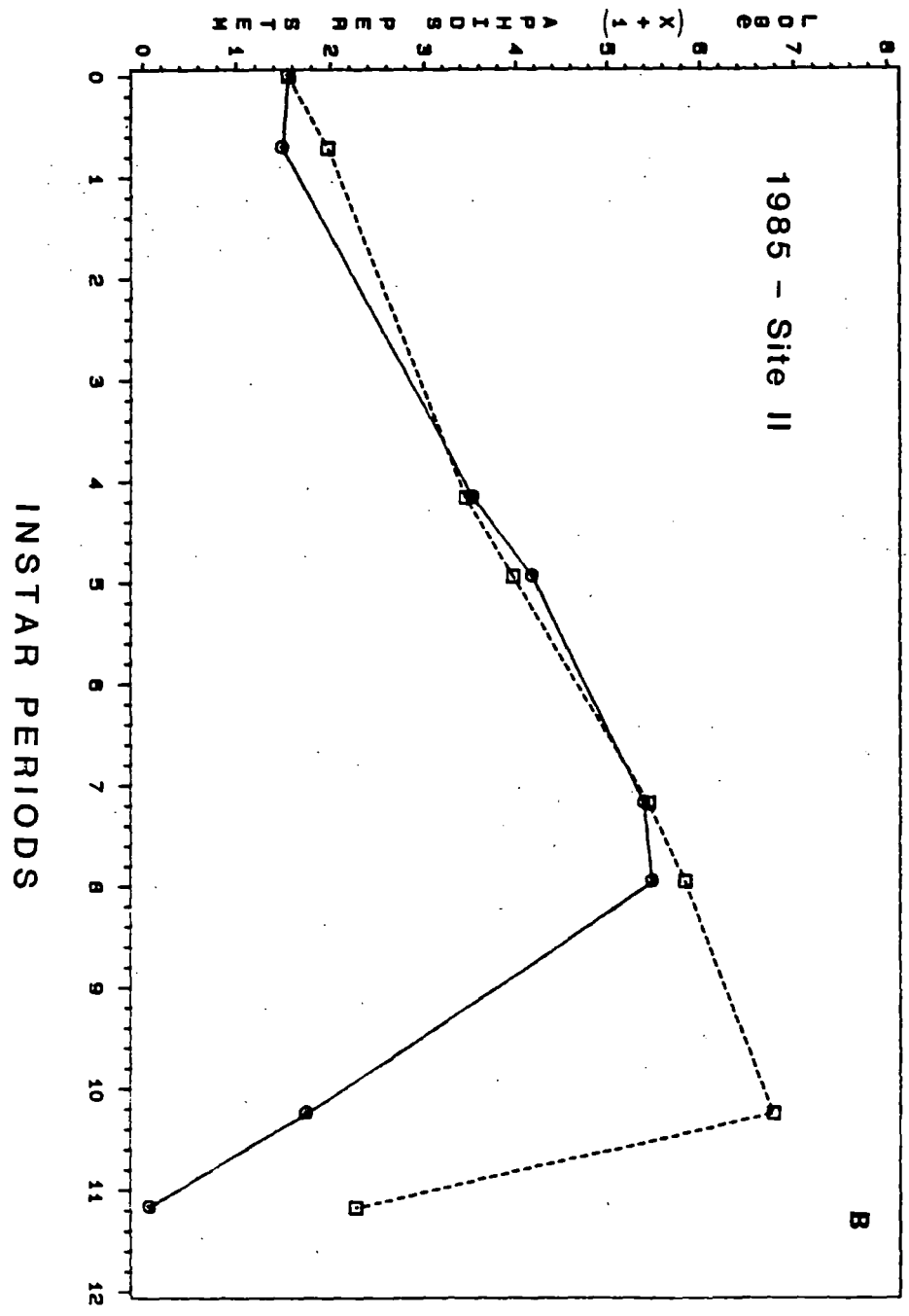
the SID throughout the season. The proportions of third and fourth instars were also distributed around SID until eighth instar period. Later in the season, however larger proportions of the populations were represented by third and fourth instars (Fig. 6 C,D). The proportions of first instar nymphs also approached the SID from instar periods 2.0 through 7.3, indicating that populations of BAA approached the SID quickly rather than converging to it over time.

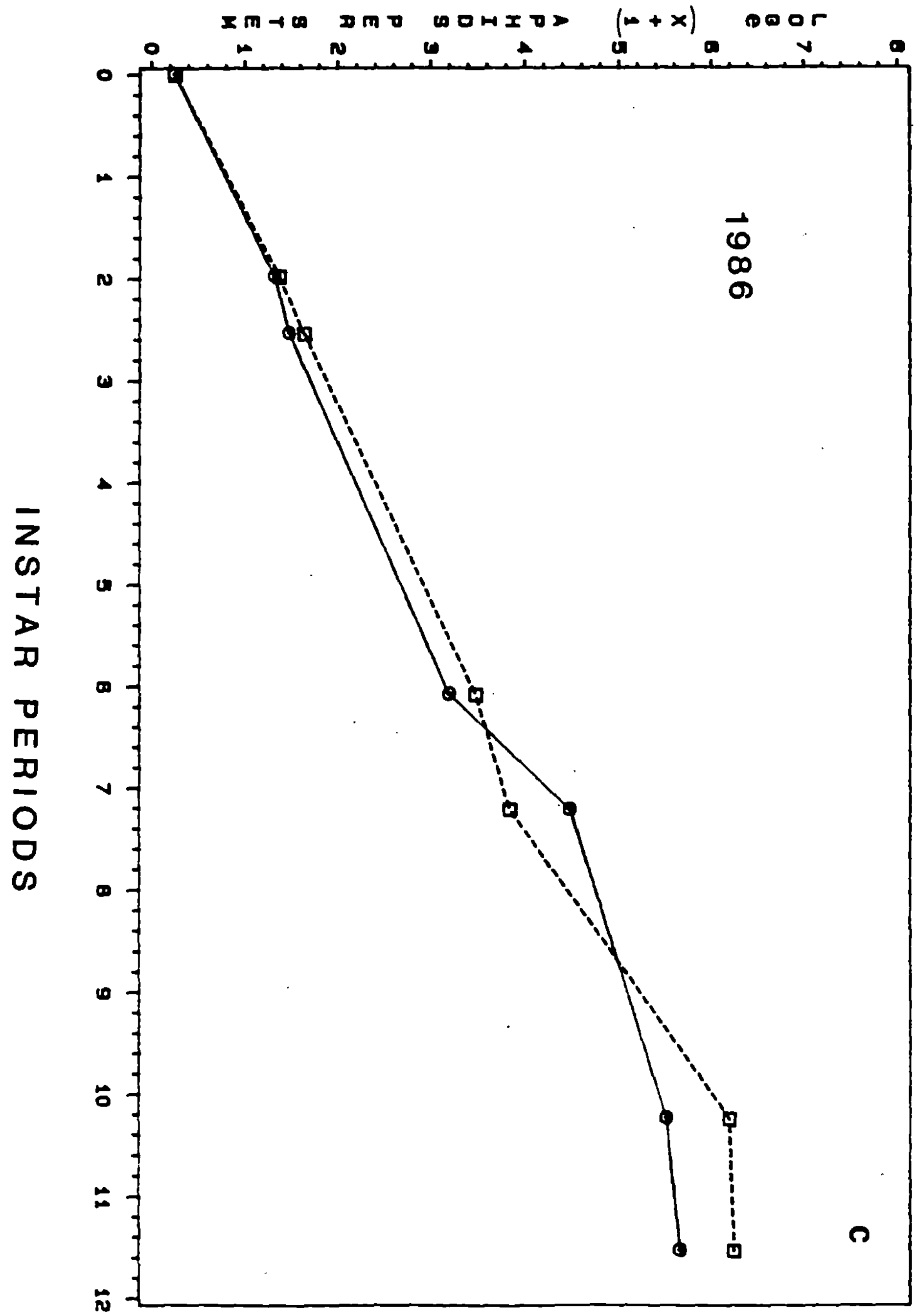
The potential and observed densities of three populations of BAA are presented in Figure 7 (A-C). During 1985 the population density increased exponentially until 1 May (7.2 instar periods) at both sites. With few deviations, the observed and projected densities during this period were similar which suggested that populations were increasing without appreciable mortality and provided a basis for using r^m as the potential rate of increase. After 1 May the observed density declined compared to the potential density at both sites. The same trend intensified later in the season and populations declined rapidly after eight instar periods. At this time the mean densities had exceeded 277 aphids/stem at site-I and 239 aphids/stem at site-II.

Although more variable than in 1985, the trends of population growth in 1986 followed a similar pattern. The density increased exponentially until instar period 7.2, after which a decline was observed in the population growth rates. Lower rates of growth became more evident as the population density increased. After instar period 11.5, when the densities had reached 238 aphids/stem, the population declined precipitously. By this time, the alfalfa stand was heavily damaged and no further sampling was possible.

Figure 7. Potential densities (based on rm = 0.565 and the expotential growth model) and observed densities of three populations of blue alfalfa aphid: 1985 site I (A); 1985 Site II (B); and 1986 (C).


A
Observed Density
Potential Density
1985 - Site I
Log e (X + 1.5)
APHIDS PER STEM
INSTAR PERIODS


1985 - Site II
B
Log e (X + 1.5)
APHIDOIDEA
STEM
0
1
2
3
4
5
6
7
8
9
10
11
12
INSTAR PERIODS


1986
C
Loge (X + 1) APHIDS PER STEM
0
1
2
3
4
5
6
7
8
0
1
2
3
4
5
6
7
8
9
10
11
12
INSTAR PERIODS

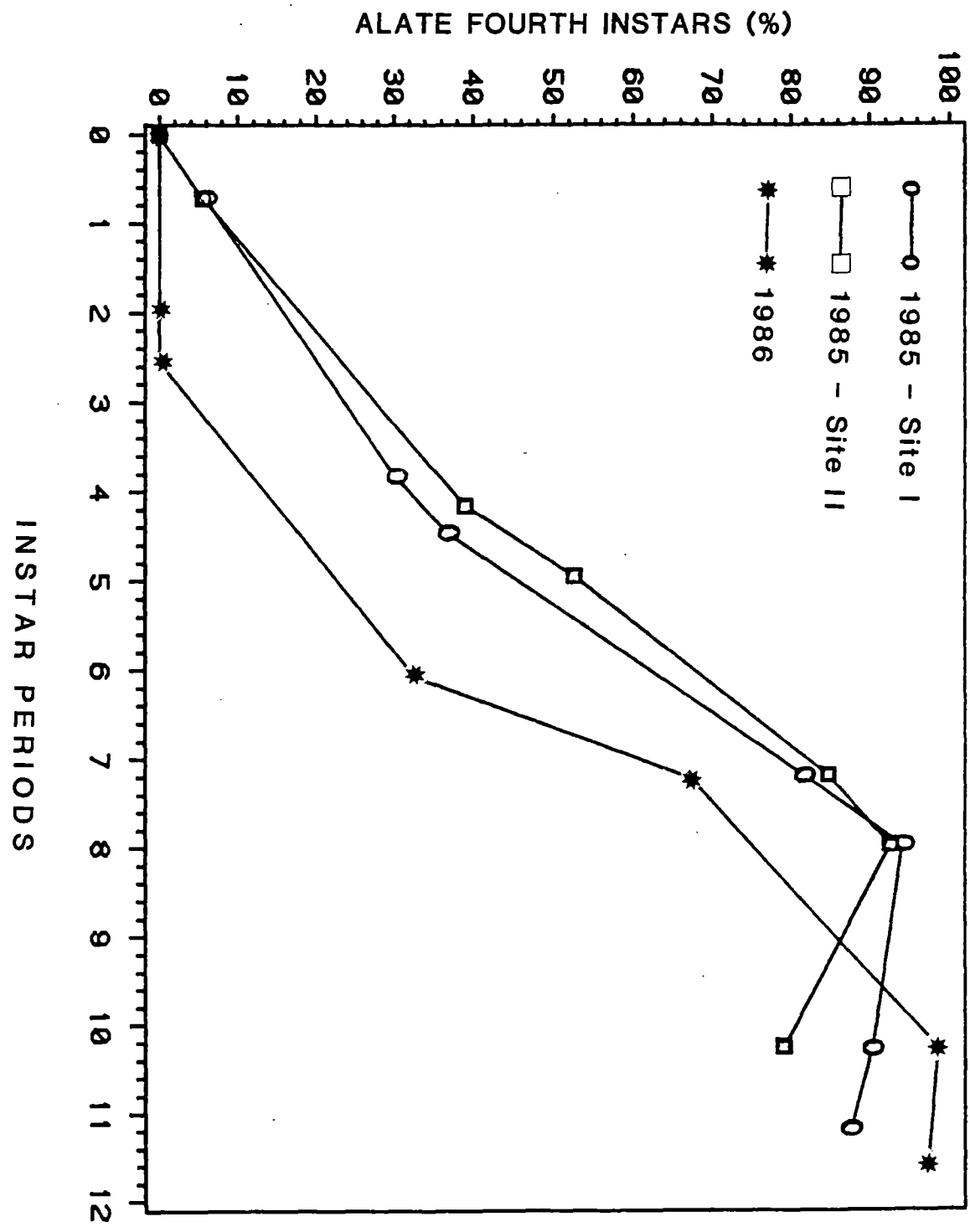
Dynamics of Mortality Factors

Emigration:

The percentage of alates among fourth instars of each population was used as a predictor of subsequent emigration by the adults. Although some alate adults may be found in a resident aphid population, Hughes (1963) suggested that these might be newly molted prereproductive individuals which would eventually leave the population. Thus all the alate adults predicted for the next sample date were considered to be lost from the population (mortality) as was the procedure of Hughes (1963). Decreased fecundity (reduction in first instars) due to emigration was assumed to be equal to the percentage of alate adults predicted to be produced during the time interval between two sampling occasions.

The dynamics of alate fourth instar nymphs in 1985 and 1986 are presented in Fig. 8. There were no alate fourth instars in the first sample in 1985 (site II) or on the first three sampling dates in 1986. Therefore, alate adults observed during sampling on these dates were considered immigrants and no mortality due to emigration was incorporated in the model. As the season progressed and densities increased, the percentage of fourth instar alates in all populations increased. After seven instar periods, the percentage of alates among fourth instars exceeded 90% for both sites in 1985. In 1986 the percentage of alates after 10 instar periods exceeded 98%. The regular increase in alates in all populations (Fig. 8) indicates that they were produced continuously in the population rather than there being alternating production of alates and apterae in successive generations. Due to difficulties of interpreting cause and effect relationships in

Figure 8. Percentage of alates among fourth instar nymphs in three populations of blue alfalfa aphid.


ALATE FOURTH INSTARS (%)
0
10
20
30
40
50
60
70
80
90
100
INSTAR PERIODS
0
1
2
3
4
5
6
7
8
9
10
11
12
1985 - Site I
1985 - Site II
1986

the field data, no direct association was attempted between the alate percentages and population densities. However, it was noted that overall increases in alates occurred in a manner similar to the population densities.

Predation:

Unlike emigration, the mortality due to predators could not be directly estimated. This mortality was therefore inferred from the magnitude of the residual mortality after emigration, predator density and age strucure of the population. The predator population densities remained higher throughout the season at both sites during 1985 than in 1986 (Table XIX). During 1985, the most common predators were adult Coccinellidae in April. Larvae of Coccinellidae were predominant in May. The predominant species of Coccinellidae was Hippodamia convergens (Guerin-Meneville). During 1986 the predators did not enter the field until 1 April after aphid densities had reached 246/stem. H. convergens was the most common species observed during 1986 also. Larvae of Syrphidae were present in low numbers on 5 April.

Despite high population densities of the BAA in all the three populations, mortality due to parasitism or infection by disease organisms was not observed either in the samples which were dissected or those reared in the laboratory.

Life Tables:

Based on the trends in population growth patterns (Fig. 7 (A-C)), three phases were arbitrarily described. The first phase extended through the first seven instar periods when virtually no mortality

TABLE XIX

POPULATION DENSITIES OF PREDATORS AND THEIR COMPOSITIONS AS OBSERVED IN THREE APHID POPULATIONS DURING 1985-1986

YEAR	SITE	DATE	INSTAR PERIOD	PREDATORS/ STEM (TOTAL)	COCCINELLIDAE	
					LARVAE	ADULTS
1985	I	15, APRIL	0.00	0.06	0.06	0.00
1985	I	23, APRIL	3.82	0.14	0.14	0.00
1985	I	01, MAY	7.18	0.21	0.11	0.08
1985	I	08, MAY	10.24	0.13	0.05	0.07
1985	II	15, APRIL	0.00	0.08	0.07	0.01
1985	II	24, APRIL	4.16	0.17	0.16	0.00
1985	II	01, MAY	7.18	0.18	0.04	0.12
1985	II	08, MAY	10.24	0.18	0.05	0.12
1986	-	23, FEB	0.00	0.00	0.00	0.00
1986	-	03, MARCH	1.98	0.00	0.00	0.00
1986	-	06, MARCH	3.82	0.00	0.00	0.00
1986	-	21, MARCH	6.08	0.00	0.00	0.00
1986	-	25, MARCH	7.21	0.00	0.00	0.00
1986	-	01, APRIL	10.24	0.04	0.03	0.00
1986	-	05, APRIL	11.53	0.09	0.05	0.01

occurred and observed densities were similar to potential densities. These condphase extended from periods seven to nine when the observed population growth rates started to decline from the potential rates of increase. The third phase marked the greatest differences between the observed and potential densities after instar period nine. Life tables were constructed for each population in each phase to explain the possible factors responsible for mortality. In life tables where observed density was equal or greater than the projected density, a column for mortality was not included.

Life Tables for 1985 (Site I)

The life table for 23-25 April (3.8 - 4.5 instar periods) was constructed for the first phase when the population growth rate was similar to the potential rate of increase (Fig. 7, A). There were no significant differences in the age structures of observed and predicted populations *(χ^2 = 1.13, DF = 5; P > 0.05) on 25 April (Table XX) indicating that there was no age-specific mortality. No parasitized or diseased aphids were observed either in rearing or dissections. The predator density was 0.14/stem but there appeared to be little effect on aphid populations. Although alate adults numbered 46% less than predicted by the model numbers are so small that this difference is not meaningful. Effects of emigration were not evident on fecundity (number of first instar nymphs) which suggested that reproductive rate of the remaining adults may have increased or presence of alates was over estimated.

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* $\chi^2 = \frac{(\text{Predicted density without mortality} - \text{Observed density})^2}{\text{Predicted density without mortality}}$

TABLE XX

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 23-25 APRIL (0.65 INSTAR PERIODS) AT SITE-I DURING 1985.

INSTAR/ MORPH	APHIDS/STEM			
	INITIAL ON 23-APRIL	PREDICTED WITHOUT MORTALITY	OBSERVED ON 25-APRIL	χ^2
I	12.8	19.7	23.7	0.6
II	7.7	11.0	11.0	0.0
III	5.3	6.8	7.6	0.1
IV - APT	2.9	3.4	3.8	0.1
IV - ALT	1.3	1.8	2.2	0.1
ADULT - APT	4.1	6.0	5.8	0.0
ADULT - ALT	0.4	0.9	0.5	0.2
MEAN APHIDS/ STEM (± SE)	34.5 (± 2.4)	49.6	54.1 (± 3.0)	1.1*

* CHI-SQUARED (DF 5, P > 0.05).

During the period of 1-3 May (7.2 - 8.0 instar periods) the growth rate in the population started declining and the aphids had virtually disappeared by 3-8 May. A life table was constructed for 1-3 May to analyze the factors which might be responsible for initiating the decline in the growth rate (Table XXI). Comparing the predicted age structure to the observed, without considering any mortality revealed significant differences (^{2} = 95.82, DF = 5, P <0.05). The major difference between observed and predicted populations during this period was in the first instars which suggested that age-specific mortality occurred at adult stage. Approximately 50.7 percent of the adults were predicted to be alates on 3 May. When decreased fecundity (reduction in the numbers of first instars due to emigration of potentially reproducing adults) and losses of alate adults (decrease in the numbers of alate adults due to emigration) were incorporated into the model about 70% of the difference* between predicted (without mortality) and observed densities was explained. No parasitized or diseased aphids were observed during this period. The remaining mortality may have been due to lady beetles whose numbers exceeded 0.19/stem.

During the period from 3-8 May (8.0 - 10.2 instar periods) the population density of BAA decreased from 277.3 to 11.4 aphids/stem (Table XXII). The observed density on 8 May was only about 1% of the predicted density (with r^m=0.565) and the age structure indicated that mortality occurred indiscriminately on all stages. Approximately 94% of the fourth instars were alates on 3 May (Fig. 8), which suggested that

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*Percent difference explained =

$$1 - \left(\frac{\text{Predicted density with mortality - Observed density}}{\text{Predicted density without mortality - observed density}} \right) X\ 100$$

TABLE XXI

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 1-3 MAY (0.78 INSTAR PERIODS) AT SITE-I DURING 1985.

INSTAR/ MORPH	APHIDS/STEM				
	INITIAL ON 1 - MAY	PREDICTED WITHOUT MORTALITY	PREDICTED WITH MORTALITY	OBSERVED ON 3 - MAY	χ^2
I	67.3	147.0	73.8	41.7	75.4
II	66.5	67.2	67.2	80.3	2.6
III	48.3	62.5	62.5	77.9	3.8
IV - APT	7.4	8.5	8.5	3.6	2.8
IV - ALT	32.7	47.6	47.6	56.3	1.6
ADULT - APT	13.3	19.1	19.1	10.7	3.7
ADULT - ALT	3.1	18.9	-	6.7	7.9
MEAN APHIDS/ STEM (± SE)	238.6 (± 18.2)	370.8	278.7	277.2 (± 18.4)	97.8*

* CHI-SQUARED (DF = 5; P < .05)

TABLE XXII

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 3-8 MAY (2.28 INSTAR PERIODS) AT SITE-I DURING 1985.

INSTAR/ MORPH	APHIDS/STEM					
	INITIAL ON 3 - MAY	PREDICTED WITHOUT MORTALITY		PREDICTED WITH MORTALITY	OBSERVED ON 8 - MAY	χ^2
		r^m=0.565	r^m=0.0			
I	41.7	413.7	0.0	41.4	0.6	412.5
II	80.3	255.2	0.0	53.7	2.1	251.0
III	77.9	88.9	30.0	18.4	4.7	79.7
IV - APT	3.6	3.7	4.2	3.6	0.3	3.1
IV - ALT	56.3	103.7	103.1	93.4	3.0	97.8
ADULT - APT	10.7	20.3	20.1	20.2	0.2	19.7
ADULT - ALT	6.7	119.7	119.6	-	0.5	118.7
MEAN APHIDS/ STEM (± SE)	277.2 (± 18.2)	1005.0	277.2	230.6	11.4 (± 18.4)	982.7*

* CHI-SQUARED (DF = 5, P < .05)

high mortality would be expected due to emigration of alate adults which would develop from alate fourth instars during 3-8 May. The decreased fecundity and losses due to emigration, when incorporated into the model, explained 78% of the differences between predicted and observed density. However, the observed density on 8 May was only 5% of the density predicted with mortality in the population due to emigration which suggested that observed decrease in the population could not be attributed to emigration alone.

At high population densities, a decrease in the reproductive potential has been reported to be a major factor in regulating population growth in many aphid species (Hughes 1963, Perrin 1976, Way and Banks 1967). To determine whether the demise in the population could have occurred due to the decrease in the reproductive rate along with emigration of alates, the density for 8 May was also projected using zero growth rate (r^m=0) (Table XXII). Comparison of predicted and observed age structures with r^m = 0 indicated that at least 157.5 aphids/stem would be expected (predicted density (with r^m=0) minus the number of alate adults (column 4, Table XXII)) if all the alates produced during this period emigrated and no reproduction occurred in the apterous adults.

Lady beetles were abundant on 1 May and 58% of them were larvae. Per capita consumption rates of lady beetles have been reported to range between 13 and 76 aphids/day depending on temperature, species and life stage of the predator and the prey used (Hamalainen et al. 1975, Chambers et al. 1983). Rautapaa (1976) reported that larvae of the lady beetles consumed more aphids than those of adults of the same species.

TABLE XXIII

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 24-26 APRIL (0.78 INSTAR PERIODS) AT SITE-II DURING 1985.

INSTAR/ MORPH	APHIDS/STEM			
	INITIAL ON 24-APRIL	PREDICTED WITHOUT MORTALITY	OBSERVED ON 26-APRIL	χ^2
I	12.1	20.8	28.1	2.5
II	6.2	10.7	14.1	1.1
III	5.8	6.1	9.0	1.4
IV - APT	2.5	3.3	3.2	0.0
IV - ALT	1.6	2.6	3.5	0.3
ADULT - APT	4.1	6.1	5.4	0.1
ADULT - ALT	0.6	1.4	0.6	0.5
MEAN APHIDS/ STEM (± SE)	32.9 (± 2.1)	51.0	63.9 (± 3.5)	5.9*

* CHI-SQUARED (DF = 5, $P < 0.05$).

Therefore, the virtual elimination of the population seemed to be a combined action of mortality due to emigration, and lady beetles.

Life Tables for 1985 (site II)

The life table for 24-26 April (4.2 - 4.9 instar periods) is presented in table XXIII. The overall observed age structure of 26 April was not significantly different ($\chi^2 = 5.8$, DF = 5, $P > 0.05$) from the age structure predicted by the model indicating that there was no age-specific mortality in the population. This was expected since no parasitized or diseased aphids were found in the population. The predator density (0.16 predators/stem) was higher than in site-I but to this point did not seem to exert a significant effect on BAA populations. Observed population density on 26 April was 63.9 aphids/stem as compared to 51.0 aphids/stem predicted by the model. Most of the difference between observed and predicted densities was contributed by an increase in the first and second instar nymphs. The lower numbers of adults in the populations and higher numbers of first instar nymphs indicated that reproductive potential of the adults was underestimated by the model.

Life table statistics for 1-3 May (7.2 - 8.0 instar periods) are presented in Table XXIV. The observed density was 29% less than the predicted density without mortality. Significant differences ($\chi^2 = 87.89$, DF = 5; $P < 0.05$) in the predicted (without mortality) and observed stage structure were also found. Major proportions of the differences in predicted and observed densities were contributed by a decrease in first instar nymphs and alate adults indicating that age-specific mortality in first instars resulted from decreased fecundity

TABLE XXIV

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 1-3 MAY (0.78 INSTAR PERIODS) AT SITE-II DURING 1985.

INSTAR/ MORPH	APHIDS/STEM				
	INITIAL ON 1 - MAY	PREDICTED WITHOUT MORTALITY	PREDICTED WITH MORTALITY	OBSERVED ON 3 - MAY	χ^2
I	62.3	134.7	65.6	38.1	69.3
II	57.7	61.3	61.3	67.0	0.5
III	45.8	55.1	55.1	68.6	3.3
IV - APT	5.3	6.6	6.6	3.8	1.2
IV - ALT	29.8	45.7	45.7	46.7	0.0
ADULT - APT	13.4	17.6	17.6	11.6	2.1
ADULT - ALT	4.1	18.5	-	3.9	11.5
MEAN APHIDS/ STEM (± S.E)	218.4 (± 21.3)	339.5	251.9	239.7 (± 21.4)	87.95*

* CHI-SQUARED (DF = 5, P < .05)

due to emigrating alate adults. In the model, when mortality due to emigration was adjusted, 88% of the difference between total observed and predicted densities (without mortality) was explained. The remaining mortality in the first instars may be attributed to decrease in numbers of apterous adults, due perhaps to death of older individuals as well as predators which exceeded 0.16/stem (Table XIX).

The life table for the rapidly declining population of BAA during 3-8 May, is presented in Table XXV. Since site I and II were within 200 meters of each other, this life table was a virtual repeat of the events recorded at site I. The observed density on 8 May was only 0.5 percent of the total predicted density without mortality for this date. On 3 May, 92% of fourth instars were alates (Fig. 8) and decreased fecundity due to emigration was expected to be the major source of mortality during this period. Since the life table was for 2.3 instar periods, the decreased fecundity affected the predicted numbers in the first three instars. Although decreased fecundity due to emigration and departure of alate adults explained 69% of the difference in the predicted and observed densities, the observed density on 8 May was only 2% of the density predicted with mortality. As was observed at site I, the decrease in the reproductive rate could not account for the tremendous decrease in aphid densities at site II.

The results from life tables constructed for 1985 site I and II, could thus be summarized as follows. The aphid populations increased without appreciable mortality until the densities had reached more than 200/stem. Although lady beetle adults were present in the field, they were not able to contain rapidly increasing populations of BAA. However, after the decline in the population growth rate had been

TABLE XXV

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 3-8 MAY (2.28 INSTAR PERIODS) AT SITE-II DURING 1985.

INSTAR/ MORPH	APHIDS/STEM					
	INITIAL ON 3 - MAY	PREDICTED WITHOUT MORTALITY		PREDICTED WITH MORTALITY	OBSERVED ON 8 - MAY	χ^2
		r^m=0.565	r^m=0.0			
I	38.1	357.7	0.0	53.0	00.4	356.9
II	67.0	220.7	0.0	58.1	1.0	218.7
III	68.6	78.3	27.4	43.7	2.1	74.2
IV - APT	3.8	8.6	8.6	8.6	0.2	8.2
IV - ALT	46.7	82.1	82.1	82.1	0.8	80.5
ADULT - APT	11.6	23.0	23.0	23.0	0.1	22.8
ADULT - ALT	3.9	98.6	98.6	-	0.1	98.4
MEAN APHIDS/ STEM (± SE)	239.7 (± 21.4)	869.0	239.7	268.5	4.7 (± 0.6)	859.7*

* CHI-SQUARED (DF = 5, P < .05)

initiated by mortality resulting from emigration of alate adults, predation by lady beetles became one of the major factors responsible for the demise of aphid populations.

Life Tables for 1986

Two life tables were constructed for the 1986 population during the phase in which the population was growing exponentially and no mortality factors were recorded. The life table for 3-6 march (2.0 - 2.5 instar periods) is presented in Table XXVI and that for 6-21 March (2.5 - 6.1 instar periods) is given in Table XXVII. The observed age structures and densities in both the life tables were similar to the expected age structures, and total densities which indicated that there was little mortality. These results agreed with the observed lack of mortality factors. No parasitized or diseased aphids were found and no predators were observed. The alate adults found during this period had not developed from the resident population as no IV-ALT were observed in the previous sampling, therefore no emigration mortality was expected.

During the period from 1-5 April (10.2 -11.5 instar periods) the growth rate of the population deviated from the projected rate due to mortality factors (Table XXVIII). The proportion of alates among adults was 98% and the expected decrease in fecundity due to emigration of alates was estimated to be 90%. The predator population density also peaked during this period (0.09/stem). The overall observed density on 5 April was 56% of the predicted density indicating that extensive mortality had occurred. The observed age structure of the population on 5 April as compared to the expected without mortality showed a decrease in first and second instars and alate adults which supported the

TABLE XXVI

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 3-6 MARCH (0.56 INSTAR PERIODS) AT CHICKASHA DURING 1986.

INSTAR/ MORPH	APHIDS/STEM			
	INITIAL ON 3-MARCH	PREDICTED WITHOUT MORTALITY	OBSERVED ON 6-MARCH	χ^2
I	1.0	1.4	1.2	0.0
II	0.6	0.8	0.9	0.0
III	0.7	0.7	0.6	0.0
IV - APT	0.2	0.5	0.4	0.0
IV - ALT	-	-	-	-
ADULT - APT	0.2	0.3	0.3	0.0
ADULT - ALT	0.1	0.1	0.1	0.0
MEAN APHIDS/ STEM (± SE)	2.8 (± 0.61)	3.8	3.4 (± 0.76)	0.0

* CHI-SQUARED (DF = 5; P > .05).

TABLE XXVII

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 6-21 MARCH, (3.20 INSTAR PERIODS) AT CHICKASHA DURING 1986.

INSTAR/ MORPH	APHIDS/STEM			
	INITIAL ON 6-MARCH	PREDICTED WITHOUT MORTALITY	OBSERVED ON 21-MARCH	χ^2
I	1.2	10.2	10.0	0.0
II	0.9	6.4	5.0	0.3
III	0.6	3.6	3.5	0.0
IV - APT	0.4	1.4	1.6	0.0
IV - ALT	0.0	0.6	0.8	0.1
ADULT - APT	0.3	2.6	2.3	0.0
ADULT - ALT	0.1	0.2	0.3	0.1
MEAN APHIDS/ STEM ($\pm$ SE)	3.5 ($\pm$ 0.8)	25.0	23.5 ($\pm$ 2.6)	0.5*

* CHI-SQUARED (DF = 5; P > .05).

hypothesis that most mortality resulted from emigration of reproducing adults. When mortality due to emigration was incorporated in the model, the observed density exceeded the potential density which suggested that emigration mortality was overestimated for this life table. This was expected because all the alate adults in the population were assumed to have emigrated whereas in actuality about 20 of the predicted 52 alate adults/stem were found in the field on 5 April (Table XVIII).

Discussion

For the past 20 years the most popular method of analyzing population dynamics of aphid species with overlapping generations has been that originated by Hughes (1963). This method assumes that a stable instar distribution (SID) is achieved in the population so that the ratio of frequencies of first and second to second and third instars is indicative of potential rate of increase. After having computed the potential rate of increase, the difference between this and the observed rate of increase is a further an estimate of mortality. This method is applied only when the observed instar distributions do not significantly differ from the calculated SID.

Carter et al. (1978) suggested that the χ^2 test for determining significant differences from the expected SID in the field as adopted by Hughes (1963) is not a stringent enough test and estimates of potential rates of increase and reproductive rates of the adults may not be valid. Based on these observations, Hutchison and Hogg (1984) suggested that independent estimates of SID based on birth and death schedules observed from simulated field conditions in the laboratory may serve as a better criteria for testing the SID in the field. They further found the

TABLE XXVIII

TIME-SPECIFIC LIFE TABLE OF BLUE ALFALFA APHID FOR 1-5 APRIL (1.29 INSTAR PERIODS) AT CHICKASHA DURING 1986.

INSTAR/ MORPH	APHIDS/STEM				
	INITIAL ON 1 - APRIL	PREDICTED WITHOUT MORTALITY	PREDICTED WITH MORTALITY	OBSERVED ON 5 - APRIL	χ^2
I	58.9	209.5	15.7	39.8	137.5
II	61.9	95.7	48.4	37.8	35.1
III	63.5	61.1	61.0	74.3	2.9
IV - APT	0.8	1.0	1.0	2.9	3.6
IV - ALT	49.0	84.1	84.1	105.7	5.5
ADULT - APT	4.4	5.5	5.5	4.6	0.1
ADULT - ALT	7.5	52.4	-	19.9	20.2
MEAN APHIDS/ STEM (± SE)	246.0 (± 25.6)	509.3	215.7	285.0 (± 18.8)	204.8*

* CHI-SQUARED (DF = 5, P < .05).

empirically determined SID useful in developing life tables for the PAA by equating the intrinsic rate of natural increase (r^m) as defined by Birch (1948), to Hughes potential rate of increase (Hutchison and Hogg 1986). Cary (1983) also based an analysis of population increase in the mite complex on cotton on the SID determined from the recruitment and survival observed in the laboratory. He suggested that the empirically determined SID is more useful becauseit is singular and could only be achieved by the constancy in recruitment and mortality rates.

My present study has shown that age distributions in BAA populations also converged ($\pm$ 5%) toward the SID for most of the sampling periods and, in the absence of mortality factors, the rate of population increase was similar to the intrinsic rate of increase as determined from the laboratory data. These results suggested that use of the intrinsic rate of increase in analyses of aphid population data as suggested by Hutchison and Hogg (1986) was valid.

Despite temporal and spatial variations, the BAA densities showed a similar pattern in all populations studied, indicating that factors affecting these populations were similar. The aphid densities increased at rates which were comparable to the intrinsic rate of increase, suggesting that this aphid is capable of realizing full reproductive potential under the field conditions.

Emigration has been reported to be one of the major factors influencing population densities of many aphid species (Hughes 1963, Perrin 1976, Walker et al. 1984, Hutchison and Hogg 1986). My study showed that the most significant mortality factor in the population dynamics of BAA was emigration, also. However, significant density-dependent decreases in the reproductive rates which were found to be

regulating factors for many aphid populations (Perrin 1976, Way and Banks 1967,) were not evident for BAA in my studies until the densities had exceeded 200/stem. From the data published by Messenger and Force (1963), the SAA also appears to have developed population densities without any feedback for density-dependent decrease in the reproductive rate (Way and Banks 1967) until host plants were severely damaged.

Variable results have been reported for role of predators in providing regulation of aphid population densities in alfalfa. Neuenschwander et al. (1975) observed a negative correlation between predator densities, especially Coccinellidae, and peak population densities of PAA and SAA and concluded that predators provided a density-dependent control of these species. Smith and Hagen (1965) reported that the precise role of lady beetles in controlling aphids in alfalfa was greatly influenced by the climate. Hutchison and Hogg (1986) found that predators played a minor role in the population dynamics of PAA in Wisconsin. Lady beetle adults in our study were predominant early in the season but could not control the developing populations of aphids. However, after the population growth rate of aphid populations had declined due to emigration, the larvae contributed to the demise of populations.

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