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THE DISPERSAL DYNAMICS OF
AMBLYSEIUS FALLACIS (GARMAN)
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THE DISPERSAL DYNAMICS OF AMBLYSEIUS FALLACIS (GARMAN) IN AN APPLE TREE ECOSYSTEM

By

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ABSTRACT

THE DISPERSAL DYNAMICS OF *AMBLYSEIUS FALLACIS* (GARMAN) IN AN APPLE TREE ECOSYSTEM

By

Donn Tiffany Johnson

The predatory mite, *Amblyseius fallacis* (Garman), is utilized in the integrated mite control program in Michigan as a biological control agent. One difficulty is that *A. fallacis* must migrate from the ground into the tree in early season to control the pest mites. Poor predator-prey synchrony in early season often necessitates an early application of a dormant oil and an acaracide. Knowledge of the early season movements of *A. fallacis* could determine if it is possible to manipulate *A. fallacis* into the tree earlier, thus enhancing the possibilities for biological control.

Studies were conducted which determined the proper grease plate trap orientation and spatial placement of plates within and beyond the orchard. Horizontal plates under the trees were more efficient in capturing mites dispersing out of the trees within the orchard, whereas vertical plates were more efficient in an open field. Plates in the east quadrant consistently captured the most mites. The north and south quadrants had similar counts, and the west captured the least. These directional quadrant differences appeared to be related to the air currents and to the differences in density of *A. fallacis* in the directional quadrants of the tree canopy. Data showed significantly more *A. fallacis* in the air near the tree trunk than at the periphery of the tree canopy. From data of aerial mite distribution under the tree, an estimate was made of the number of grease plates required to give a desired precision level.

Studies of early season dispersal dynamics of *A. fallacis*, i.e. prior to tree colonization by *A. fallacis*, showed that its density in the air was low in comparison to other periods during the season and that mite density in the air tended to be correlated with mite density in the ground cover. This suggests that *A. fallacis* may colonize the tree via the air.

Bean plant trap data and a restricted mite movement experiment showed that *A. fallacis* move into the tree predominantly via the tree trunk and to a lesser degree via the air. Tree colonization by *A. fallacis* was related to the prey density within the tree and the cumulative DD_{54} (degree days base = 54°F) value. A prey density > 1 *P. ulmi* equivalent/leaf was a prerequisite for tree colonization by *A. fallacis* in addition to an accumulation of 469 DD_{54}.

Mid season, i.e. up to peak prey density in the tree, was a period of numerical buildup within the tree for both the prey and predator. Immature stages of _A_. _fallacis_ predominated in the tree during mid season. Associated with this buildup were increased numbers of _A_. _fallacis_ in the air (mostly adult females), on the trunk, and in the ground cover.

Late season, i.e. after peak prey density in the tree, movements and habitat densities of _A_. _fallacis_ were highly dependent upon the declining prey population in the tree. The distribution of _A_. _fallacis_ stages in the air changed from mostly adult females in early and mid season to include more immatures and males. Increased air dispersal was attributed to starvation due to localized depletion of prey within the tree.

_A_. _fallacis_ was detected dispersing in the air up to 100 m or more away from the orchard. Seasonally, density on the plates decreased exponentially with distance away from the orchard.

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INTRODUCTION

In Michigan many commercial apple growers follow an integrated mite control program (Croft 1975, Croft and McGroarty 1977) which reduces the number of acaricide applications to control the European red mite, *Panonychus ulmi* (Koch), the two-spotted spider mite, *Tetranychus urticae* Koch, or the apple rust mite, *Aculus schlechtendali* (Napela). This is accomplished by using a selective spray program that has only minor deleterious effect upon the highly adaptive predator, *Amblyseius fallacis* (Garman). *A. fallacis* has developed strains resistant to at least 15 organophosphorous insecticides (Croft and Brown 1975, Croft et al. 1976a), DDT and methoxychlor (Smith et al. 1963), and carbaryl (Croft and Meyer 1973). *A. fallacis* is also adapted to prey effectively upon the tree infesting mites *P. ulmi*, *T. urticae*, and *A. schlechtendali* (Smith et al. 1963, Swift 1968).

One difficulty with the integrated mite control program used in Michigan relates to predator-prey synchrony within the tree. The overwintering habitat of *A. fallacis* is principally in the ground cover beneath the apple tree or on the trunk, whereas that of its prey is near and or under the buds of the apple tree. It has been observed that *A. fallacis* does not colonize the apple tree until June or early

July (Croft 1975). Late colonization of the tree by *A. fallacis* necessitated the application of a dormant oil and occasionally a reduced rate of an acaricide in early season. The result is a reduction in the pest mite density in the tree until migrating populations of *A. fallacis* enter the tree and multiply to a density that can control the pest mites. Croft and McGroarty (1977) studied the predator-prey interaction for several years, and reported that only a small difference in the initial number of *A. fallacis* colonizing the tree could make the difference between effective biological control or the need to control the pest mites chemically (Croft and McGroarty 1977). Presently, the mechanism by which *A. fallacis* moves into the tree in early season and the factors that affect this movement are unknown. If manipulation of *A. fallacis* movement into the tree in early season was possible, possibilities for biological control could be enhanced greatly.

The objective of this study was to determine what factors or trends in mite populations influence the movement of *A. fallacis* into and out of the apple tree. More specifically they included investigations of: 1) the mode of movement of predators from the ground into the apple tree; 2) the effects of temperature, relative density of *A. fallacis* in the ground cover and prey per apple leaf on predator colonization of the apple tree; 3) the relationship between prey density within the apple tree and the rate and stage distribution of predators moving out of the tree through time; 4) the mode and distance of dispersal of predators both within and beyond apple orchards.

LITERATURE REVIEW

Dispersal or diffusion of organisms has been discussed (Johnson 1969, Mitchell 1970, Wolfenbarger 1975), but little research is available on the consequences of this dispersal to the individual or a population of individuals (Gadgil 1971). Also studies have related acarine air dispersal to environmental factors (Boyle 1957, Duffy 1956, Ebeling 1934, Fleschner et al. 1956, Hussey and Parr 1963, Johnson 1969, Johnson and Croft 1975 and 1976, Marle 1951, Mitchell 1970, Nault and Styer 1969, Nelson and Jorgensen 1968, Newell 1941).

The biology of the predaceous mite, *A. fallacis*, has been studied extensively for its effectiveness as a biological control agent (Ballard 1954, Croft and McGroarty 1977, McClanahan 1968, Smith and Newsom 1970). The effects of selected environmental factors on reproduction of *A. fallacis* are known. Rock et al. (1971) found that a critical photophase of 12 hours or less induced reproductive diapause in a strain of A. fallacis from New Jersey (40°N latitude) reared at 15.6°C. They also showed that diapause could be terminated in 60 to 70 days at 15.6°C. Lee (1972) stated that diapause termination was move variable in *A. fallacis*. Once egg production begins, the generation time of A. fallacis varies from 6.1 to 10 days at 25°C and 20°C, respectively (Lee 1972). The oviposition rate varies according to prey density and temperature. It has been demonstrated that A. fallacis responds both functionally and numerically to the density of its prey; this reponse is enhanced as the temperature is increased. Functional and numerical responses of A. fallacis to T. urticae were three times greater at 26.7°C than at 21.1°C or below (Croft and Blythe 1979). Given ample prey (i.e. 15 or more T. urticae eggs/female/day an A. fallacis female will lay from one to three eggs/day at 15.6°C and 26°C, respectively (Croft and Blythe 1979). In the field, the male to female sex ratio is as low as 0.2 (Rock et al. 1971) or as high as 0.5 (Lee 1972).

Biotic and abiotic environmental factors influence the dispersal movements of organisms (Fraenkel and Gunn 1964, Johnson 1969). In early season A. fallacis moves from the ground into the tree, later in the season the prey become depleted in the tree and the predator returns to the ground cover to overwinter (Croft and McGroarty 1977). Similar observations were reported for Tetranychus pacificus McGregor (Newell 1941), and T. urticae (Hussey and Parr 1963).

Starvation, due to a lack of prey for predaceous mites or a chlorotic condition of the plant host for phytophagous species, affects their dispersal. If food is readily available, only preovipositing females of phytoseiids (Johnson and Croft 1976, Croft and McMurtry 1972) and tetranychids (Boyle 1957, Hussey and Parr 1963, Marle 1951, Mitchell 1970) dispersed to found new colonies. If food is unavailable, dispersal of other stages of *T. urticae* (Boyle 1957, Hussey and Parr 1963), *P. ulmi* (Marle 1951), and the eriophyid mite, *Aceria tulipae* (Keifer) (Nault and Styer 1969) occurs.

Wind is a major environmental factor affecting air dispersal in mites. Adult females of *A. fallacis* exhibited a dispersal behavior between air speeds of one to ten miles per hour (M.P.H.) in a wind tunnel. Active release of *A. fallacis* into the air without spinning threads occurred between six and ten MPH (Johnson and Croft 1976). Many tetranychids behave similarly with regard to dissemination by air currents. Adult females of *P. ulmi* were observed to spin a thread down from leaves and hang freely in the air and disperse during periods of gentle air currents (Boyle 1957, Marle 1951). The tetranychids, *T. urticae* (Boyle 1957), *T. pacificus* (Newell 1941), and the phytoseiid, *A. fallacis* do not spin threads for bouyancy during air dispersal. Long body hairs of *T. pacificus* (Newell 1941) or the aerodynamic body shape of *A. fallacis*, provide some bouyancy which facilitate aerial dispersal. Thus it appears that many tetranychid mites and their phytoseiid predators have evolved similar means of aerial dispersal.

Croft and McGroarty, who studied the relationship between ground cover and tree inhabiting populations of _A. fallacis_ and spider mites in commercial apple trees proposed a hypothetical model of _A. fallacis_ movement (Croft and McGroarty 1977, McGroarty 1979). They presented a graphical representation of _A. fallacis_ population dynamics within the ground cover and apple fruit tree ecosystem (Figure 1) including dispersal features. I quote their interpretation of the dynamic process involved in this representation: "At time (a), _A. fallacis_ may be slowly increasing or simply maintaining its overwintering level in the ground cover understory (i.e. of the apple orchard). The presence of these measurable populations seems to be critical if complete biological control is to be achieved later during the growing season. At point (b), _P. ulmi_ begins to increase in the tree, but most often there is a lag in predator response (c) because there is a certain minimum threshold density of prey which must be attained before the predator can find enough food to first survive and then later increase in the tree system. At point (c) there is often a temporary decline or flattening of the ground cover population curve for _A. fallacis_ and this appears to correspond to the rapid migration of predators into the fruit tree.... At point (d), an equilibrium point between predator dispersal from the ground cover, and a non-behavioral dispersal from the tree back to the ground is achieved.

The latter event appears to be related to the random probability of predators being blown from the tree and is closely correlated with predator densities in the tree independent of the prey available as long as these food sources are not limiting. This is indicated by the parallel slope increase of predators and prey between time (d) and (e). At (f), the ratio of predators to food prey is beginning to become limited on certain leaves even though the mean tree interaction has not peaked with repect to predator density. At this point, a specific dispersal causes predators to leave the tree at a faster rate than they are increasing or migrating into the tree. As prey are controlled, within-tree predator populations decline and there is a major dispersal back to the ground cover (g). Eventually a suppression and regulation of predators and prey is imposed on the within-tree predator-prey system in late season, while ground cover populations greatly increase, undergo high mortality, or enter diapause (g) depending on when the within-tree interaction has been terminated. These late season dynamics (g-h) greatly affect what levels of prey overwinter in the tree and what level of predators enters the overwintering period in the ground cover."

It should be recognized that their study was based only on correlations between ground cover and tree populations of _A_. _fallacis_ in time and they did not in fact measure populations of dispersing mites. In this research, attempts were made to directly relate dispersal rates of _A_. _fallacis_

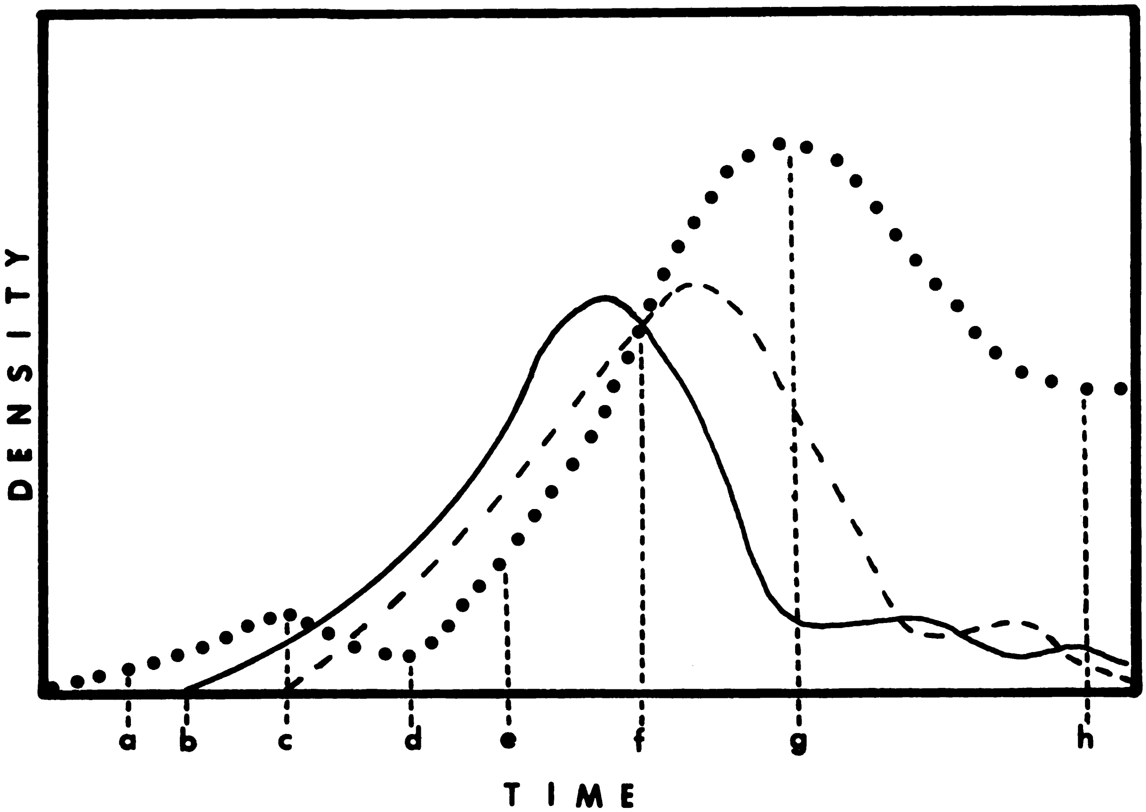

Figure 1.: A generalized plot of the seasonal densities of P. ulmi in the tree (-) in the ground cover (· · ·) and the tree (--) of a commercial apple tree (from Croft and McGroarty 1977).

to changes in density in these orchard ecosystem habitats. More specifically, the study was concerned with the movements of predators occuring between times (a-e) as proposed by Croft and McGroarty (1977) (Figure 1) and to a lesser extent during the remainder of the season.

METHODS

The relative densities of A. fallacis in the air both within and beyond apple orchards were estimated using grease plates ($10cm^2$) as the catching surface. Orientation (vertical or horizontal) of the plates relative to capturing efficiency was evaluated both within and beyond orchards and at different height locations below 2 meters above the ground level. The mean density of A. fallacis/grease plate/day was counted directly from plates using a stereomicroscope.

Plate location under individual trees was studied in several experiments. All tests were run in four blocks in three commercial apple orchards (i.e. Klackle, Rasch, and Graham Station). In 1974 (Klackle's orchard), four plates were placed in four directional quadrants. Concurrently, the density of A. fallacis/apple leaf was estimated in the lower hemisphere of each directional quadrant of the same trees by collecting ten apple leaves/quadrant in an equidistant manner from the interior to the periphery of the tree. The lower hemisphere is known to have a higher density of predators and prey (Croft et al. 1976). In 1975 (Rasch's orchard), plates were set out under trees either near (<1m) or far (>3m) from the tree trunk and sampled. The latter design was used to determine the difference between catch in relation to the proximity to the tree trunk. In 1976 (Rasch's orchard), four trees were monitored with 20 grease plates/tree set in from the trunk. The sample mean per plate ($\bar{x}$) was derived from two, ten plate sample estimates. The variance (s_i^2) associated with each $\bar{x}_i$ were used together to calculate the value for mean crowding:

$$\overset{*}{m} = \bar{x}_i + s_i^2/\bar{x}_i - 1 \; .$$

A linear regression was calculated for the relationship of the $\bar{x}_i$ to its corresponding $\overset{*}{m}_i$. The linear regression was represented by the equation: $\overset{*}{m} = \alpha + \beta\bar{x}_i$, where α is the y-intercept and β is the slope of the line; together, both α and β give an indication of the type of distribution the data approximate. The sample size (n) for a desired standard error of the $\bar{x}$ ($S.E._{\bar{x}}$) was calculated by:

$$n = t_i^2/D^2 \; ((\hat{\alpha} + 1)/\bar{x}_i + (\hat{\beta} - 1))$$

where t is the critical value of the Student's t- distribution for a given D (the $S.E._{\bar{x}_i}$) and degrees of freedom ($\bar{x}_i$) (Iwao and Kuno 1968). Estimates of n were calculated for a range of D from 0.1 to 0.5, and $\bar{x}_i$ from 0.1 to 100.

Several sampling methods were used to estimate population densities of *A. fallacis* and its prey in various habitats of the apple tree ecosystem. In the ground cover beneath the tree *A. fallacis* levels were determined by scanning broad leaf plants for six-one minute periods/tree. Broad leaf sampling by this technique provided 25% precision in estimating the density of *A. fallacis* according to McGroarty and Croft (1975). Another method used was to scan ten apple sucker leaves/tree for *A. fallacis*. The latter method provided a higher degree of precision in estimating the density of *A. fallacis* in the ground cover than does the broadleaf counting technique (McGroarty and Croft 1975).

The relative density of *A. fallacis* at four heights on the tree trunk was estimated using the two leaf stage of harvestor bean plants infested with *T. urticae*. These plants were stapled to the tree trunk in plastic bags of moist soil at four different heights (i.e. 1,2,3, and 5 feet). In 1975, four plants were placed at each height (i.e. 16 plants/orchard). In 1976, ten plants were placed at each height (i.e. 40 plants/orchard). Bean plants were scanned for *A. fallacis* and replaced weekly. Data was collected weekly for all sampling methods since the generation time of *A. fallacis* and its prey is from seven to nine days (Smith and Newsom 1970).

The relative weekly density and the stage distribution of *A. fallacis* in the air was estimated by grease plates set under apple trees. In all cases, plates were placed in the horizontal position. In 1975 and 1976, 16 and 20 plates/tree, respectively, were monitored at weekly intervals.

The relative density and the stage distribution of predators/apple leaf and the number of _P_. _ulmi_ equivalents[1]/ apple leaf were estimated by collecting apple leaves from the tree as described earlier. In 1975 and 1976, a 50 or 100 leaf samples/tree, respectively, were collected. Ten leaves were collected from five or ten radii of the tree. Initially 100 leaves were sampled, but once the population density exceeded 0.3 predators/apple leaf, then only 50 leaves were taken (in 1976 and 1977). At least four trees were monitored each year from 1975 to 1977. Although each leaf count gave only a relative measure of mite densities (due to minor variations in leaf size), they would very closely approximate those taken on a surface area basis.

Counts of _A_. _fallacis_ from the ground, trunk, air and apple leaf were compared to establish relationships and trends between populations. Grease plate counts were compared to tree counts taken the previous week. Grease plate counts are cumulative over seven days. Density trends at the four trunk levels were used to describe the colonization of the tree by _A_. _fallacis_ in early season. Mid and late season trends of predator levels on the trunk were compared to the density changes in the tree, the air and the ground cover.

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[1] _P_. _ulmi_ equivalent = No. _P_. _ulmi_ + No. _T_. _urticae_ + (No. _A_. _Schechtendali_/15) (Croft, unpublished data).

An exponential curve fit was used to estimate the value of cumulative degree days above 54°F (DD_{54}) for the time A. fallacis was first detected in the apple tree (ca. 0.04 predators/apple leaf the curve was derived from data points relating cumulative DD_{54} to the number of A. fallacis/apple leaf up to 1.5 predators/apple leaf) (Brownlee 1965). Tree colonization by A. fallacis was estimated in other ways. A comparison was made of the date A. fallacis appeared at the 5 foot trunk height they were detected within the tree. Also measured on these two dates were the P. ulmi equivalents/leaf within the tree. A multiple regression was calculated to determine which factors contributed the most to explaining the variation observed in the initial appearance and density of A. fallacis in the apple tree. The variables analyzed were: 1) the density of A. fallacis in the ground cover; 2) the relative density of P. ulmi equivalents/apple leaf in the tree; and 3) the cumulative DD_{54} which was correlated to the other variables.

One experiment determined the principal means (e.g. walking and/or air) whereby A. fallacis colonizes the apple tree in early season. This experiment consisted of four treatments: 1) unrestricted movement of A. fallacis into the tree; 2) restricted movement to the trunk by enclosing nursery trees in a mite-proof screen cage; 3) restricted movement to the air by covering the trunk with Stickem®; 4) restricted movement into the tree via the trunk and air by both caging and applying Stickem®. Initially, 24 Prince

Red Delicious nursery trees (4 to 6 feet tall) were sprayed with Sevin® to insure that no mites or insects were on the trees prior to the experiment. Then four trees were planted under each of six commercial apple trees (Delicious) in an orchard near Sparta, Michigan. Trees were set out on May 15, 1978, and infested with *T. urticae* (a food source for *A. fallacis*) weekly over the next three weeks. Once *A. fallacis* was detected in orchard trees, all the leaves on the nursery trees were scanned for *A. fallacis*. The number of leaves/nursery tree varied from 40 to 200 leaves. Only those leaves infested with *T. urticae* were used in the sample. Ten leaf samples/tree were used to estimate the mean predator numbers/apple leaf.

Samples from the nursery tree study were taken weekly for a three week period. From the variation exhibited in the leaf counts, it was found that the distribution of *A. fallacis* in these trees approximated a negative binomial distribution (k = .58). Therefore, the means for each replication were transformed by log $(\bar{x}_i + 1)$ before being analyzed by ANOVA procedures. Four replicates of each treatment were used in the analysis as a result of dropping the lowest and the highest replicate in each experiment. The Student-Newman-Kuel's multiple range test was used to distinquish between treatment means at the 0.05 level (Ostle 1963).

Mid to late season population density changes were described by comparing the seasonal trends in the stage distribution of A. fallacis/apple leaf in the tree with its trends in stage distribution in the air (grease plate samples). Trends in the tree population were also compared to the density trends at the four trunk levels and in the ground cover.

In 1976 and 1977, a seasonal study was conducted to determine the relationship between counts/grease plate and distance beyond the apple orchard. In 1976, 5 grease plates were set out monthly in a horizontal plane at positions 5, 10, 15, 20, and 100 meters beyond the orchard. Weekly, in 1977, ten plates were set out vertically at 3.8, 8.4 meters, and 15 plates at 19, 42, and 72 meters beyond the orchard. In both 1976 and 1977, plates were set out horizontally under the trees. At each distance, the mean number of A. fallacis/grease plate was determined. Data was analyzed by ANOVA and Student-Newman-Kuel's multiple range test used to differentiate between mean counts at .05 level. Power curve regression equations were fit to the 1976 seasonal data set (i.e., May 19 to August 30) and each of the 5 weekly data sets of 1977. Weekly curves were compared for within seasonal differences in density at various distances, and between season differences of the regression curves for 1976 and 1977.

RESULTS AND DISCUSSION

Grease Plate Sampling Procedures. Grease or sticky plates have been used in many dispersal studies of mites (Fleschner et al. 1956, Johnson and Croft 1975, Marle 1951, Newell 1941, Nault and Styer 1969) and are satisfactory tools for measuring relative densities of insects in the air for a wide range of air velocities (Johnson 1950, Taylor 1962). For passively blown organisms such as mites, these techniques would be even more precise. Preliminary studies indicated that horizontal placement of grease plates was better for beneath tree sampling or within orchard studies while the vertical orientation was more effective for obtaining beyond orchard estimates. These results were expected considering that within the orchards the majority of mites are originating and falling downward by gravity from above the catching surface (i.e. in the tree). It is unlikely that such small organisms fall straight down, but they also are probably influenced by air currents.

No differences in plate catch in preliminary experiments were noted within orchards at different plate height levels, except one occasion during peak mite dispersal from the tree. Apparently the vertical density of these mites in the air is similar under most conditions when the principle source of migrating mites is from the tree.

For density studies beyond the orchard (i.e., a field), the vertical plate position sampled mites primarily moving parallel with the wind. These mites originated from the ground vegetation or field periphery. Nault and Styer (1969) and Taylor (1962) also positioned their grease plates or cylinders vertically for greatest catch of eriophyid mites or aphids, respectively, in an open field.

Seasonal data on _A_. _fallacis_/grease plate recorded in four cardinal directions under the tree in 1974 are given in Table 1; data for seasonal densities of _A_. _fallacis_/apple leaf in each corresponding tree quadrant during the same period are plotted in Figure 2. The plate data showed a directional effect with the east capturing more _A_. _fallacis_ than the others, while the south and north being equivalent but greater than the west. These results can be explained in at least two ways: 1) the directional densities of predators differed within the canopy causing differential fallout; or 2) as the predators dispersed out of the tree the air currents distributed the greatest number of mites in the eastern quadrant and the least in the western. Evidence of both explanations are found by comparing specific dates in Figure 2 and Table 1. August 15 in Figure 2 shows the greatest tree density in the southern quadrant, but Table 1 (August 22) show east as the greatest, which indicates an effect of air currents. A comparison of September 5 in Figure 2 to September 12 in Table 1 shows both have the

TABLE 1: Comparison of the number of *A. fallacis*/grease plate from different quadrants under the apple tree (1974).

DATE	QUADRANT			
	N	E	S	W
8/09	6.0±0.9[a]	4.0±0.6	1.8±0.5	1.8±0.5
8/22	8.0±0.9	11.5±1.1	8.0±1.0	8.3±1.0
8/29	19.3±1.5	18.0±1.6	18.5±1.4	13.0±1.3
9/05	11.3±1.3	18.5±1.4	17.8±1.3	17.5±1.2
9/12	17.0±1.4	26.0±2.0	20.5±1.6	17.3±1.7
9/19	25.0±1.6	32.8±1.9	25.5±1.8	22.5±1.6
9/25	29.3±1.8	41.3±1.4	31.5±1.7	27.3±1.6
TOTAL[b]	115.9	152.1	123.6	107.7

[a] Average number of *A. fallacis*/grease plate week ±5.0

[b] Total number of *A. fallacis*/grease plate/season

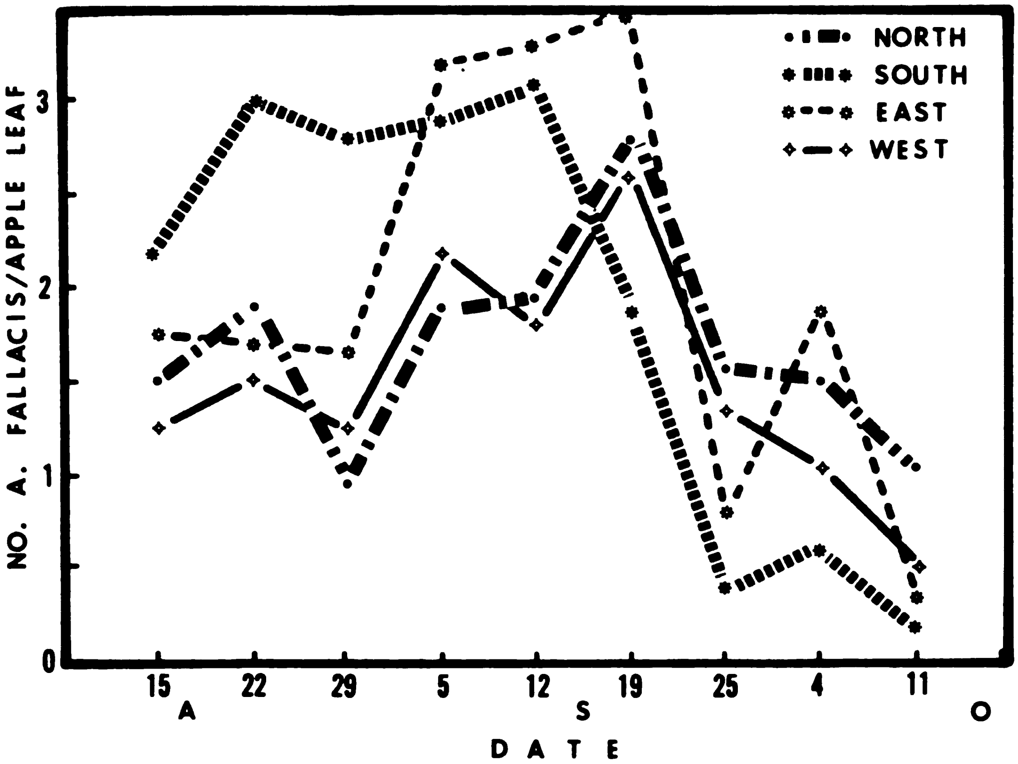


Figure 2: Comparison of the late seasonal densities of *A. fallacis*/apple leaf in each directional quadrant of the tree (1974).

eastern quadrant giving the greatest counts which indicates an effect of differential density in tree quadrants. McGroarty (1977) found from two independent analyses significant differences between the ground cover densities of _A_. _fallacis_ in the four directional quadrants. The north and east quadrants, most often, had the highest density, but generally all quadrants were similar. He also attributed these difference to the effect of air currents on dispersal.

Another spatial comparison of plate location was that of plate proximity to the tree trunk. It was felt that the vertical densities of _A_. _fallacis_ in the tree canopy would be higher in the center as mentioned previously. Table 2 illustrates the comparison of counts betwen grease plates from sites either near or far from the tree trunk. At all dates, more mites were collected on the near than on the far plates as expected. In comparison, McGroarty (1977) found seasonal differences in ground cover density of _A_. _fallacis_ in relation to proximity to the trunk. Early season counts showed predators at significantly higher densities near the trunk, mid season densities were almost equal, and during predator emigration from the tree the ground cover densities were greater at the periphery.

The discrepancy between McGroarty's ground cover data and these grease plate results relative to proximity to the tree trunk is probably due to the fact that grease plate counts are cumulative over seven days, but the ground cover counts are cumulative over the season. It is believed that

TABLE 2: Comparison of the number of *A. fallacis*/grease plate set either near (<1m) or far (>3m) from the tree trunk (1975).

DATE	TREE No.	PROXIMITY TO TRUNK NEAR	PROXIMITY TO TRUNK FAR
7/24	E2	12.0±10.2[a]	5.3± 7.2
7/31	E2	22.7± 8.7	7.5± 2.1
8/07	S	36.8±12.4	17.0± 5.3
8/07	E2	54.5± 7.5	24.0±18.1
8/21	E2	12.0±11.8	4.3± 9.3
TOTAL[b]		1121	963

[a] Average number of *A. fallacis*/grease plate ±5.0.

[b] Total number of *A. fallacis* caught either near or far.

as the mites fall out of the tree, they fill the available feeding and overwintering sites nearest the trunk first since greater numbers land in this area. Overpopulation in the area of the trunk forces a wave of mites to move away from the trunk. This wave may account for the larger counts in the periphery than near the trunk later in the season. Eventually the mites scatter equally throughout the ground and air of the apple tree ecosystem.

Based on preliminary studies of orientation and placement, it was possible to obtain a standard sampling method and estimate the sample size required to achieve a desired precision level ($S.E._{\bar{x}}$) with the grease plates. Estimations of sample size required knowledge of the distribution of mites in the universe sampled. Mites impacted on individual grease plates randomly (Figure 3), indicating that no ambulatory dispersal via the supporting poles occurred, and that no differential impaction due to wind deflection around the plate surface was influencing catch to any great extent. Mites were found to be randomly distributed among grease plates (Figure 4) at a lower range of plate counts (i.e. zero to ten mites/plate/week) as shown by the values of $\alpha = 0.3$ and $\beta = 0.9$ from the linear regression in Figure 4. At plate counts above ten mites/plate/week, mites were more aggregated as shown by the values of $\alpha = 5.78$ and $\beta = 1.13$ also from Figure 4.

Estimates of the sample size required for a desired $S.E._{\bar{x}}$ were calculated using the above α and β values in the

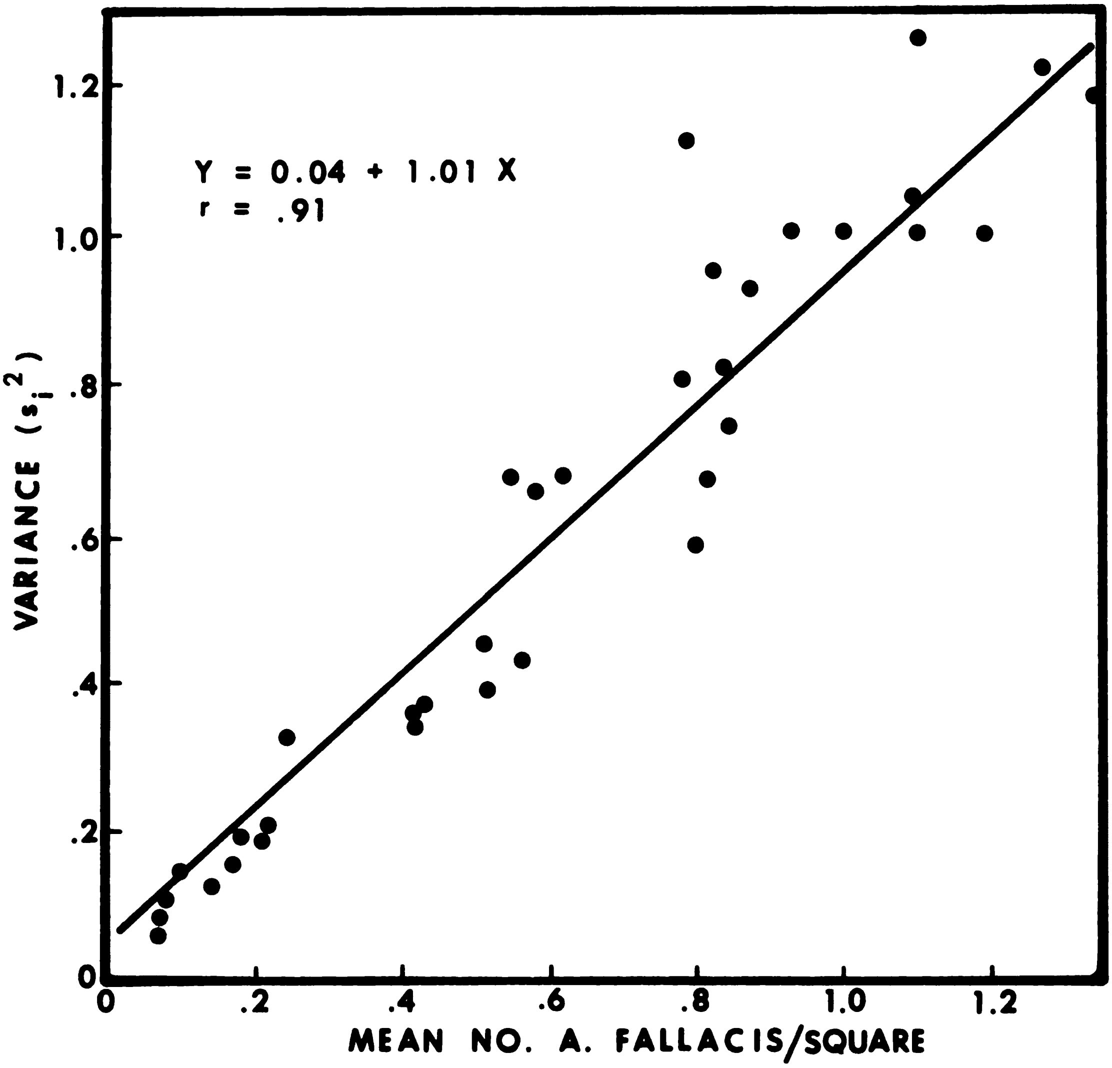


Figure 3: Comparison of the variance (s_i^2) to the mean ($\bar{x}_i$) number of <u>A</u>. <u>fallacis</u>/square of grease plate.

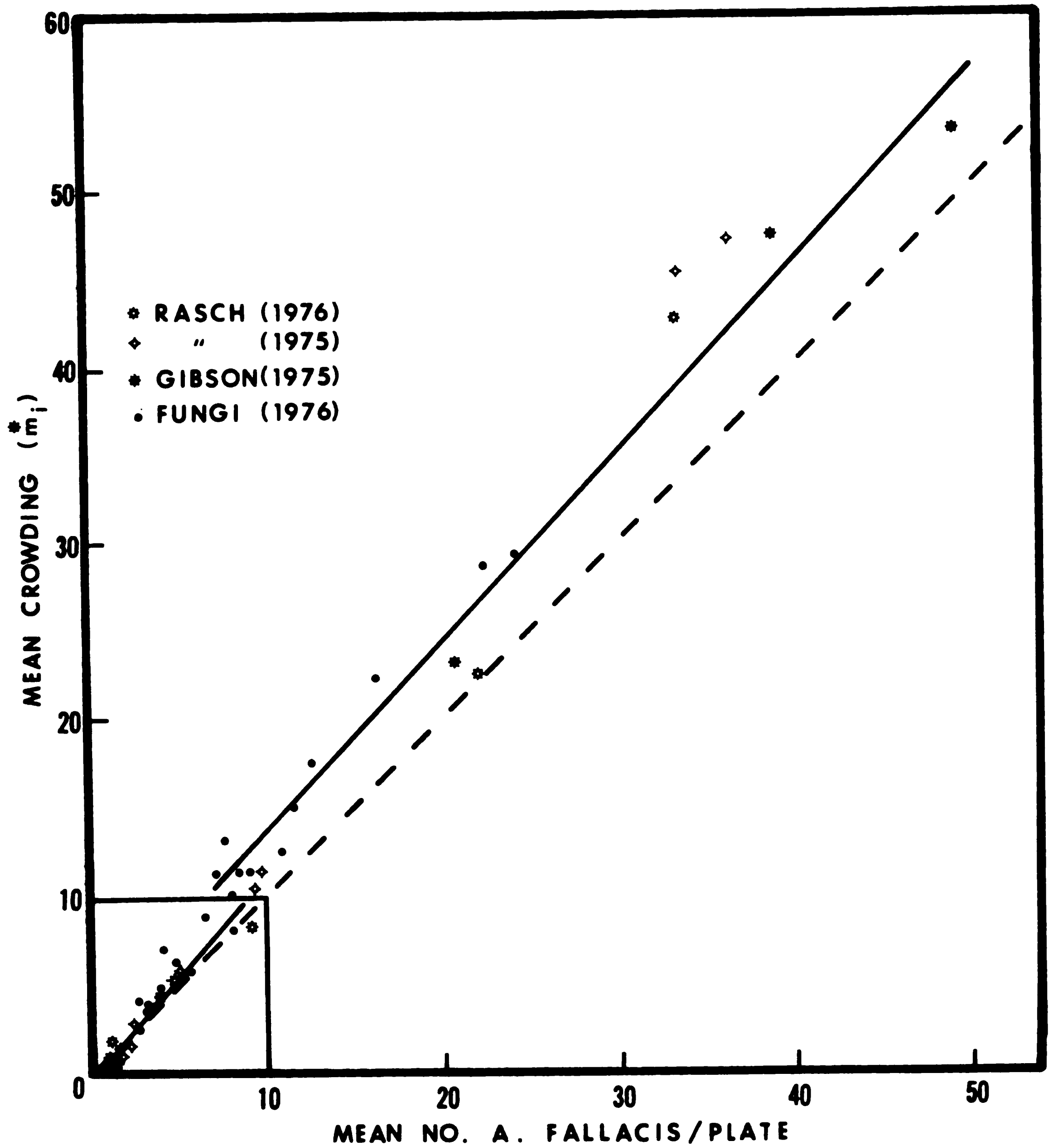


Figure 4: Comparison of the mean crowding ($\overset{*}{m}$) to the mean ($\bar{x}_i$) taken from grease plate samples in three orchards (1975-76).

equation described by Iwao and Kuno (1968). The minimum sample size needed for a given level of precision (i.e. $S.E._{\bar{x}}$ range from 0.1 to 0.5) for a wide range of mean plate counts (i.e. from 1 to 10 and 10 to 100 mites/plate) is given in Table 3.

General Seasonal Dynamics. The life history and dispersal patterns of *A. fallacis* within the apple tree ecosystem can be described as three interrelated seasonal events (Figure 1). The first is the early season activity of predators prior to their detection the apple tree. These mites occur in the ground cover understory, upon the tree trunk, and in the air mostly under the apple tree. Mid season activities included all events up to and including the time of peak prey abundance in the tree. Events included in this period are increased activity of *A. fallacis* in the understory, and on the tree trunk; its numerical response to prey within the tree canopy; and both ambulatory and air dispersal within and from the tree. Late season activities pertained to the dispersal dynamics of predators which occur as prey abundance in the tree declines due to predation.

A basic model of *A. fallacis* movements between habitats in the apple ecosystem and the effects of certain factors on these movements are presented in Figure 5. Seasonal summaries of the density counts of *A. fallacis* within each orchard subcomponent and dispersal activities within the apple tree ecosystem are presented in Figures 6 through 9.

TABLE 3: Sample size or number of plates required to estimate the plate density of *A. fallacis* under the canopy of an apple tree.

Density	Acceptable Standard Error of the Mean (D)				
	.10	.20	.30	.40	.50
0.1[a]	2.2×10^6	5.4×10^4	9076.8	1304.3	408.9
0.5	3.1×10^4	1436.0	304.4	59.1	20.6
1.0	4944.1	291.3	67.8	14.6	4.9
2.0	481.7	50.2	13.6	4.0	1.5
5.0	67.4	9.0	2.7	0.9	0.4
10.0	10.8	1.6	0.5	0.2	0.1
10.0[b]	265.3	38.0	10.7	3.9	1.6
20.0	139.6	20.6	5.9	2.2	0.9
40.0	84.9	12.7	3.7	1.4	0.6
60.0	67.9	10.2	3.0	1.1	0.5
100.0	54.4	8.2	2.4	0.9	0.4

[a] A density of 0.1 to 10 mites/plate had $\alpha = 0.33$, and $\beta = 0.9$.

[b] A density of 10 to 100 mite/plate had $\alpha = 5.78$, and $\beta = 1.13$.

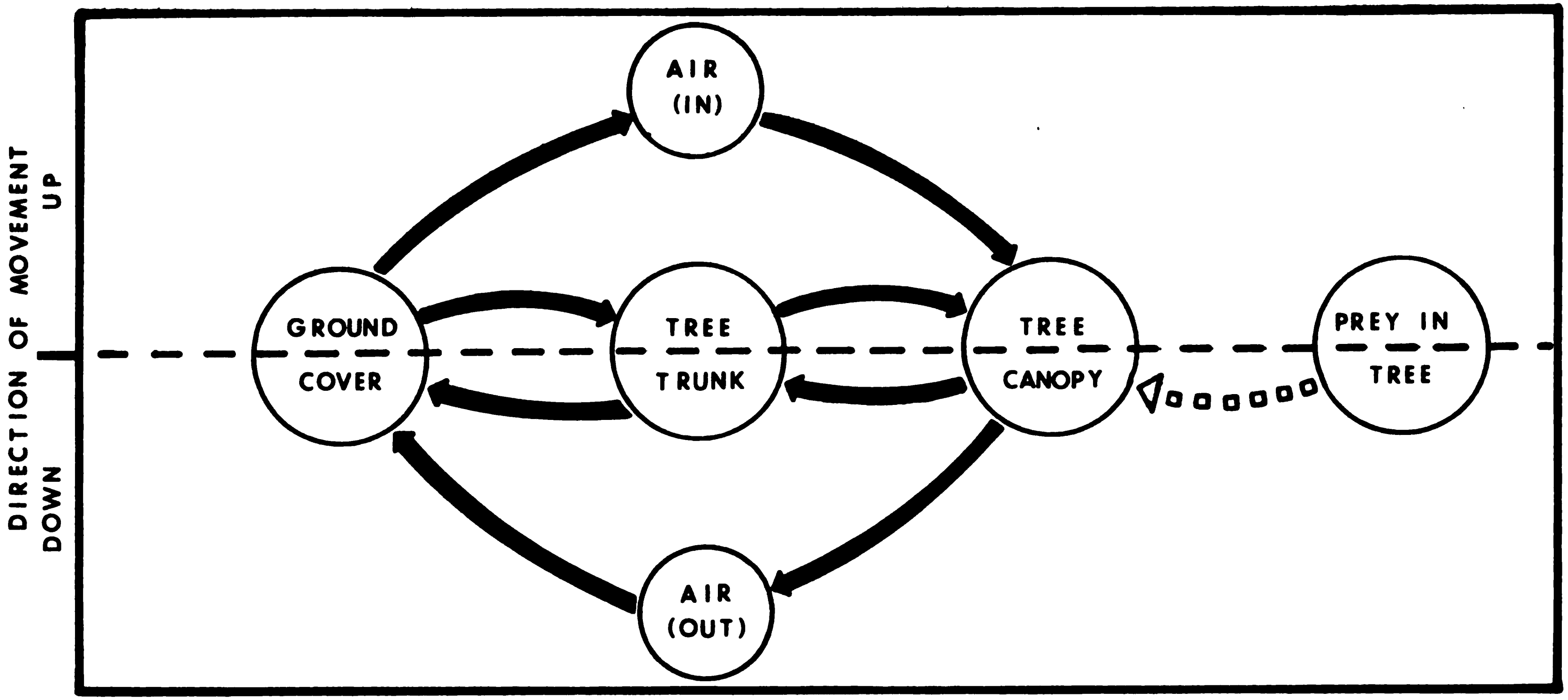


Figure 5. A basic model of the various directional movements (solid arrows) made by *A. fallacis* either up or down (--), their relative density *in each habitat* (circles), and the influence (open arrows) of prey density on the movement of *A. fallacis*.

These figures will be referred to periodically hereafter as each dispersal activity phase is described in greater detail.

Early Season Dynamics. Generally early season ground cover densities of populations were low (i.e. < 0.02 mites/ apple sucker leaf) in comparison to later in the growing season (Figures 6, 8 and 9). Ground cover populations, however, are very important sources for later within tree populations as shown by Croft and McGroarty (1977) and their presence is necessary if biological control of *P. ulmi* population is to be accomplished later in the tree (compare with data in Figures 6, 8 and 9 versus 7).

In 1975 and 1976, a total of only five *A. fallacis* were captured on grease plates (16 plates/tree/week under eight trees in three orchards = 384 total plates counted) during the early season period indicating minimal air-borne dispersal was occurring. *A. fallacis* was not present in the tree so most mites dispersing in the air during this period most likely originated from sites in the ground cover. Ground to air dispersal would generally imply a horizontal trajectory of the mites in the air. The use of vertical grease plates probably would present more surface area to the air flow and be more efficient in capturing mites blown horizontally. However, the horizontal plates were presumed to be less effective than vertical plates in early season which probably resulted in the low capture in early season samples.

In an attempt to document this early season migration

Figure 6. Seasonal summary of data on relative densities of A. *fallacis* in the ground cover, on the trunk, on the grease plate, and in the tree verses prey in the tree (1975).

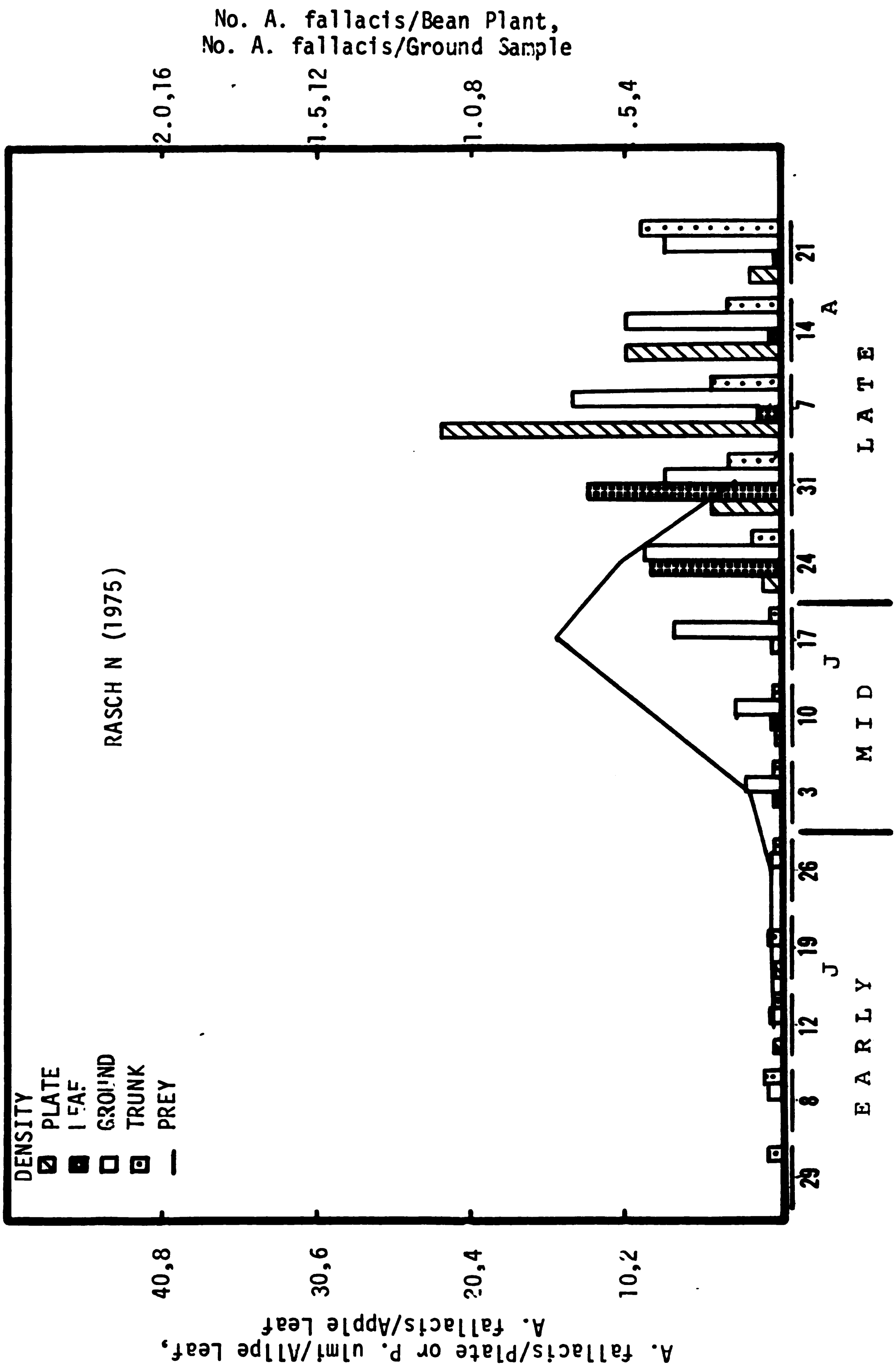

No. A. fallacis/Bean Plant,
No. A. fallacis/Ground Sample
2.0,16
1.5,12
1.0,8
.5,4
RASCH N (1975)
DENSITY
▨ PLATE
■ LEAF
□ GROUND
▣ TRUNK
| PREY
29
8
12
J
19
26
3
10
J
17
24
31
7
14
A
21
EARLY
MID
LATE
40,8
30,6
20,4
10,2
A. fallacis/Plate or P. ulmi/Allpe Leaf,
A. fallacis/Apple Leaf

Figure 7. Seasonal summary of data on relative densities of A. fallacis in the ground cover, on the trunk, on the grease plate, and in the tree versus prey in the tree (1975).

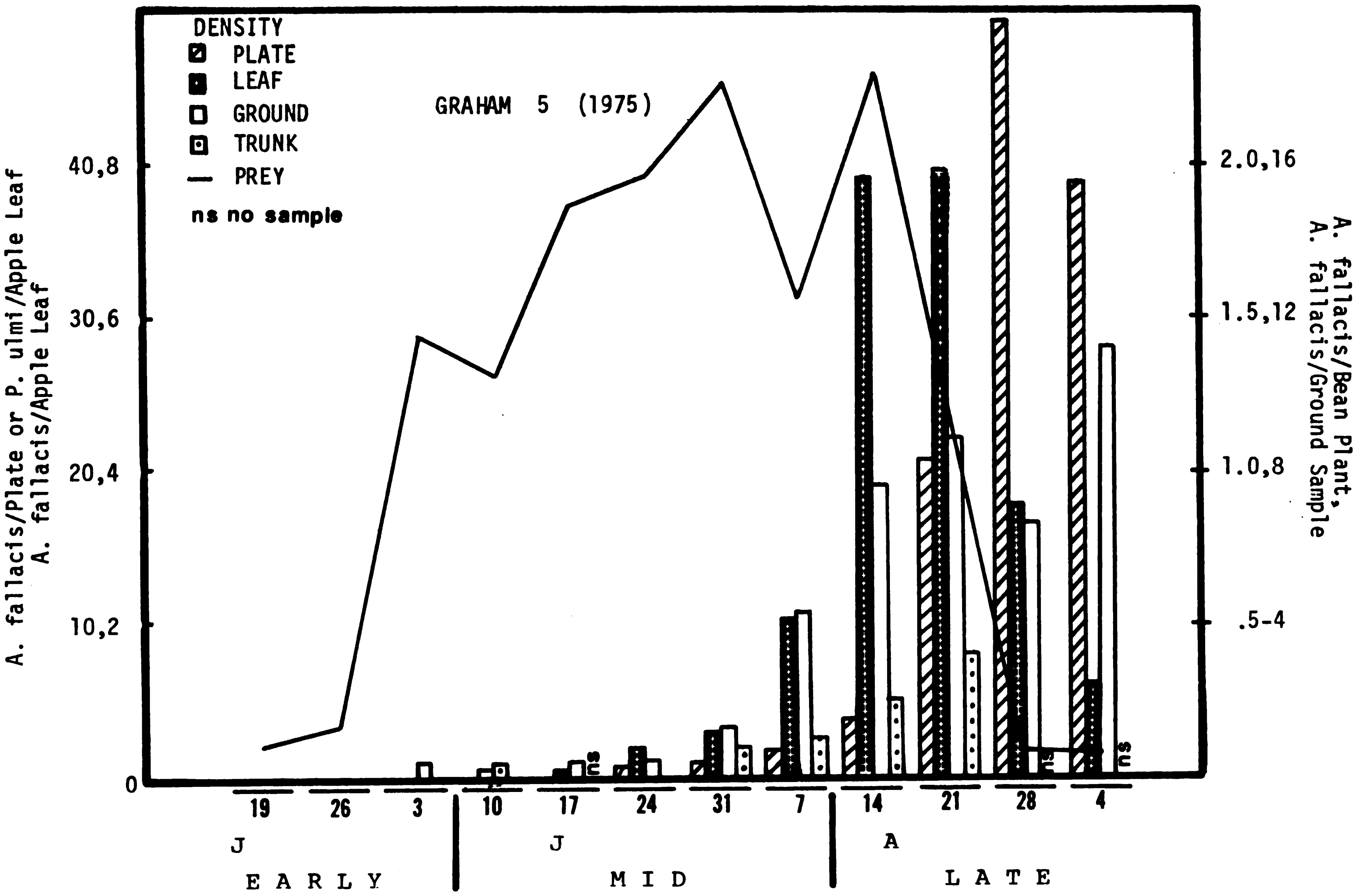

DENSITY
▨ PLATE
■ LEAF
☐ GROUND
⊡ TRUNK
— PREY
ns no sample
GRAHAM 5 (1975)
A. fallacis/Plate or P. ulmi/Apple Leaf
A. fallacis/Apple Leaf
40,8
30,6
20,4
10,2
0
A. fallacis/Bean Plant,
A. fallacis/Ground Sample
2.0,16
1.5,12
1.0,8
.5-4
ns
ns
ns
19
26
3
10
17
24
31
7
14
21
28
4
J
J
A
EARLY
MID
LATE

Figure 8. Seasonal summary of data on relative densities of *A. fallacis* in the ground cover, on the trunk, on the grease plate, and in the tree prey versus prey in the tree. (1976).

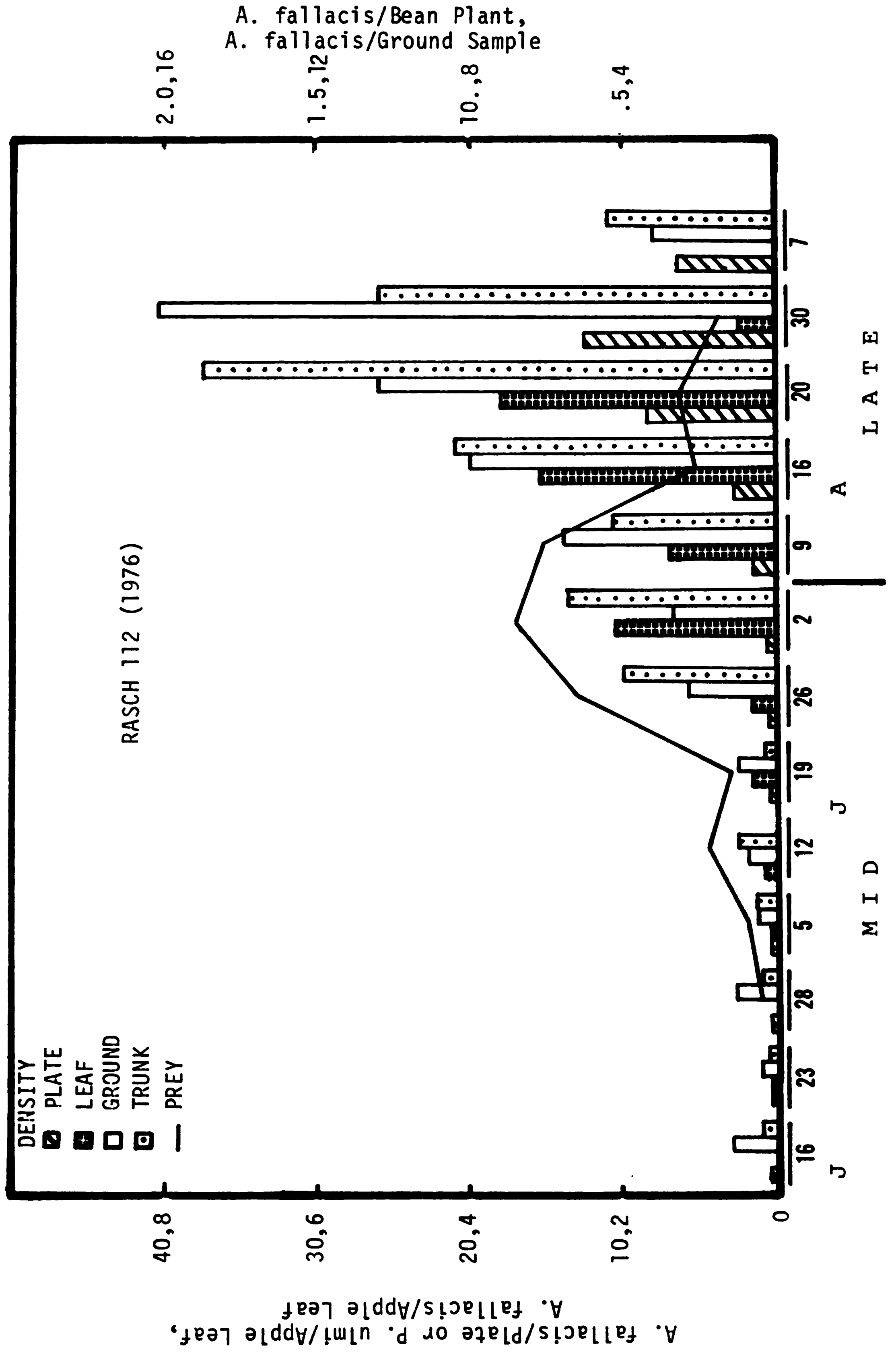
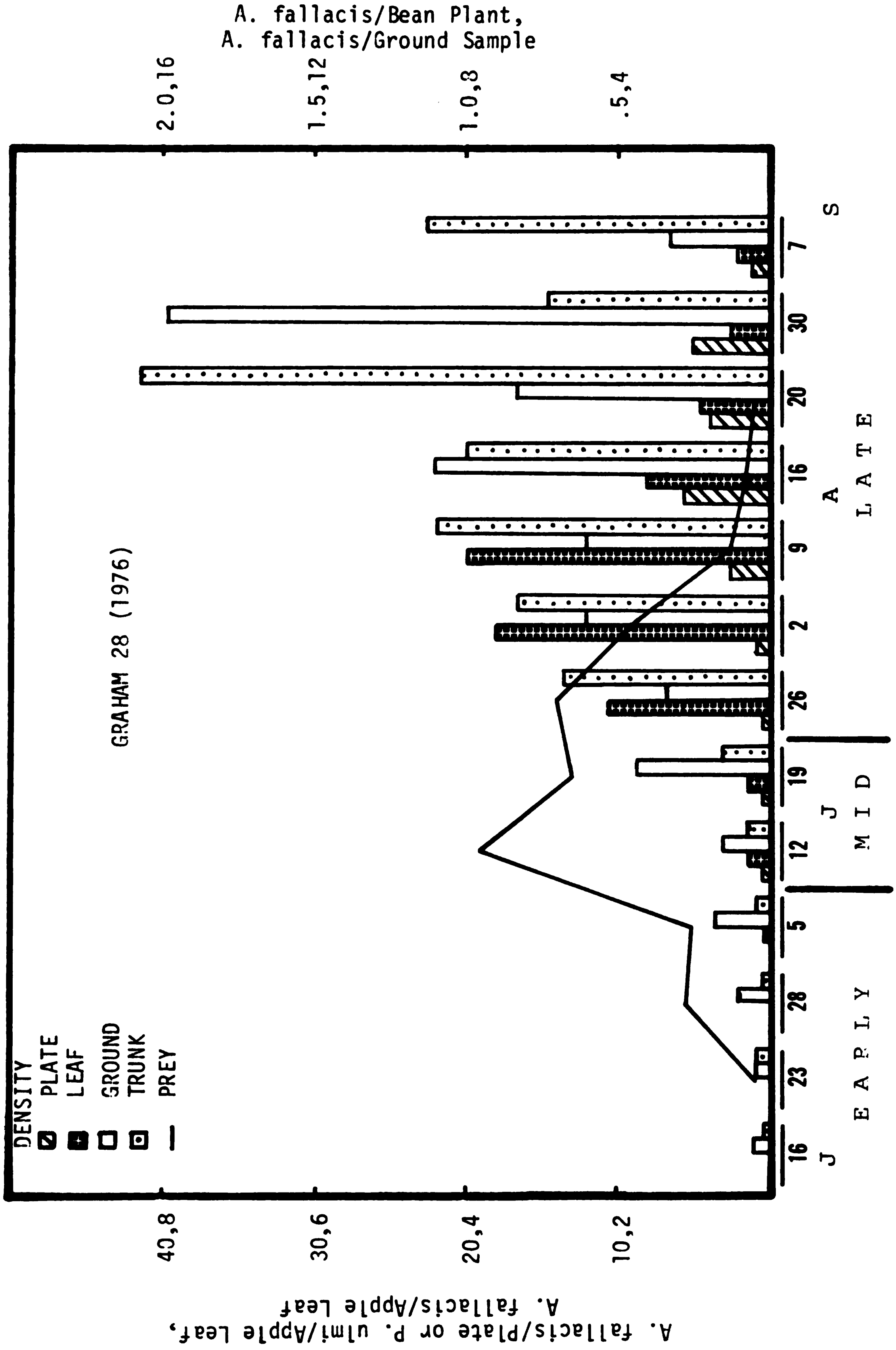

A. fallacis/Bean Plant,
A. fallacis/Ground Sample
2.0,16
1.5,12
10.,8
.5,4
A. fallacis/Plate or P. ulmi/Apple Leaf,
A. fallacis/Apple Leaf
40,8
30,6
20,4
10,2
0
RASCH 112 (1976)
DENSITY
PLATE
LEAF
GROUND
TRUNK
PREY
16
23
28
5
12
19
26
2
9
16
20
30
7
J
MID
J
A
LATE

Figure 9. Seasonal summary of data on relative densities of *A. fallacis* in the ground cover, on the trunk, on the grease plate, and in the tree versus prey in the tree (1976).

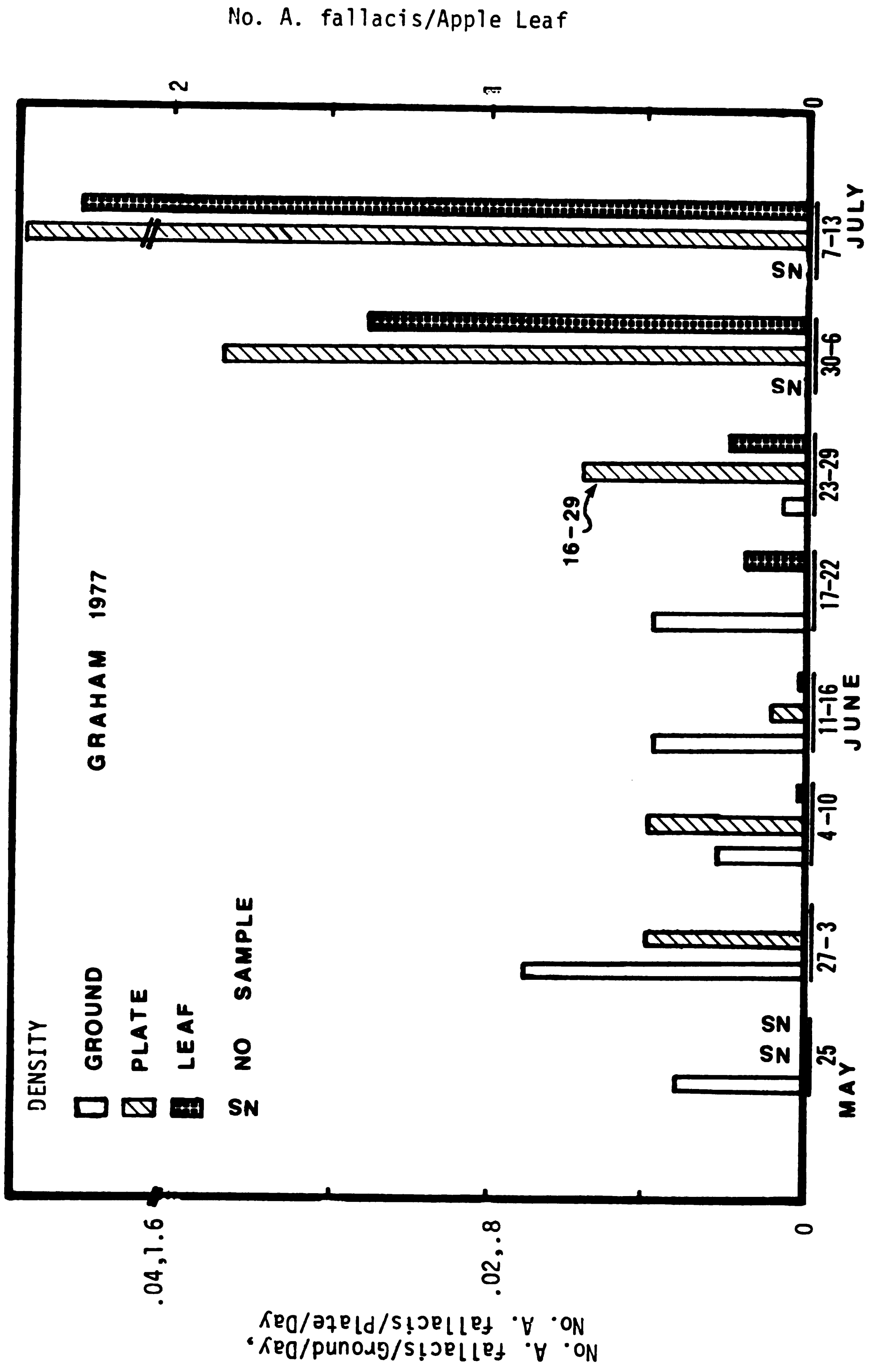

A. fallacis/Bean Plant,
A. fallacis/Ground Sample
2.0,16
1.5,12
1.0,8
.5,4
GRAHAM 28 (1976)
DENSITY
PLATE
LEAF
GROUND
TRUNK
PREY
16
23
28
5
12
19
26
2
9
16
20
30
7
J
J
A
S
EARLY
MID
LATE
40,8
30,6
20,4
10,2
A. fallacis/Plate or P. ulmi/Apple Leaf,
A. fallacis/Apple Leaf

more precisely, 80 grease plates were placed horizontally under a single tree in 1977. Figure 10 illustrates the comparison of grease plate counts of A. fallacis to tree ground cover counts and apple leaf counts of A. fallacis. From May 27 to June 29, the grease plate counts tended to be closely correlated with the ground cover counts (note: the plate catch represents the cumulative number of A. fallacis captured during the previous seven days, therefore it relates best to the previous ground or tree sampling date). Once A. fallacis became established in the trees (see June 22), the grease plate counts were more closely related to the increasing density of A. fallacis in the apple tree (see Figures 6 through 9, also).

A number of other studies support the occurrence of aerial dispersal of A. fallacis. For example, variable removal of ground cover beneath the tree from 0% cover to 100% cover or the restriction of mite movement on the trunk and in air was observed to only slightly delay colonization of the tree by A. fallacis (Croft and McGroarty 1977). Such habitat manipulations primarily limited the movement of A. fallacis into the tree from the ground cover under the tree.

Specific studies concerned with the mode of early season movement of A. fallacis into the apple tree determined the contribution made to colonization of the tree by trunk and/or air dispersal movements. Early season trunk densities of A. fallacis as measured by the bean plant - T. urticae

Figure 10. Summary of the early to mid season relationship between the relative density of *A. fallacis* in ground cover (□), in the air (⧄) and in the tree (■) (1977).


No. A. fallacis/Apple Leaf
2
1
0
No. A. fallacis/Ground/Day,
No. A. fallacis/Plate/Day
.04,1.6
.02,.8
0
DENSITY
GROUND
PLATE
LEAF
SN NO SAMPLE
GRAHAM 1977
MAY
25
SN
SN
27-3
4-10
11-16
JUNE
17-22
23-29
16-29
30-6
SN
7-13
JULY
SN

techniques are presented in Figures 11 through 14. The density of A. fallacis on bean plants at heights one, or two feet were considered to be comparable to the ground cover density. Plants at three feet appeared to be a transition zone between the lower and upper trunk area, i.e. their first catch occurred slightly after that of the lower heights or the same week as the five foot height (see Figure 12, August 7; Figure 11, May 29; and Figure 14, June 23). Density of A. fallacis at five feet was considered to reflect the density in the canopy. The earliest activity of A. fallacis on the trunk was usually at the lower two heights (see Figure 12, July 10; and Figure 14, prior to July 5).

In most cases, A. fallacis appeared at the 5 foot level from one to three weeks prior to its detection (colonization) in the tree (Figures 6 through 9). The power of detection of low densities of A. fallacis by bean plant traps was considered to be greater than that of the tree leaf counting method. This may account for the difference between the date of first appearance of A. fallacis on the trunk at five feet and in the canopy.

Another factor influencing the difference when predators were detected at the five foot trunk level versus the tree canopy is related to the availability of food in each habitat. For example, food was always available on the trunk (i.e. on infested bean plants), but within the tree prey may be absent or less dense than one mite/leaf. Other

Figure 11. Relative density and proportion of A. *fallacis* on the tree trunk at various levels (1975).

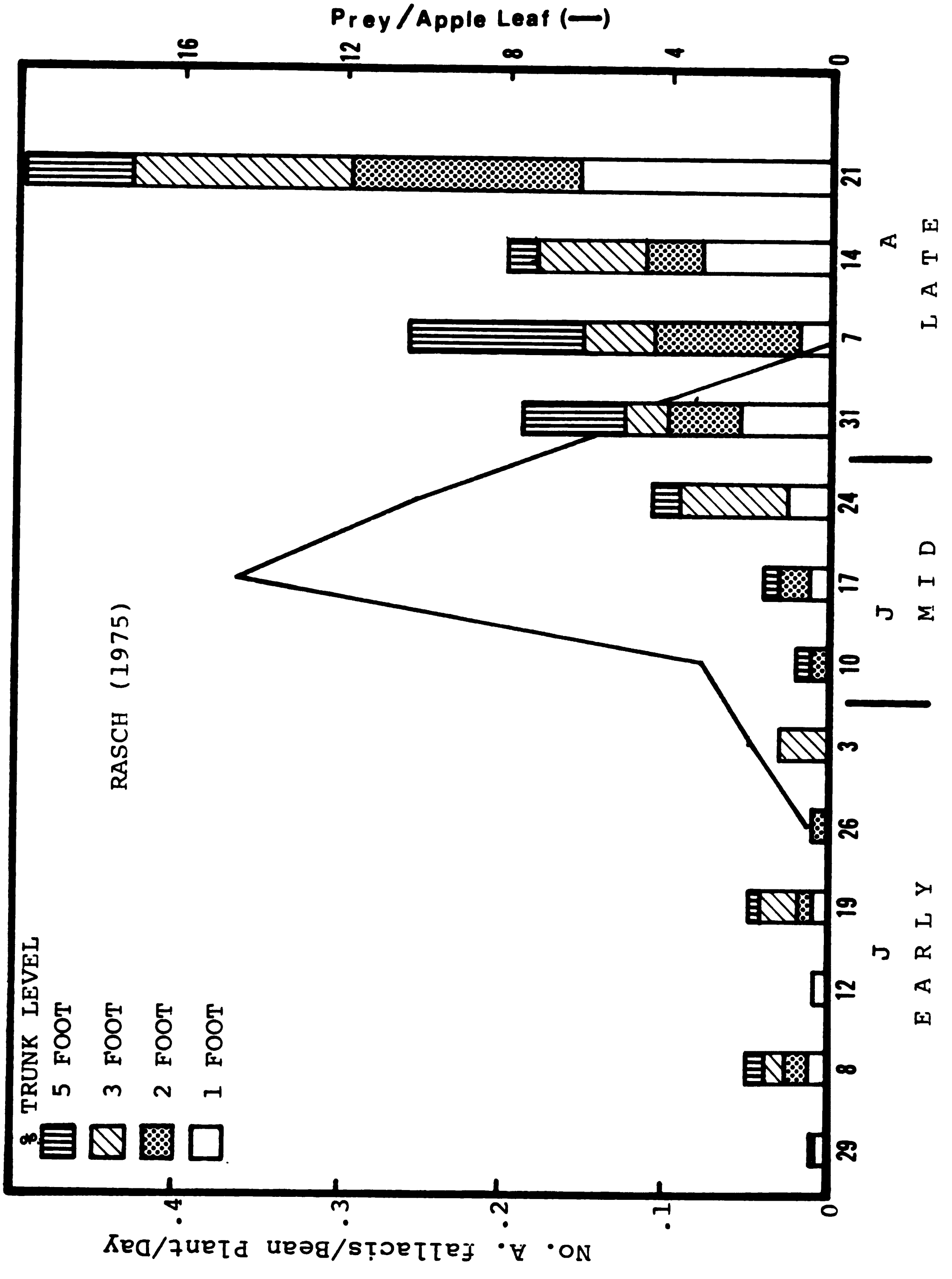

Prey/Apple Leaf (—)
0
4
8
12
16
No. A. fallacis/Bean Plant/Day
0
.1
.2
.3
.4
▤ 5 FOOT & TRUNK LEVEL
▨ 3 FOOT
▩ 2 FOOT
☐ 1 FOOT
RASCH (1975)
29
8
12
19
26
3
10
17
24
31
7
14
21
J
J
A
EARLY
MID
LATE

Figure 12. Relative density and proportion of A. *fallacis* on the tree trunk at various levels (1975).

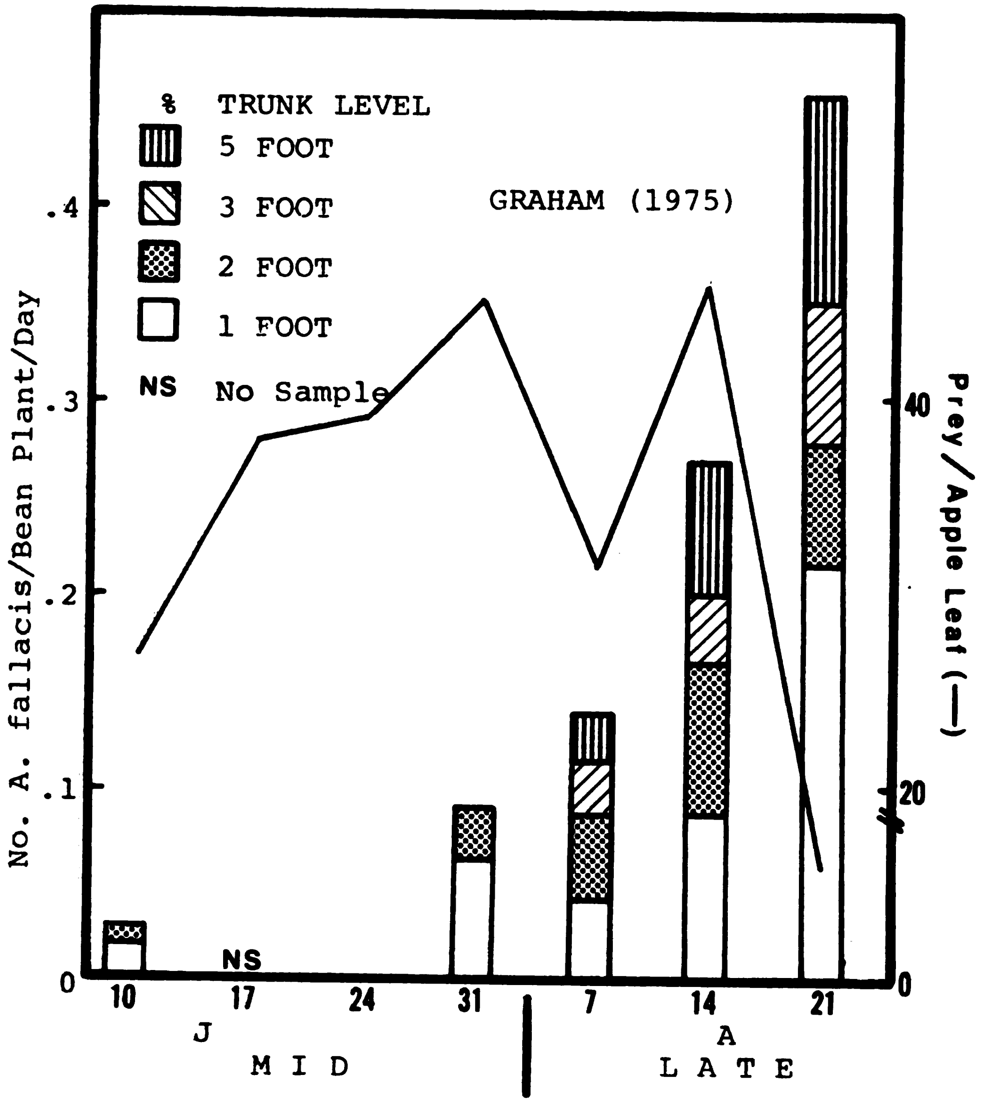

% TRUNK LEVEL
5 FOOT
3 FOOT
2 FOOT
1 FOOT
NS No Sample
GRAHAM (1975)
No. A. fallacis/Bean Plant/Day
.4
.3
.2
.1
0
Prey/Apple Leaf (—)
40
20
0
NS
10
17
24
31
7
14
21
J
A
M I D
L A T E

Figure 13. Relative density and proportion of _A_. _fallacis_ on the tree trunk at various levels (1976).

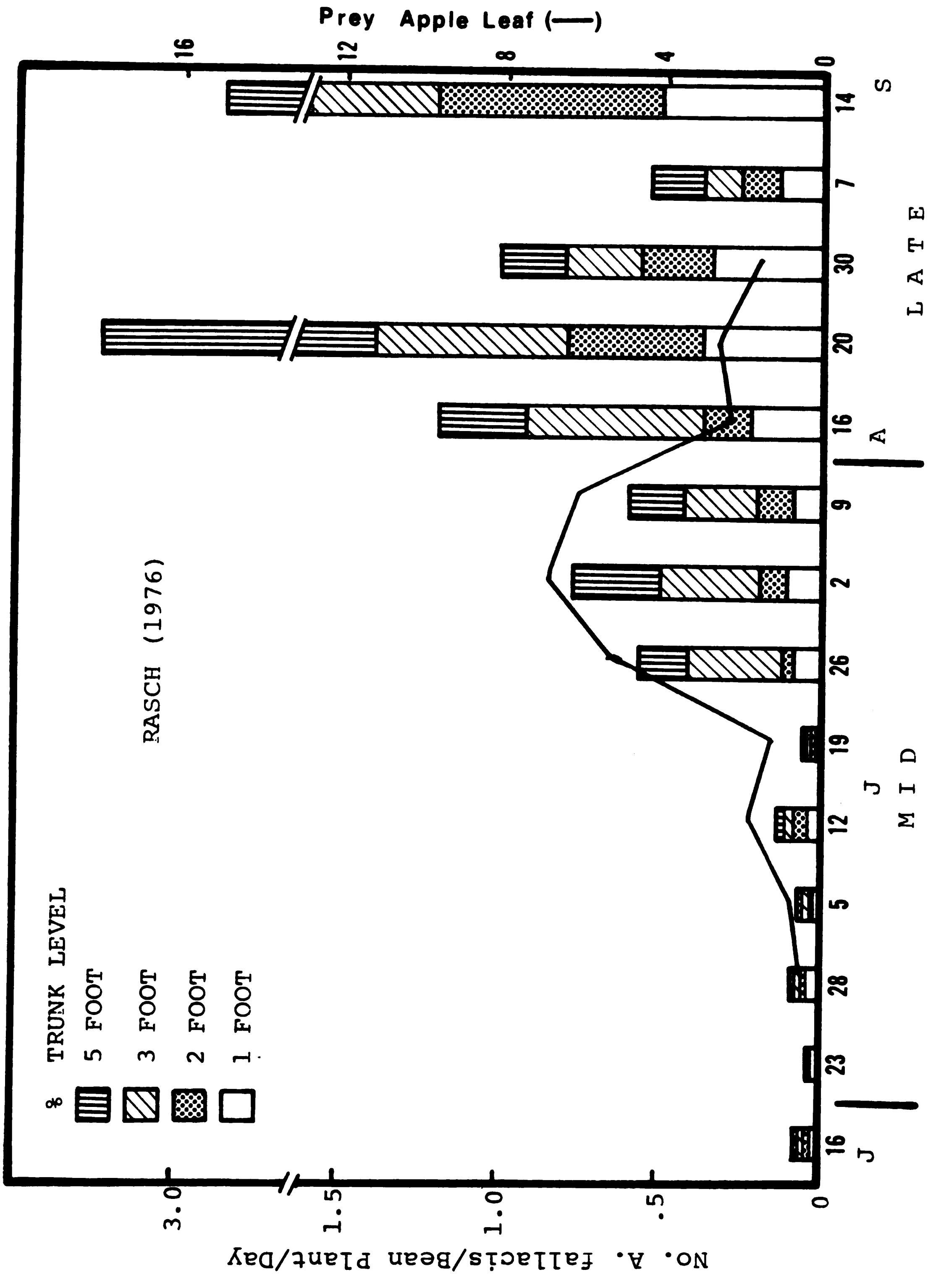
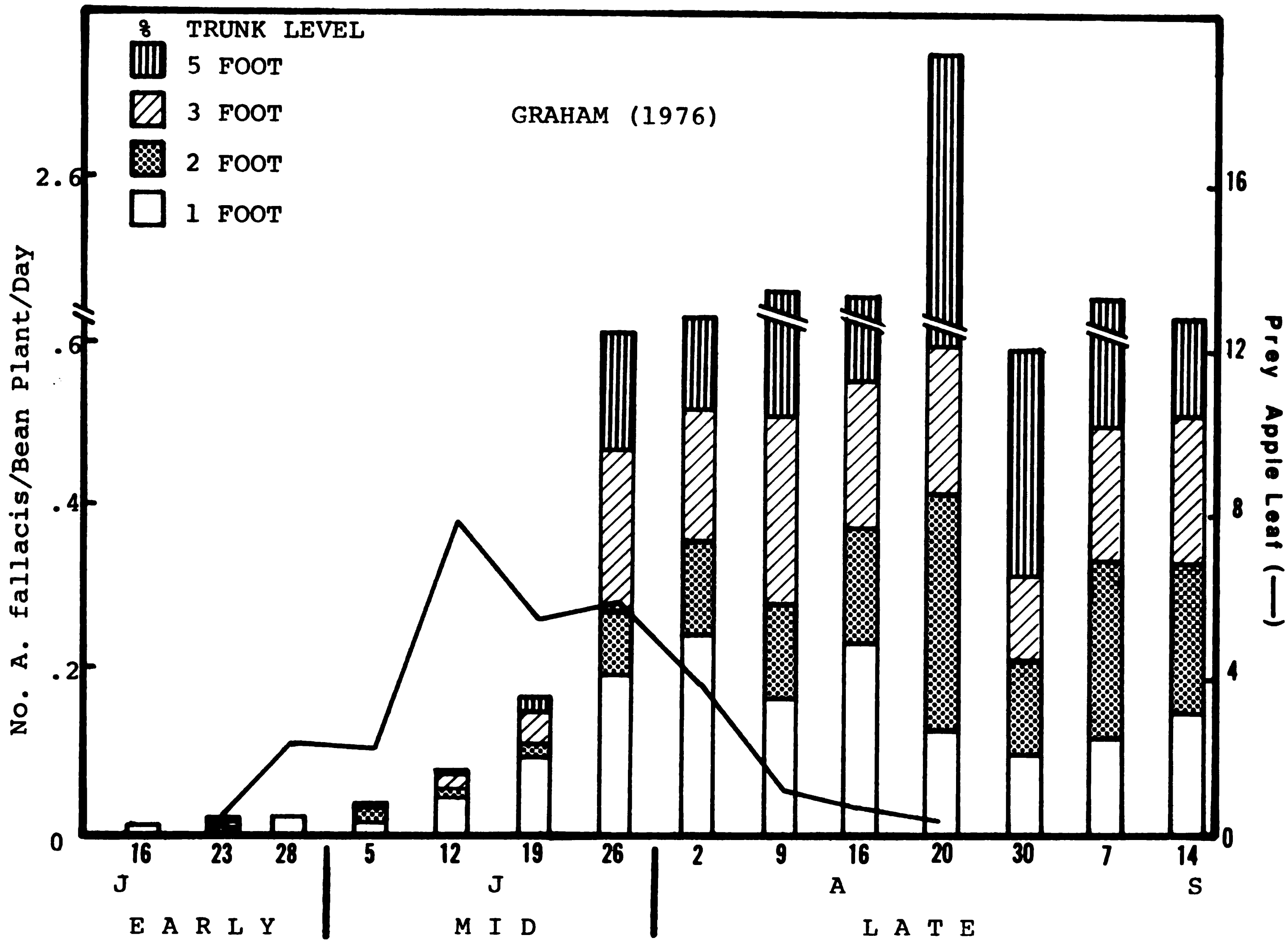

Prey Apple Leaf (—)
16
12
8
4
0
% TRUNK LEVEL
5 FOOT
3 FOOT
2 FOOT
1 FOOT
RASCH (1976)
No. A. fallacis/Bean Plant/Day
0
.5
1.0
1.5
3.0
16
23
28
5
12
19
26
2
9
16
20
30
7
14
J
J
A
S
MID
LATE

Figure 14. Relative density and proportion of *A. fallacis* on the tree trunk at various levels (1976).


% TRUNK LEVEL
5 FOOT
3 FOOT
2 FOOT
1 FOOT
GRAHAM (1976)
No. A. fallacis/Bean Plant/Day
2.6
.6
.4
.2
0
Prey Apple Leaf (—)
16
12
8
4
0
16
23
28
5
12
19
26
2
9
16
20
30
7
14
J
J
A
S
E A R L Y
M I D
L A T E

studies (unpublished, Croft and McGroarty 1977) have shown that prey densities below one mite/leaf are usually insufficient to allow _A_. _fallacis_ to persist and increase numerically within apple trees. A similar effect was noted by comparing dates of detection of _A_. _fallacis_ at the five foot trunk height and within the tree. Generally, _A_. _fallacis_ was present at the five foot trunk level from five days to a month prior to their detection in the tree. The only difference noted was that when more than one prey/apple leaf were present in the tree the agreement between the date of first appearance of _A_. _fallacis_ on the trunk and within the tree was very close. Conversely, they were very far apart in time if prey were less than one/leaf in the tree when predators were first detected at the five foot level on the trunk.

Table 4 gives the results of the restriction experiment to assess the relative contribution that trunk and/or air dispersal makes to tree colonization. In the four treatments, it was found that the major mode of dispersal into the tree was via the trunk (treatment 2) which was equivalent to counts from the unrestricted movement (treatment 1). Total exclusion of mites was not obtained even in treatment 4. This indicated the effectiveness of _A_. _fallacis_ dispersal into the tree. Air movement (treatment 3) was equivalent to the counts from maximum restriction (treatment 4). This implied that air dispersal plays no significant role in early season colonization of the apple tree in

TABLE 4: Summary of the restricted mite movement experiment giving the absolute density of A. fallacis found in each treatment.

TREATMENT	7/04/78	7/11/78
1 (all)	.52 a[1]	.72 a b[2]
2 (trunk)	.55 a	.79 a
3 (air)	.21 b	.53 a b
4(none)	.15 b	.42 b

[1] Expressed as log (mites/apple leaf + 1).

[2] Data followed by the same letter(s) were not significantly different at .05 level.

comparison to the trunk movement although on July 11, there were slightly more mites in treatment (3) than (4)(Table 4). The fact that A. fallacis principally moves up the trunk agrees with similar reports by Newell (1941) and Nelson and Jorgensen (1968) for certain tetranychids.

The early season dispersal movements of A. fallacis were measured in relation to three variables: 1) prey density in the tree; 2) cumulative DD_{54}; and 3) density of A. fallacis in the ground cover. Multiple regression between the number of A. fallacis/apple leaf and the three variables mentioned above, showed that prey density in the tree explained @63% of the variation in the density of A. fallacis/apple leaf when it was first detected in the tree (Table 5). Cumulative DD_{54} and predators in the ground contributed little more to the full regression model.

An attempt was made to predict the first detectable appearance of A. fallacis in the tree given ample prey for colonization. An exponential curve was fit to the data representing the comparison between cumulative DD_{54} and the number of A. fallacis/apple leaf (i.e. $\leq$ 1.5 mites/apple leaf) (Figure 15). Since the early growth phase of A. fallacis is best represented by exponential growth. The cumulative DD_{54} value of 469 was derived as an estimate when 0.04 A. fallacis/apple leaf could be detected (i.e. the lowest detectable density of A. fallacis with a 100 leaf sample/orchard). Table 6 gives the earliest, average, and latest dates for which A. fallacis would be expected to appear in

TABLE 5: ANOVA for the multiple regression model containing three variables.

Source of Variation	d.f.	Estimated Regression Coefficient	F	r
Prey	1	.0022	7.98**	.63
Cumul. DD_{54}	2	-.000027	0.21	-.02
_A_._f_. Ground	3	-.012	0.08	-.26
FULL MODEL		.034 (constant)	3.24*	.64

* significant at .05 level

** significant at .01 level

TABLE 6: The date that *A. fallacis* will first appear in apple trees based on a 469 degree days (base = 54) approximation and sampling error[a] at ten apple growing stations in Michigan.

	DATE		
STATION	EARLIEST	AVERAGE	LATEST
East Lansing	June 17	June 22	June 29
Eau Claire	June 10	June 14	June 21
Grand Haven	June 19	June 25	June 30
Greenville	June 14	June 18	June 23
Hart	June 20	June 25	July 1
Holland	June 12	June 17	June 23
Kalamazoo	June 8	June 13	June 18
Ludington	June 27	July 3	July 8
Manistee	June 25	July 1	July 7
Traverse City	June 25	June 30	July 5

[a] Based on a 100 leaf/tree sampling method; 10 trees and 10 leaves/tree.

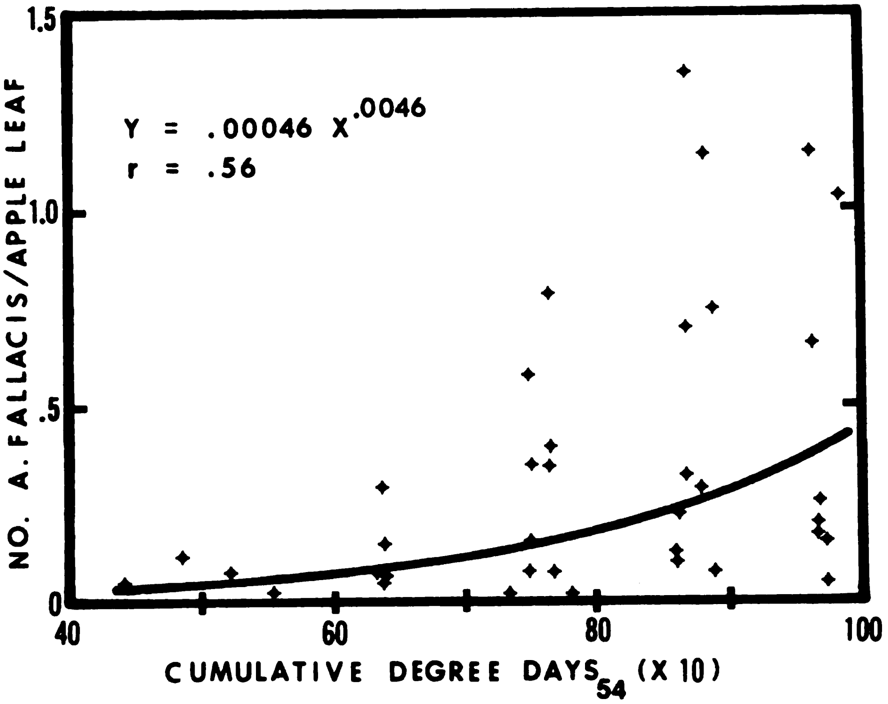


Figure 15. Comparison of cumulative DD (base = 54) and the density of A. *fallacis*/apple leaf immediately after it colonizes the tree.

ten commercial apple growing stations in Michigan. The range of dates for each station includes the variability expected due to both weather variation and sampling error. Such information would be helpful to growers and mite control personnel in estimating when A. fallacis would appear in the trees if prey are present. It also would enable them to minimize the use of pesticides deleterious to A. fallacis.

Data taken on the first appearance of A. fallacis in apple trees in Michigan based on population growth counts over a five to ten year period by Croft and McGroarty (1977) indicated that this predator is never found in appreciable numbers until early June or thereafter. Tree colonization by A. fallacis is in marked contrast to most other phytoseiid mites occurring in North America which usually overwinter on the tree and are active often before bloom (T. occidentalis, Hoyt 1969). With A. fallacis, attempts at ground cover management, modifying the climatic environment or manipulating prey levels in either the ground cover or tree have generally had little effect on the timing of the first appearance of A. fallacis in the tree (Croft and McGroarty 1977).

Relative to the means of dispersal from the ground into the tree in early season, ambulatory movement via the trunk, hanging branches or up weeds contacting the tree are probably the major route into the tree. However, the possibilities for aerial dispersal could not be discounted. Trunk dispersal has long been suspected since the first predators in the trees can usually be detected on leaves in the lower tree canopy near the trunk. Also, under certain conditions, clean cultivation tests verses the presence of 100% vegetation ground cover comparisons relative to A. fallacis dispersal into trees have shown significantly earlier observations of predators in the tree when vegetation was present (Croft and McGroarty 1977). Clean cultivated plots beneath the tree canopy (still there is vegetation between the rows) still allow for colonization of trees by predators which strongly suggests that air dispersal does occur (Croft and McGroarty 1977).

In these experiments, ambulatory dispersal was implicated as the major means of entry into trees in both field sampling experiments and restriction studies. Although aerial dispersal appeared to be less important, two points in this regard should be made. First, it is believed that although horizontally placed grease plates were more effective in monitoring aerial dispersal of A. fallacis from the apple trees, they were probably relatively less effective in the early season when the source of predators primarily originates from weeds or other ground cover plants. These mites would be blown parallel to the wind (i.e. horizontal). For this reason, it is believed that the sampling procedure (i.e., horizontal plates) used may have greatly underestimated air dispersal during this period. Secondly, it should be remembered that A. fallacis has an extremely high reproductive rate (r = .279/day at 25°C, Croft unpublished data).

Small numbers of mites entering trees can, within two or three weeks, result in enormous tree populations of the magnitude commonly observed in the field. This potential for reproductive increase indicates that even minor aerial dispersal of mites may result in effectve biological control of tree feeding mites.

Remaining questions then are - what factors account for the delayed entry of A. fallacis into the apple trees in early season and can these mites be managed so as to encourage earlier colonization of the tree? (Several factors should be considered in such an evaluation): Early season control of phytophagous mites in the apple tree by A. fallacis appears to be limited for a number of reasons. First and foremost is that A. fallacis overwinters in the ground cover and pest mites overwinter in the tree. Predator-prey asynchrony has been commented on earlier. Second, the developmental threshold of A. fallacis is relatively high in comparison to its prey and other phytoseiid mite predators (Table 7). A high developmental threshold results in a slower generation time for A. fallacis than for P. ulmi early in the season, even though it exceeds P. ulmi in development at temperatures above 21°C during mid season (Lee 1972, Smith et al. 1963). Cool temperatures result in delayed completion of the first generation of A. fallacis (from overwintering females) until May 20th at the earliest (1977), June 10th on the average (1976) and June 18th at the latest (1974) (Figure 16). Delayed development minimizes the

TABLE 7: Comparison of the developmental thresholds of certain phytophagous mites and their phytoseiid predators all from the continental United States.

Species	Developmental Threshold (°C)	Reference
Panonychus ulmi	9.3	Mori (1957)
Typhlodromus pyri	10.6	McMurtry (1970)[1]
T. occidentalis	9.2	Tanigoshi(1975)[1]
A. fallacis	12.2	Lee (1972)

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[1] Calculated from their data using Uvarov's (1931) developmental zero equation and only using temperatures resulting in >2% development/day.

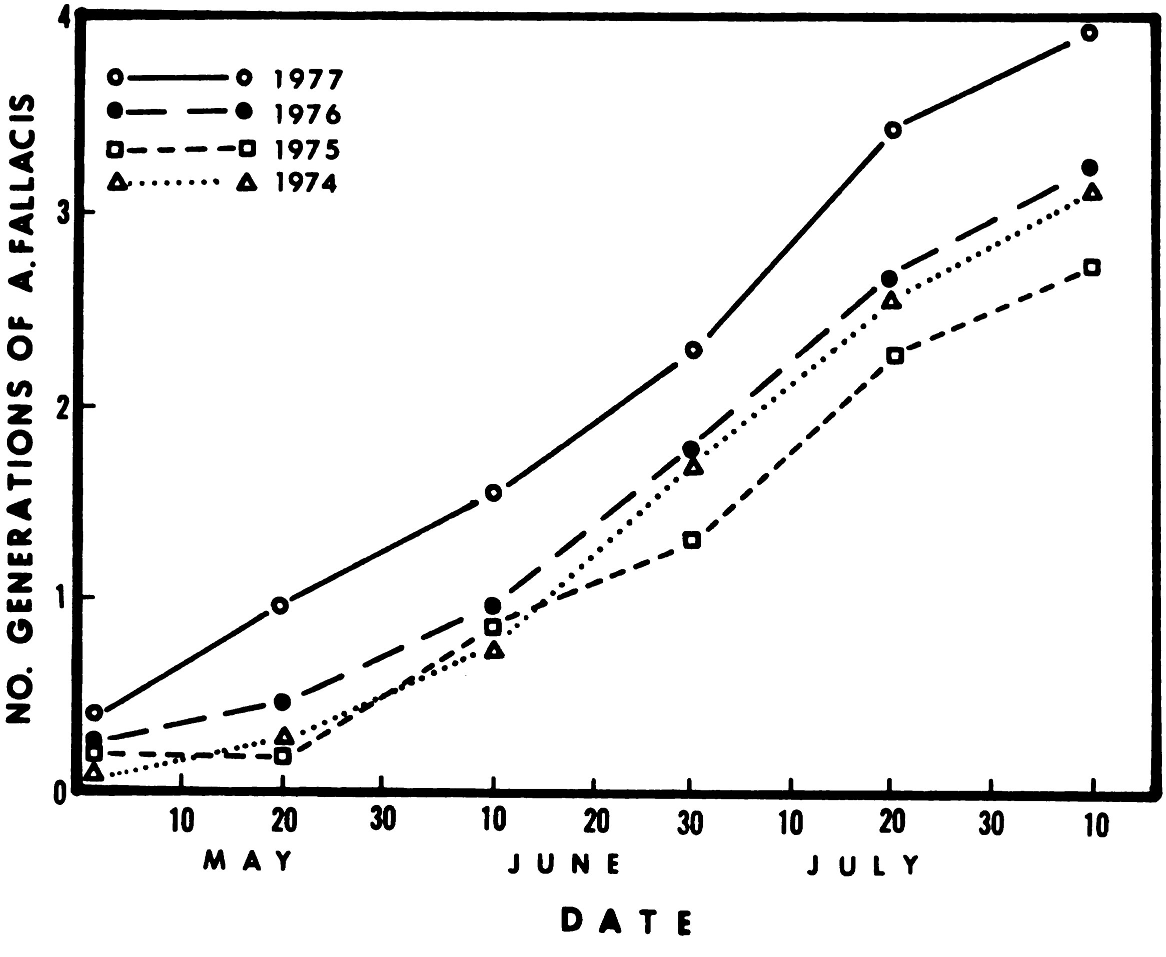


Figure 16. A computer model run of *A. fallacis* development (generations) in the ground cover of 4 different years (based on data given in Dover et al. 1978).

initial reproductive growth by *A. fallacis* in the ground cover.

A third factor may be the existence of a reproductive diapause in *A. fallacis*. According to Rock et al. (1971), *A. fallacis* terminated diapause spontaneously after 56 days at 15.6°C and a photophase of 11.25 hours (Table 8). Rock et.al. (1971) found that females of *A. fallacis*, transferred from a photophase of 9 hours to 14 hours on the 40th day, commenced oviposition 19 days later at 15.6°C. Lee (1972) showed that transferring diapausing females from a photophase of 8 hours to 16 hours at 20°C resulted in oviposition in 6 days. Lee (1972) stated that *A. fallacis* may be composed of individuals with different diapause potentials.

Photophase in the northern hemisphere exceeds 12 hours from March 21st to September 23rd. Thus, reproductive diapause in *A. fallacis* can not be induced by temperature during this period and early season temperatures terminate the reproductive diapause. Figure 17 is a plot of the average monthly temperatures for Grand Rapids, Michigan. Note that not until April does the man maximum temperature exceed 15°C. Given a mean daily temperature of 15°C from May 1st on, reproductive diapause could be terminated as early as May 20th (Lee 1972). In this study immatures were noted in the field my mid May (also by Putman, 1959).

An atmospheric humidity differential between the ground cover and the tree canopy in early season was initially hypothesized to be a factor limiting the initial dispersal

TABLE 8: The number of days required to terminate the reproductive diapause of *A. fallacis* exposed to different photophase and temperature regimes (Rock et al. 1971).

Light : Dark (Hours)	Temperature (°C)	Days To Terminate
9 : 15	15.6	70
11.25 : 12.75	15.6	56
9 : 15	21.7	36
9 : 15	26.7	26

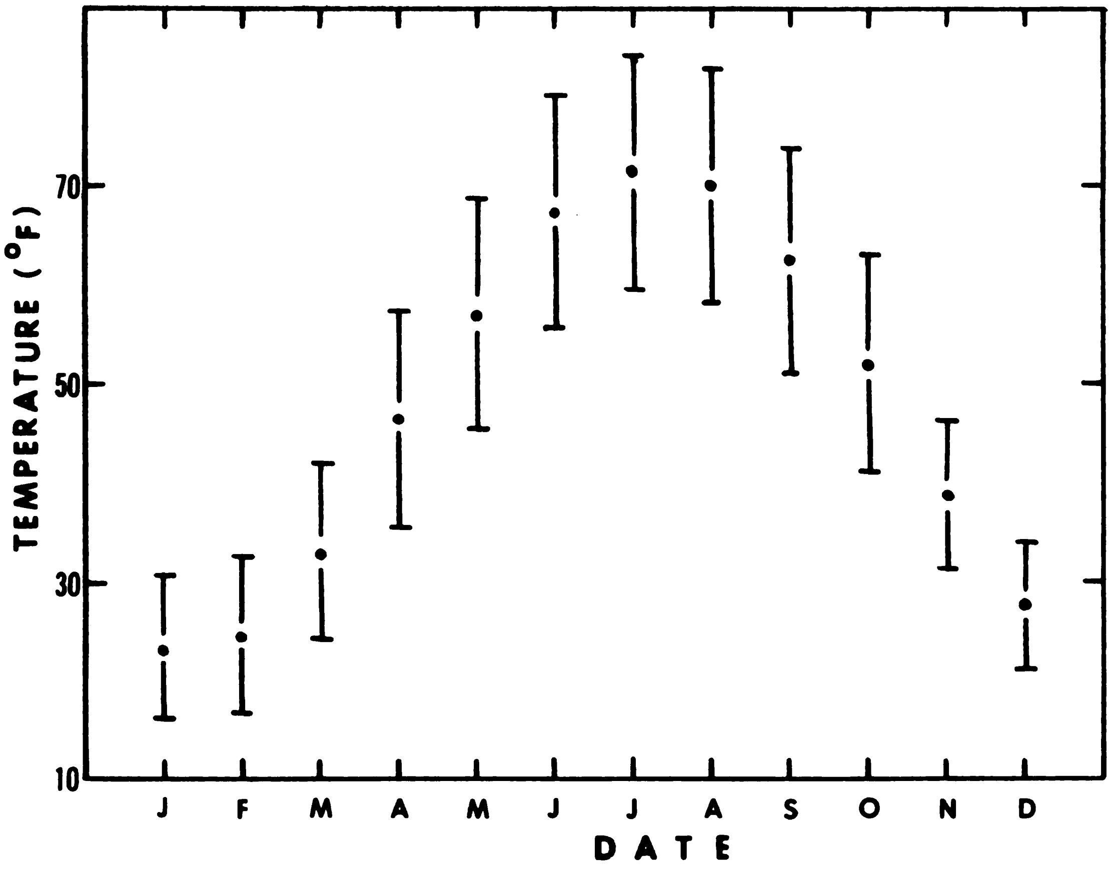


Figure 17. Plot of the 30 year average monthly temperatures (°F) and their respective average maximum and minimum for Grand Rapids, Mich. (NOAA,1973).

movements of A. fallacis into the tree. Figure 18A shows that the relative humidity of the ground habitat remained slightly higher all season than that in the tree canopy. However, there was not an appreciable difference between these habitats in early season. In addition, cumulative DD_{54} in the ground cover were only one to five days behind those of the tree (Figure 18B). Such temperature differential of one to five days would slightly favor reproduction of the pest mites in the tree over that of A. fallacis in the ground cover and also lessen the early season ambulatory searching activities of the predator in the ground cover. In general, it would appear that cultural practices that increased the ground cover or even the tree canopy temperatures (i.e., pruning trees to increase light penetration to the leaves and ground cover) might hasten the appearance of A. fallacis and improve the possibility for biological control of P. ulmi.

Mid Season Dynamics. Once A. fallacis has colonized a tree and sufficient prey were present (i.e. 1/leaf), there was exchange of predators between ground cover, tree trunk and the tree canopy populations. This system was influenced by the high rate of predator reproduction in the tree, while in the ground cover and trunk regions, predators were only maintaining a replacement reproductive rate. Concerning these dynamic changes, the present study supports the hypotheses of Croft and McGroarty (1977) relative to predator population in the various orchard ecosystem components (see

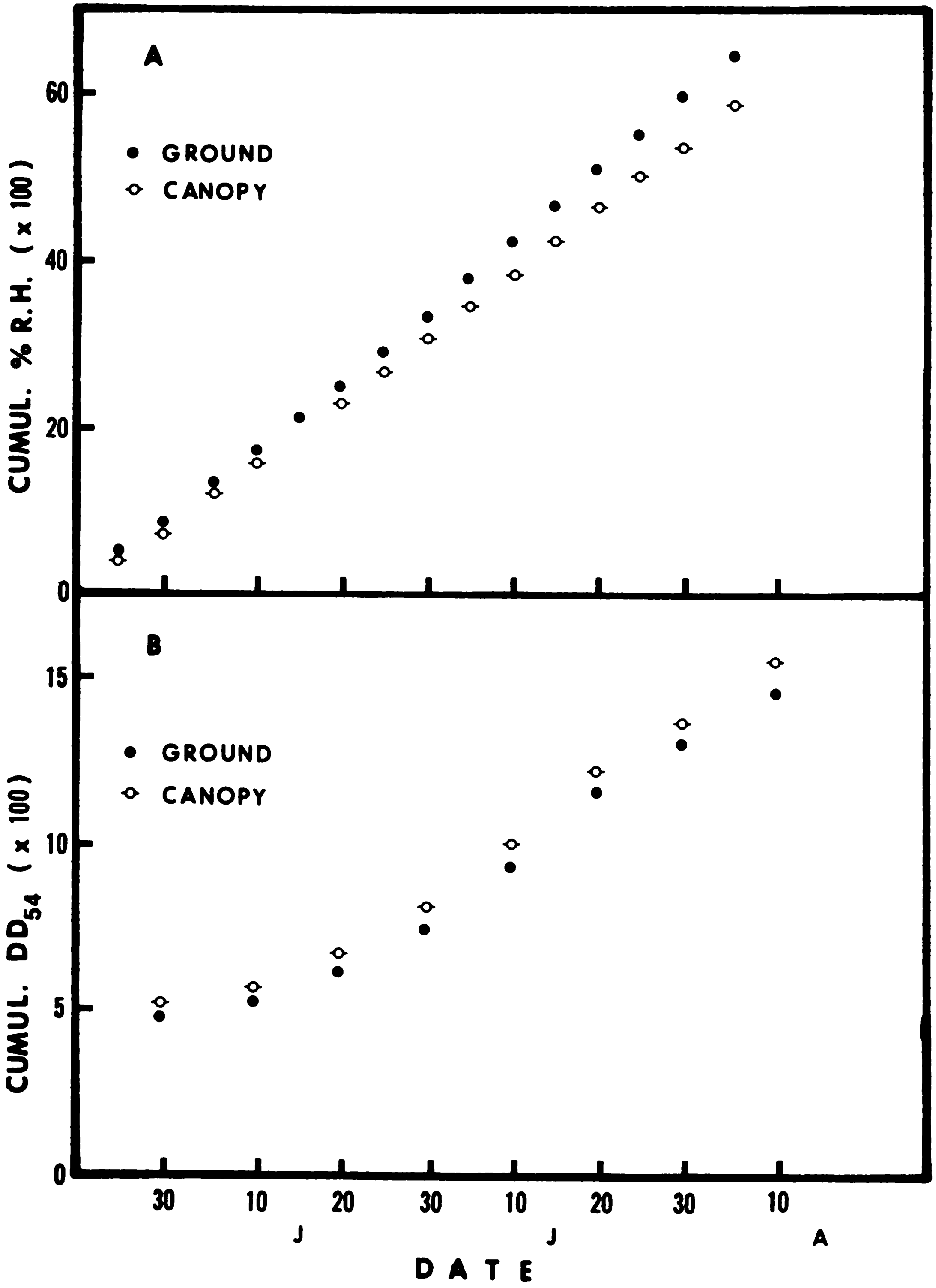


Figure 18. The seasonal cumulative area under the % R.H. curve (A), and the cumulative DD_{54} at ground level (•) and in the tree canopy (-o-) (Graham orchard, 1977).

the quote on page 5 concerning the time period d through e from Figure 1).

Data presented in Figures 6 through 14 show a gradual increase in the density of A. fallacis in the ground cover, on the plates, and on the tree trunk during mid season. These increases were due to reproduction of predators within the tree and what is believed to be a passive air dispersal of immature predators and possibly a more direct movement by preovipositing females (Johnson and Croft 1976). Plots of density and percent stage distribution counts for the tree and grease plate samples during this period are given in Figures 19 through 22. Reproductive activity in the tree was reflected by the high percentage of the population of A. fallacis that was immature forms (see July 19 to August 2 in Figure 19, July 26 to August 20 in Figure 20, July 19 to July 26 in Figure 21, and prior to July 26 in Figure 22). High percentages of immatures were noted on apple leaves when the prey density for the previous week exceeded two/leaf, whereas the combined proportion of adult females and males rarely exceeded 50% (Tables 9-12). The seasonal average male : female sex ratio per apple leaf was 0.4 and ranged from 0.2 to 0.7 and agreed with that reported previously by Lee (1972).

The density and percent stage distribution in the air under the tree canopy was closely related to the previous week's densities of A. fallacis in the tree (Figure 6 through 9). Prior to August 9 in Figures 19 through 22, the

Figure 19. Seasonal summary of the density and percent stage distribution of A. fallacis/apple leaf and /grease plate and the corresponding prey/apple leaf (1976).

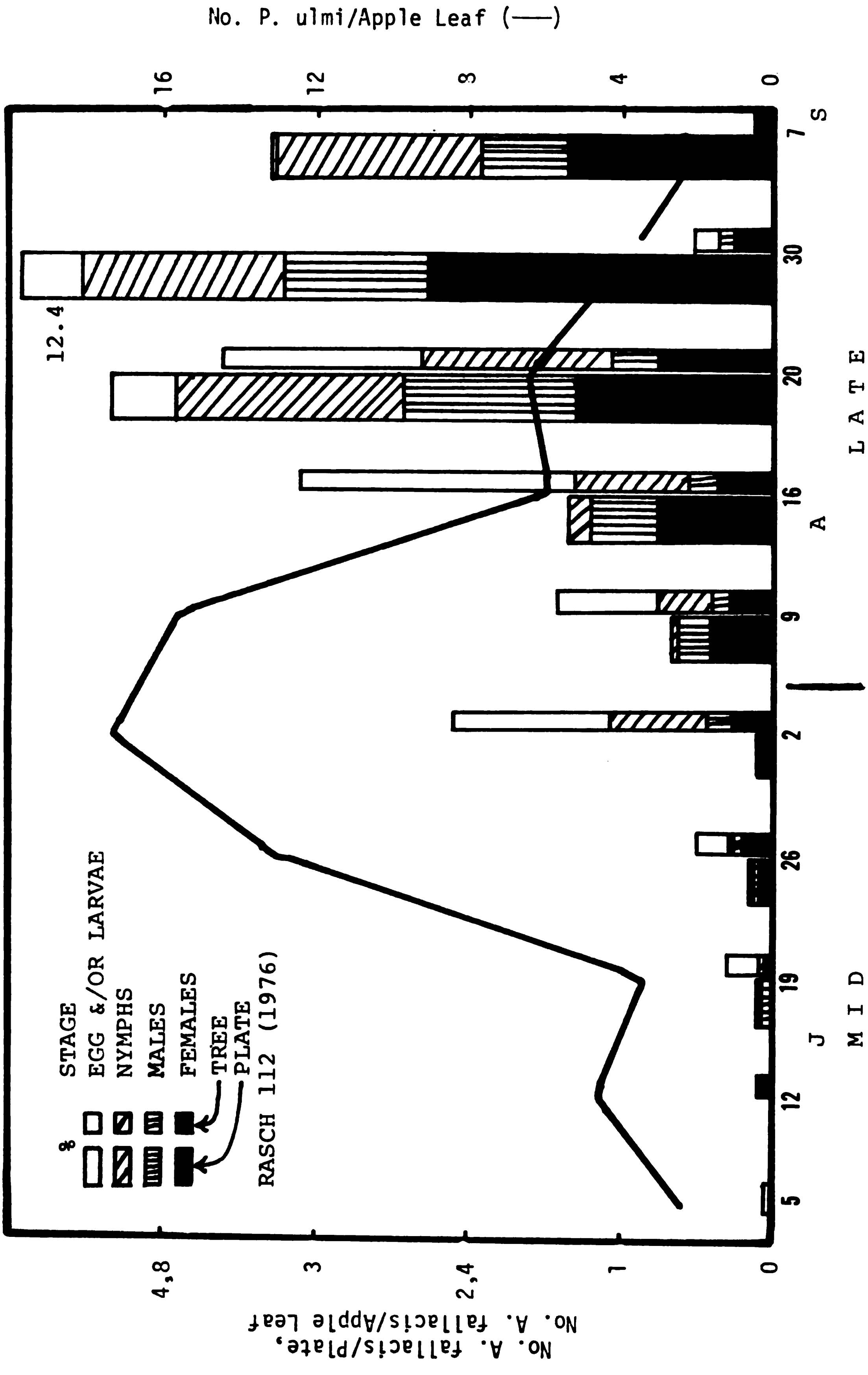

No. P. ulmi/Apple Leaf (——)
16
12
8
4
0
No. A. fallacis/Plate,
No. A. fallacis/Apple Leaf
4.8
3
2.4
1
0
%
STAGE
EGG &/OR LARVAE
NYMPHS
MALES
FEMALES
TREE
PLATE
RASCH 112 (1976)
12.4
5
12
19
26
2
9
16
20
20
30
7
J
A
S
MID
LATE

Figure 20. Seasonal summary of the density and percent stage distribution of A. *fallacis*/apple leaf and /grease plate and the corresponding prey/ apple leaf (1976).

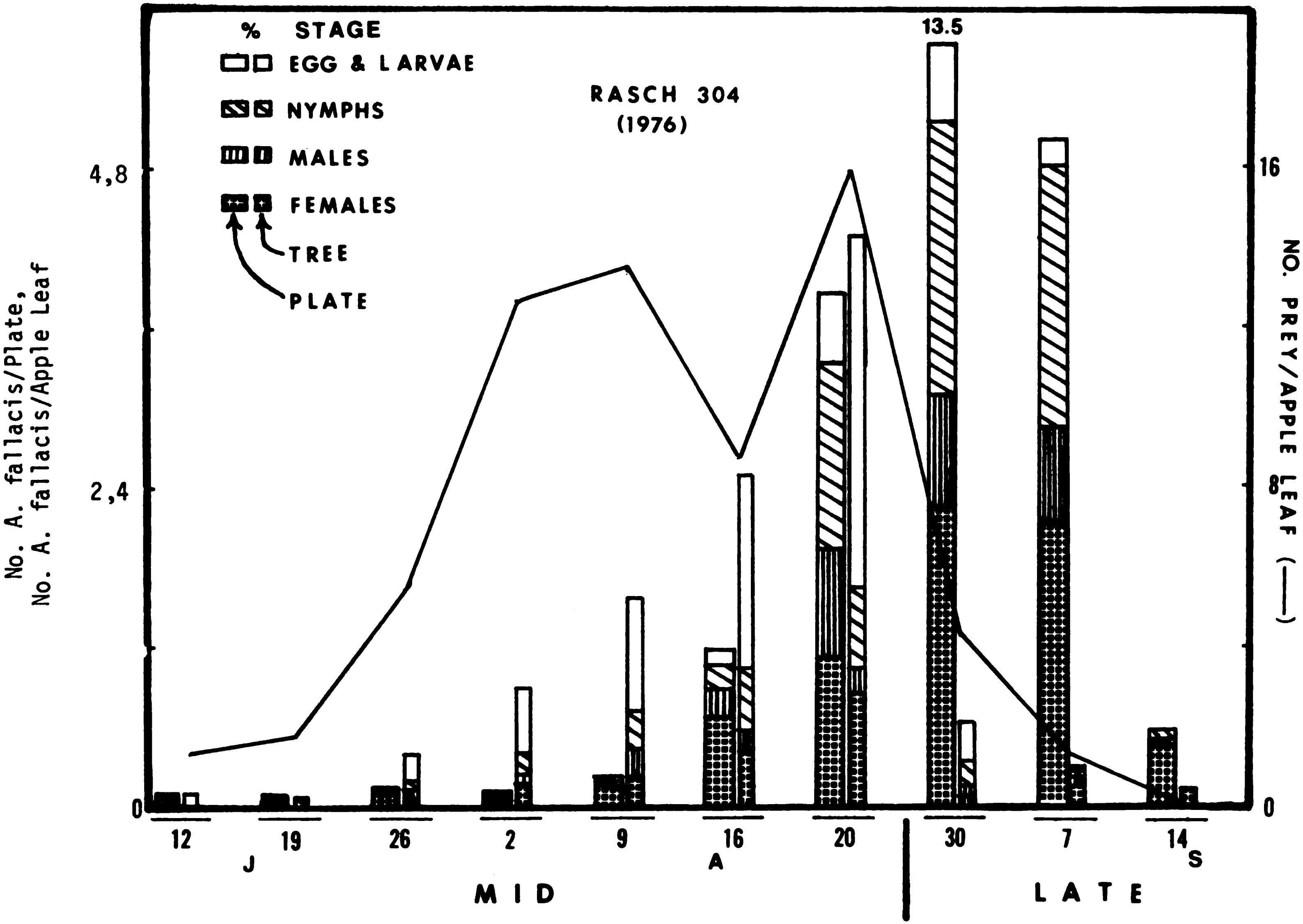

% STAGE
EGG & LARVAE
NYMPHS
MALES
FEMALES
TREE
PLATE
RASCH 304
(1976)
13.5
4,8
2,4
0
No. A. fallacis/Plate,
No. A. fallacis/Apple Leaf
16
8
0
NO. PREY/APPLE LEAF (——)
12
J
19
26
2
9
16
A
20
30
7
14
S
MID
LATE

Figure 21. Seasonal summary of the density and percent stage distribution of *A. fallacis*/apple leaf and /grease plate and the corresponding prey/ apple leaf (1976).

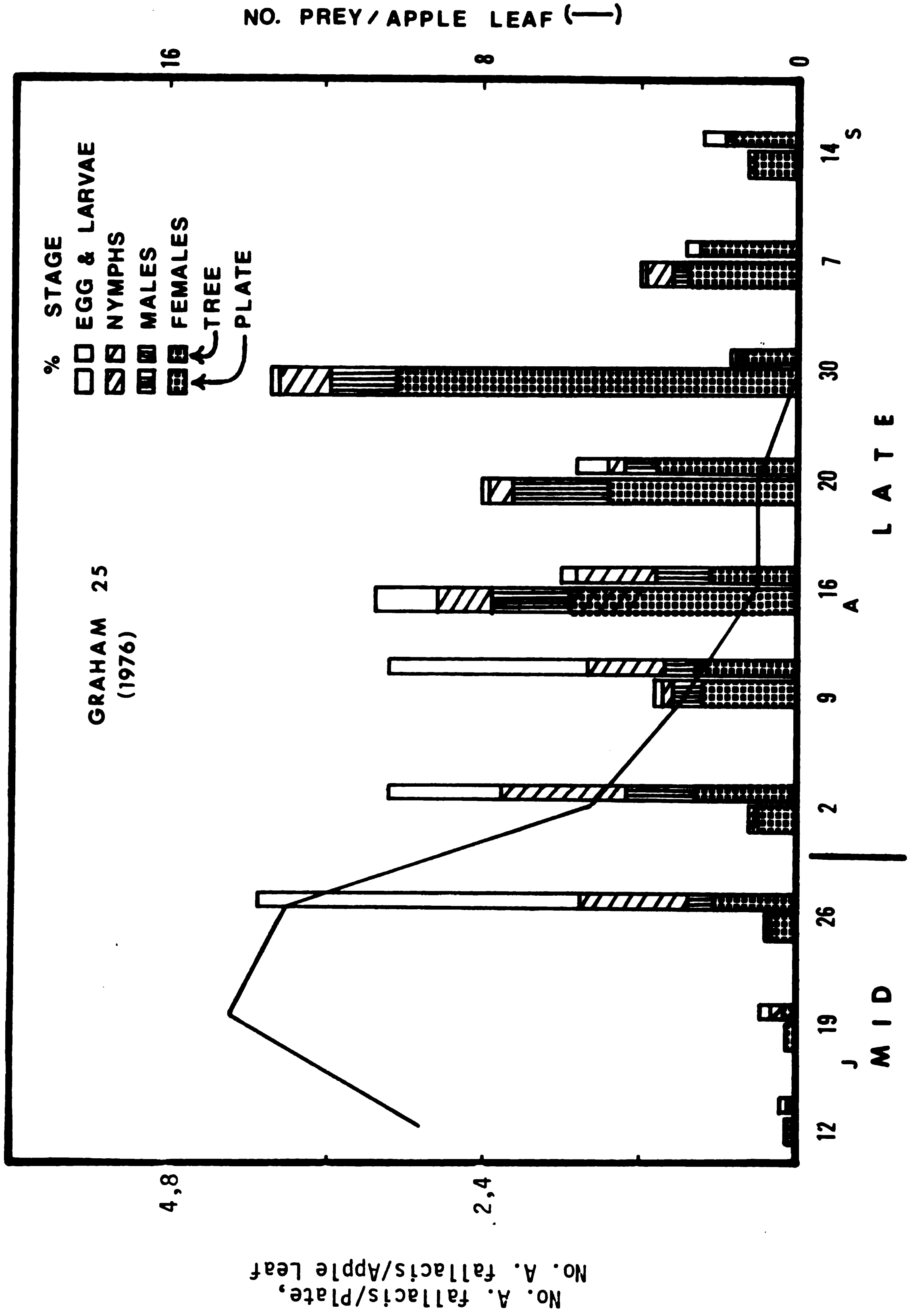

NO. PREY / APPLE LEAF (—)
16
8
0
% STAGE
EGG & LARVAE
NYMPHS
MALES
FEMALES
TREE
PLATE
GRAHAM 25
(1976)
12
J
19
MID
26
2
9
16
A
20
LATE
30
7
14
S
4,8
2,4
No. A. fallacis/Plate,
No. A. fallacis/Apple Leaf

Figure 22. Seasonal summary of the density and percent stage distribution of A. *fallacis*/apple leaf and /grease plate and the corresponding prey/ apple leaf (1976).

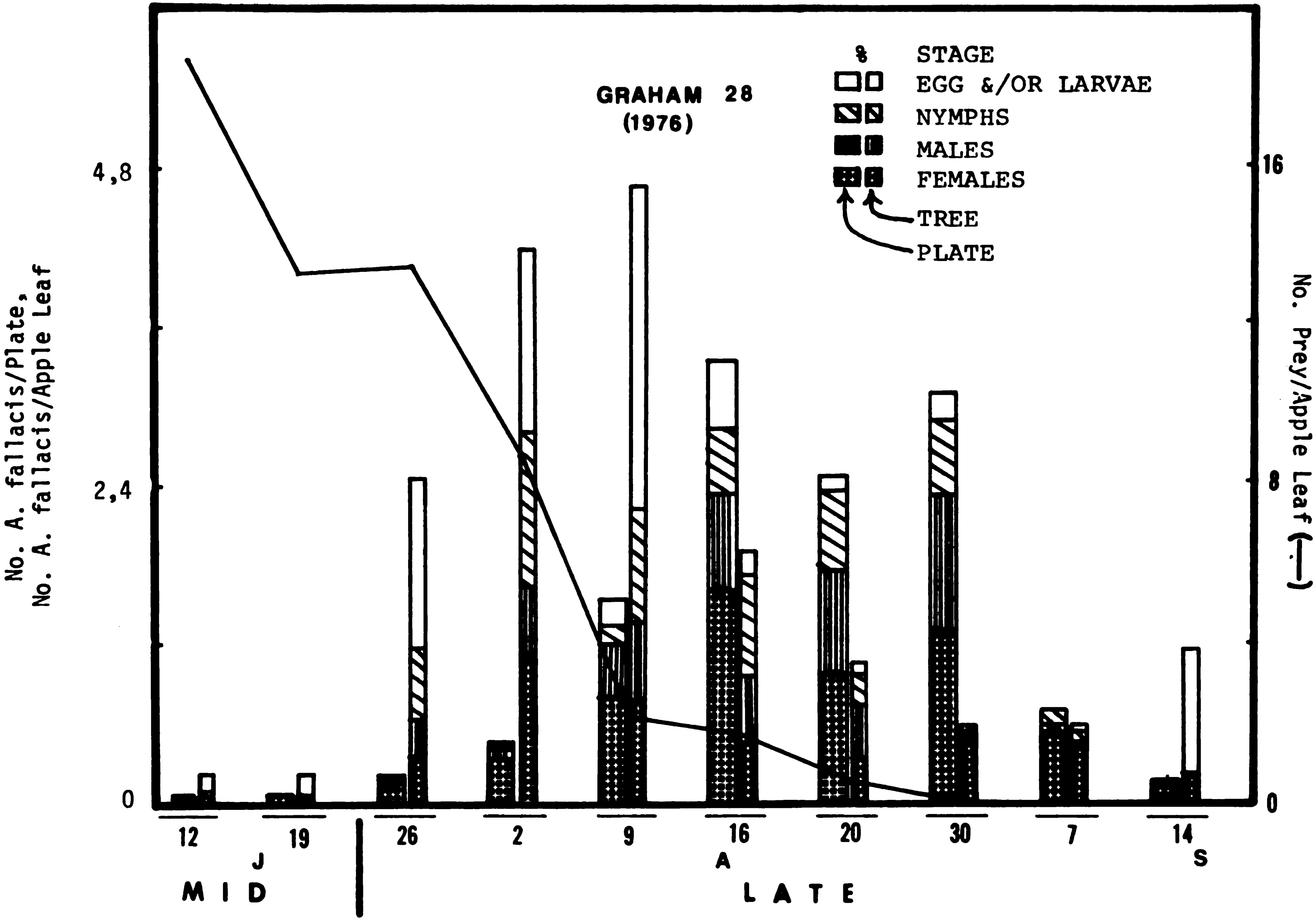

GRAHAM 28
(1976)
% STAGE
EGG &/OR LARVAE
NYMPHS
MALES
FEMALES
TREE
PLATE
No. A. fallacis/Plate,
No. A. fallacis/Apple Leaf
4,8
2,4
0
No. Prey/Apple Leaf (—)
16
8
0
12
19
26
2
9
16
20
30
7
14
J
A
S
MID
LATE

TABLE 9: Seasonal summary of the density and percent stage distribution of _A_. _fallacis_/ apple leaf (tree 112, 1976).

STAGE	DATE									
	7/12	7/19	7/26	8/02	8/09	8/16	8/20	8/30	9/07	9/14
E[a]	50.0[b]	36.4	64.0[c]	38.5	34.0	38.9	43.1	20.0	0	0
L	50.0	9.1	8.0	3.9	15.1	8.3	15.0	16.1	0	0
P-D	0	27.3	20.0	11.5	31.1	25.0	24.2	34.4	32.0	0
o	0	9.1	0	7.7	7.5	8.3	6.5	9.4	20.0	0
o	0	18.2	8.0	38.5	12.3	19.4	11.1	20.0	48.0	100
$\bar{X}$[d]	.02	.1	.3	.5	2.1	1.4	3.1	3.6	.5	.1
PREY[e]	2.2	4.6	3.4	13.0	17.3	15.6	5.8	6.4	3.7	1.5

[a] E = egg, L = larvae, P-D = nymphs, o = adult male, ^{o} = female

[b] 100 leaf sample giving percentage of each stage in population

[c] 50 leaf sample after 7/19

[d] mean number of _A_. _fallacis_/apple leaf

[e] mean number of _P_. _ulmi_ equivalents/apple leaf

TABLE 10: Seasonal summary of the density and percent stage distribution of *A. fallacis*/apple leaf (tree 304, 1976).

STAGE	DATE 7/12	 7/19	 7/26	 8/02	 8/09	 8/16	 8/20	 8/30	 9/07	 9/14
E[a]	100	0	35.7	37.8	47.0	49.5	43.5	33.3	0	0
L	0	0	21.4	13.5	9.1	8.4	17.0	16.7	33.3	0
P-D	0	100	14.3	18.9	18.2	18.7	14.8	29.2	0	0
o	0	0	21.4	8.1	13.6	5.6	4.9	8.3	20.2	0
o	0	0	7.1	21.6	12.1	17.8	19.8	12.5	53.3	100
$\bar{X}$ *A.f.*[d]	.01	.01	.3	.7	1.3	2.1	3.6	.5	.2	.1
$\bar{X}$ *P.u.*[e]	1.2	1.7	5.4	12.6	13.1	8.7	15.8	4.4	1.3	1.1

[a-e] Same as in Table 9, above.

TABLE 11: Seasonal summary of the density and percent stage distribution of _A_. _fallacis_/apple leaf (tree 25, 1976).

STAGE	DATE 7/12[b]	7/19	7/26[c]	8/02	8/09	8/16	8/20	8/30	9/07	9/14
E[a]	33.3	19.1	44.3	22.3	43.1	4.4	7.3	0	7.6	21.0
L	11.1	14.3	16.1	5.4	5.4	1.1	7.3	7.1	4.6	4.8
P-D	22.2	38.1	19.5	30.8	19.2	44.0	7.3	0	0	0
o	0	0	5.2	17.7	7.7	19.8	14.5	14.3	0	4.8
o	33.3	28.6	14.9	23.9	24.6	30.8	63.8	78.6	87.9	69.4
$\bar{X}$ _A_._f_.[d]	.1	.2	3.5	2.6	2.6	1.8	1.4	.3	.7	.6
$\bar{X}$ _P_._u_.[e]	9.7	14.5	13.0	5.2	2.8	.9	.9	0	0	0

[a-e] Same as in Table 9, above.

TABLE 12: Seasonal summary of the density and percent stage distribution of A. fallacis/ apple leaf (tree 28, 1976).

STAGE	DATE									
	7/12[b]	7/19	7/26[c]	8/02	8/09	8/16	8/20	8/30	9/07	9/14
E[a]	43.5	55.6	37.1	22.0	43.8	6.1	6.5	0	6.5	55.0
L	13.0	22.2	14.3	10.2	7.2	3.7	0	0	0	10.0
P-D	13.0	16.7	22.9	28.3	19.6	40.2	23.9	8.0	10.9	0
o	0	0	10.3	13.0	12.9	25.6	34.8	4.0	0	0
o	30.4	5.6	15.2	26.6	16.5	24.4	34.8	88.0	82.6	35.0
$\bar{X}$ A.f.[d]	.2	.2	2.1	3.5	3.9	1.6	.9	.5	.5	1.0
$\bar{X}$ P.u.[e]	18.7	13.0	13.5	8.7	2.2	1.7	.5	0	0	0

[a-e] same as in Table 9, above.

TABLE 13: Seasonal summary of the density and percent stage distribution of A. fallacis/ grease plate (tree 112, 1976).

STAGE	DATE								
	7/19	7/26	8/02	8/09	8/16	8/20	8/30	9/07	9/14
L[a]	20.0[b]	3.0	0	9.0	11.5	9.2	7.6	1.4	0
P-D	0	3.0	0	9.9	10.8	34.8	27.3	41,1	12.3
o	80.0	9.1	20.0	24.3	22.3	26.3	19.9	17.7	7.0
o	5.0	84.9	8.0	56.8	55.4	29.7	45.2	39.7	80.7
$\bar{X}$ A.f.[c]	.04	.3	.2	1.3	2.6	8.6	12.5	6.6	.7
No. of Plates	20	18	20	12	8	12	11	12	12

[a] L = larvae, P-D = nymphs, o = males, o = females

[b] Percent of population that are a given stage

[c] Mean number of <u>A</u>. <u>fallacis</u>/grease plate/day

TABLE 14: Seasonal summary of the density and percent stage distribution of *A. fallacis*/ grease plate (tree 304, 1976).

STAGE	DATE									
	7/12	7/19	7/26	8/02	8/09	9/16	9/20	9/30	9/07	9/14
L[a]	0[b]	0	0	0	3.2	8.9	12.5	10.9	3.5	0
P-D	14.3	0	4.8	27.8	12.9	14.3	32.4	33.7	40.2	9.3
o	0	16.7	28.6	11.1	25.8	18.5	25.6	14.2	13.8	8.0
o	85.7	83.3	66.6	61.1	58.1	58.3	29.5	41.2	42.5	82.7
$\bar{X}$ *A.f.*[c]	.05	.04	.2	.1	.4	2.0	6.5	13.3	8.4	.9
No. of Plates	20	20	18	20	12	12	12	12	12	12

[a-c] Same as in Table 13, above.

TABLE 15: Seasonal summary of the density and percent stage distribution of A. fallacis/ grease plate (tree 25, 1976).

STAGE	DATE									
	7/12	7/19	7/26	8/02	8/09	8/16	8/20	8/30	9/07	9/14
L[a]	0[b]	0	0	0	5.9	14.5	3.1	1.9	1.6	0
P-D	0	0	2.2	8.1	6.5	12.6	20.7	10.1	17.8	0
o	0	0	11.1	2.7	21.6	17.8	16.6	13.3	10.8	12.0
o	100	100	86.7	89.2	66.0	55.1	59.6	74.7	69.7	88.0
$\bar{X}$ A.f.[c]	.03	.01	.3	.5	1.8	5.4	4.0	6.8	1.9	.6
No. of Plates	20	20	20	20	12	12	12	12	12	12

[a-e] Same as in Table 13, above.

TABLE 16: Seasonal summary of the density and percent stage distribution of A. fallacis/ grease plate (tree 28, 1976).

STAGE					DATE					
	7/12	7/19	7/26	8/02	8/09	8/16	8/20	8/30	9/07	9/14
L[a]	0[b]	0	6.0	2.8	12.4	16.7	4.7	6.1	0	0
P-D	0	0	4.0	3.7	8.3	13.9	24.9	19.5	11.4	10.0
o	0	0	20.0	18.5	28.9	21.9	32.6	19.3	11.4	10.0
o	100	100	70.0	75.0	50.5	47.5	37.8	55.2	77.2	80.0
$\bar{X}$ *A.f.*[c]	.04	.06	.4	.8	2.6	5.6	4.0	5.1	1.1	.2
No. of Plates	20	20	20	12	12	12	12	12	12	12

[a-c] Same as in Table 13, above.

predominant stage of _A_. _fallacis_ that impacted upon the plates was the adult female (>60%) and to a much lesser extent the adult male (<20%). Rarely were the immatures captured on the plates at this time (combined total <10%) (see Tables 13 through 16 for actual percentages). This supports the belief that the adult females were actively dispersing when prey were available and that other stages did so rarely and only passively (Johnson and Croft 1976).

The density of _A_. _fallacis_ on the trunk and in the ground cover were shown to increase similarly in Figures 6 through 9. Their numbers in the ground and on the trunk were increasing at a rate that appeared to be greater than that of those in the tree. The increased numbers on the trunk may represent the mite moving into the tree plus the addition of some dispersing from the tree to the ground cover.

Late Season Dynamics. The decline of prey in the tree was followed by increased densities of _A_. _fallacis_ on the trunk, in the air and in the ground cover (Figures 6-14). Also, the numbers migrating via the air between these habitats was greatly increased (Figures 19-22). It is obvious from these figures that _A_. _fallacis_ densities in all these habitats are directly influenced by the predator-prey interaction in the tree. The reproductive increase of _A_. _fallacis_ in the tree increased until the prey declines to < one/leaf (Figures 19-22). Prior to the reproductive decline of _A_. _fallacis_, due to limited prey levels in the tree, the percent stage distribution of _A_. _fallacis_ dispersing in the air changes from the usual adult female and some males to include an increasing proportion of immature and male stages (Figure 19-22, and Tabe 13-16). During mid season, the prey and predator are distributed in a similar manner throughout the tree canopy with favorable levels of food for both. However, during late season there is increasing local populations of _A_. _fallacis_ exposed to a limited food supply. The local prey extinctions results in starvation of _A_. _fallacis_., which induces an increase in adult female and male searching for food and subsequent air dispersal activity (Croft and McMurtry 1972, Johnson and Croft 1976). It is probable that immature stages are affected similarly and that starvation increases their searching activity and the duration of their life stage both which increase the density being blown from a leaf. The stage proportion of _A_. _fallacis_ impacting on the plates as immatures, males or females during this period varied (see Tables 13-16). After August 30 (Tables 9-12), reproduction of _A_. _fallacis_ in the tree was minimal (i.e. < 30% immatures), which corresponds with the increase in the proportion of adult females air dispersing (i.e.80% on and after September 14 in Figures 19-22 and Tables 13-16). Figures 19 to 22 show the changes in prey density in the tree and the subsequent changes in the percent stage distribution of predators noted on the grease plates.

Occasionally, larger counts of _A_. _fallacis_ were caught at the five foot trunk height (August 7 in Figure 11, August 20 in Figure 13 and 14). These dates were associated with the peak air dispersal of _A. fallacis_ (Figures 19-22) and possibly peak ambulatory movement in the canopy. The combination of air dispersal and ambulatory movements out of canopy were believed to produce higher densities of _A. fallacis_ at the five foot height. Preliminary studies have shown significant movement of _A. fallacis_ from the ground cover up the poles at this time (Johnson, unpublished data). However, data were not collected concerning the predominant direction of movement, although it is assumed to be downward.

Dispersal Distance Study. The last study dealt with the air density of _A. fallacis_ at various distances away from the orchard border during the season. Table 17 summarizes the relative density of _A. fallacis_ impacting on grease plates at six distances outside of an orchard. In early and mid season, prey levels were favorable for _A. fallacis_ during the weeks of July 13 and July 20. Data for these weeks showed a decline in the number of _A. fallacis_/plate at successively greater distances away from the orchard (Figure 23, lines A-C). Food was limiting in the trees after July 27, the period that corresponded to air dispersal of _A. fallacis_ and significantly greater counts at all distances. By August 3, in comparison to previous weeks, a significant density of A. fallacis was noted in the air over the grassy field outside of the orchard (Figure 23, square symbols). The plate counts found at all distances were attributed to the minimal air dispersal out of the tree (see counts from

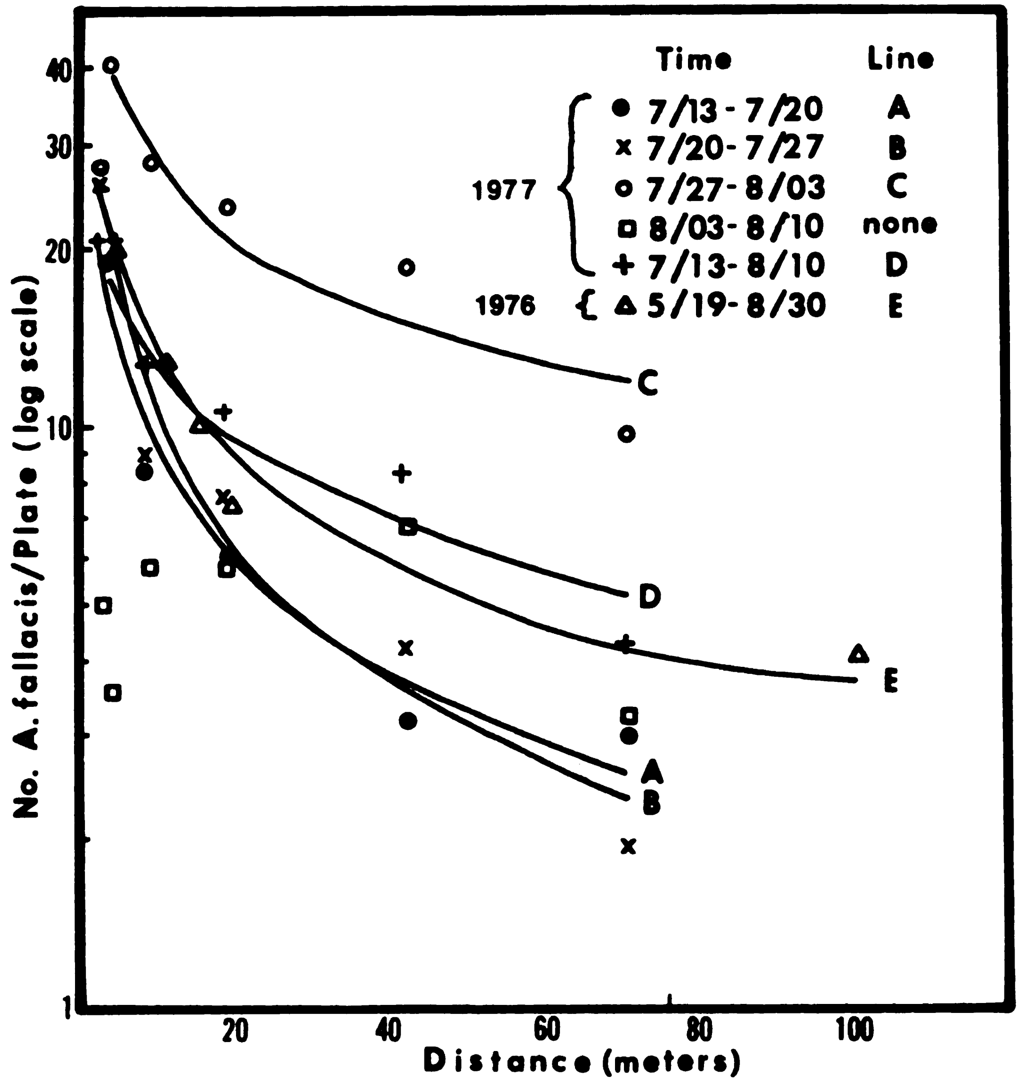

Time
Line
1977
● 7/13-7/20
A
× 7/20-7/27
B
○ 7/27-8/03
C
□ 8/03-8/10
none
+ 7/13-8/10
D
1976
△ 5/19-8/30
E
No. A. fallacis/Plate (log scale)
40
30
20
10
1
20
40
60
80
100
Distance (meters)
C
D
E
A
B

Figure 23.

zero to 4m from the tree in Figure 23) and the supposition that A. fallacis was distributed equally in the ground cover away from the orchard. The mites noted on the plates may have come from the ground cover near the plates. Slightly greater counts, August 3, at eight to 40m away from the tree illustrate a wave of A. fallacis dispersing away from the over-populated understory of the tree where major counts occurred earlier in the season. The greater counts of A. fallacis outside of the orchard increases the likelihood that an individual will locate sites containing food and overwintering sites.

Power curves in Figure 23 were fit to the data in Table 17. Lines E (1976) and D (1977) represent the cumulative seasonal density of A. fallacis from zero to 70 or 100 meters away from the orchard. The equations of these curves are presented in Table 18 along with their correlation coefficients (r). These curves agree with similar distance dispersal curves presented by Wolfenbarger for other small organisms (1975).

TABLE 17: Summary of the density of _A. fallacis_ that dispersed via the air to various distances away from the orchard border in Graham station (1977).

Date	Distance From Orchard In Meters					
	Origin	3.8	8.4	19.1	41.9	72.4
7/13-7/20	24.0_{a}[1]	19.1_{b}	8.4_{c}	$5.9_{c,d}$	3.3_{c}	3.0_{d}
7/20-7/27	25.8_{a}	19.6_{b}	8.9_{c}	7.6_{c}	4.4_{d}	1.9_{e}
7/27-8/03	27.1_{b}	41.6_{a}	28.1_{b}	$23.5_{b,c}$	18.5_{c}	9.3_{d}
8/03-8/10	$4.9_{a,b,c}$	$3.5_{b,c}$	$5.7_{a,b}$	$5.8_{a,b}$	6.7_{a}	3.3_{c}
7/13-8/30[2]	20.5	21.0	12.8	10.7	8.2	4.4

[a-e] Represent significant differences at .05 level, with _a_ being the largest and _e_ being the smallest value.

[1] Mean number of mites/10cm x 10 cm grease plate.

[2] Mean number of mites/plate during whole sampling season (7/13 to 8/30).

TABLE 18: The regression equations and their correlation coefficients (r) for the predicted curves in Figure 23.

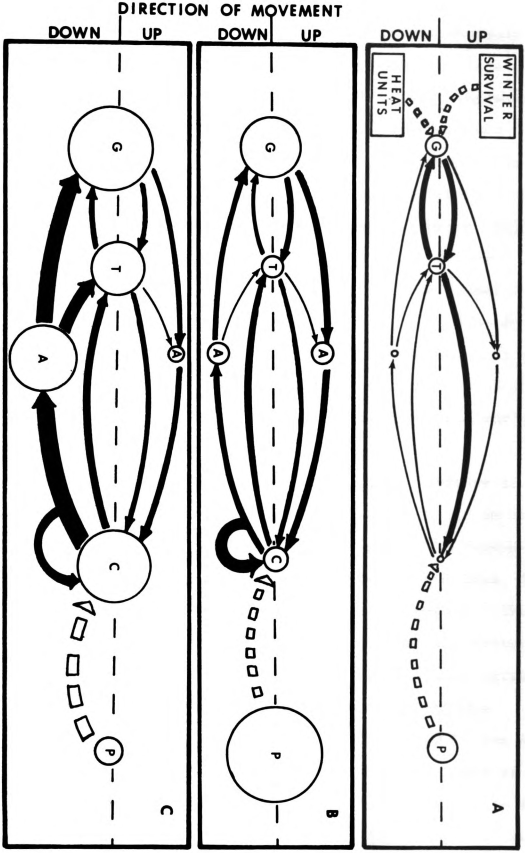
DATE	YEAR	LINE	REGRESSION EQUATION	r
7/13-7/20	1977	A	$Y = 43.6\ \mathrm{EXP}\ (-0.66)$	.97
7/20-7/27	1977	B	$Y = 53.7\ \mathrm{EXP}\ (-0.73)$	.96
7.27-8/03	1977	C	$Y = 78.2\ X^{(-0.45)}$	.95
OVERALL	1977	E	$Y = 18.9\ \mathrm{EXP}\ (-0.12)$	.96
OVERALL	1976	D	$Y = 43.7\ \mathrm{EXP}\ (-0.54)$	.98

OVERALL DISPERSAL MODEL OF *A. FALLACIS*: A SUMMARY

A generalized model of the seasonal movements of *A. fallacis* and factors that affect their migration is presented in Figure 24 (A-C) was briefly mentioned earlier (Figure 5). Specifically for Figure 24, each subcomponent is divided into two horizontal segments indicating the movements of *A. fallacis* up or down inspace. The circles represent estimates of magnitude of the densities of *A. fallacis* in each subcomponent including the ground cover (G), on the tree trunk (T), in the air(A) or in the tree canopy (C). The circle containing the (P) is the density of prey in the tree. The width of the solid arrows between circles gives the direction and relative amount of interhabitat movement among submodels, and the open arrows express the magnitude of influence that a certain factor (e.g., winter survival, heat or prey density) has on these movements.

Early Season Submodel. The ground cover density of *A. fallacis* appears to be dependent upon its winter survival, subsequent environmental conditions and available food resources such as *T. urticae*, other mite species, pollen or honeydew. With the onset of warmer weather there is more reproductive and ambulatory activity in the ground cover which increases the probability of mites randomly moving

Figure 24. Seasonal model of the movements (solid arrows) of *A. fallacis*, the relative densities (circles) of mites in each habitat (G = ground, T = trunk, A = air, C = canopy, P = prey in canopy), and the influence (open-boxed arrows) of the environmental factors on these movements.


DIRECTION OF MOVEMENT
DOWN
UP
DOWN
UP
DOWN
UP
HEAT UNITS
WINTER SURVIVAL
G
T
A
C
P
A
B
C

onto the tree trunk and into the canopy. Also, air dispersal may occur from the ground or the trunk. This increased activity was found to be related to the amount of heat accumulated (DD_{54}). After a minimum cumulative DD_{54} exposure in the field, A. fallacis presence in the tree occurred more often. Colonization of the tree is dependent upon the presence of a minimum threshold density of prey/apple leaf. If the prey level in the tree was inadequate, then _A_. _fallacis_ would eventually return back to the trunk or ground. At this time, there may be an equilibrium between the number of mites in the air dispersing into or out of the tree if no food is present. In comparison, the movement up the trunk is considered to be predominantly upward. Colonization of the tree by _A_. _fallacis_ signifies the transition from early to mid season.

Mid Season Submodel. Prey in the tree increase to their peak population followed by a one to two week lag in the numerical response of _A_. _fallacis_. During the reproductive phase of _A_. _fallacis_ population increase in the tree, its numbers in the air and on the trunk also increase. The major dispersing stage in the air and on the trunk are probably the adult preovipositing females. These observations agree with those of Croft and McMurtry (1972) for _Typhlodromus occidentalis_ Nesbitt and Johnson and Croft (1976) for _A_. _fallacis_. In both species, the preovipositing females were found to have a greater rate of searching and be more difficult to confine to a colony than ovipositing females or other stages. The increased searching activity of preovipositing females is independent of the food available. In comparison to the early season, the directional movement on the trunk is believed to be close to equilibrium, and the air dispersal is predominantly out of the tree. Some of these mites reach (i.e., via air or walking) leaves within the same or in adjacent trees (see Figure 24B, the arrow originating from the tree and returning to it). The remaining ovipositing females continue to oviposition, and evidently disperse only when prey are limiting. After the peak of the prey population in the tree, there is a delayed effect on the dispersal of _A_. _fallacis_ marking the beginning of the late season.

Late Season Submodel. A decline in prey due to predation by _A_. _fallacis_ results in a mass net movement via the air or trunk of _A_. _fallacis_ to the ground cover. As food becomes limiting, the percent stage distribution of _A_. _fallacis_ in the air changes to include additional immatures and males. Localized extinction of prey causes all stages of _A_. _fallacis_ to starve and to disperse in the air. Starvation is assumed to increase the searching activity of all stages and the likelihood that they are detached from the leaf into the air. The tendency to exhibit dispersal behavior and actively release themselves into the air in the laboratory was affected by starvation in only the ovipositing female and to a lesser extent in the male; whereas the immature stages rarely exhibited a dispersal behavior in the laboratory and did not actively release into the air (Johnson and Croft 1976). Without food, the duration of each immature stage would be increased so that the probability of being blown off the leaf would be increased. Air dispersal between trees would not result in successful colonization at this time since biological control between treees is inclose synchrony and food would probably be limiting in adjacent trees also.

Trunk and ground cover populations of *A. fallacis* peak during this period and remain high well after the decline of the *A. fallacis* population in the tree. There appears to be an equilibrium between the movements to and from the lower levels of the trunk and the ground cover. There is also a spreading of *A. fallacis* from the surrounding habitats so that the air density of mites is similar at most locations (i.e. up to 100m). Again, it would be adaptive for *A. fallacis* to disperse from food limiting locales to places where reproduction could continue until diapause occurred. Dispersal to new sites increases the likelihood that some of the individuals in the population locate viable overwintering sites.

Understanding the factors affecting the early season colonization of the apple tree by *A. fallacis* may enable researchers to determine which factor(s) may be manipulated to produce a more synchronized interaction between *A. fallacis* and its prey in the apple tree. These studies indicated that given a detectable early season population of *A. fallacis* in the ground cover and a minimum threshold density of prey in the tree, the heat accumulation correlates with the searching activity of _A_. _fallacis_ in early season. Future research should include studies of the effects of compatible cultural methods (e.g., pruning or manipulation cover vegetation) that increase the microhabitat temperature of or perhaps radiation reaching the ground cover and the trunk. Comparisons of heat accumulation and date of colonization of the tree by _A_. _fallacis_ for various methods of manipulating these enviornments should yield a strategy that results in the more effective biological mite control.

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