This is to certify that the

thesis entitled

FACULTATIVE DISPERSAL OF THE APPLE MAGGOT,
RHAGOLETIS POMONELLA, (WALSH)
(DIPTERA: TEPHRITIDAE)

presented by

JANYCE MARIE RYAN

has been accepted towards fulfillment
of the requirements for

___Masters___ degree in __Entomology__

Stuart H Gage
Major professor

Date _May 17, 1990_

PLACE IN RETURN BOX to remove this checkout from your record.
TO AVOID FINES return on or before date due.

DATE DUE	DATE DUE	DATE DUE
~~JAN 1996~~ 1996		
MAY 1 5 1957		
MAY 2 3 1999		

c:\circ\datedue.pm3-p.1

FACULTATIVE DISPERSAL OF THE APPLE MAGGOT,
RHAGOLETIS POMONELLA, (WALSH)
(DIPTERA: TEPHRITIDAE)

By

Janyce Marie Ryan

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Entomology

1990

ABSTRACT

FACULTATIVE DISPERSAL OF THE APPLE MAGGOT, *RHAGOLETIS POMONELLA* (WALSH) (DIPTERA: TEPHRITIDAE)

By

Janyce Marie Ryan

Apple maggot damage in commercial orchards is often caused by emigrant flies from unmanaged apple trees. Understanding this dispersal can lead to more effective management. This study examines temporal and spatial dynamics of movement, and factors initiating apple maggot dispersal. Apple maggot flies immigrating into an unsprayed orchard were captured on red sticky spheres and yellow Pherocon ®AM traps for 3 summers. Females and males were caught in similar proportions. Overall preferences for red spheres, and the predominance of gravid females suggested that flies were in search of sites for mating and oviposition rather than food. Fruit drop was indicated as the single most important factor initiating dispersal, as changes in host fruit density were highly correlated with declines in trap catch. Lastly, flies were attracted to sticky traps within a circular arena of potted apple trees, but no clear directedness in movement could be concluded from angles of recapture.

To Gus, who saw me through it all

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Introduction

Dispersal is fundamental to animal movement in that it allows individuals to maximize their resources and respond to adversity. Ecologically, it functions in the regulation of population density (Taylor & Taylor 1977). Dispersal also provides an evolutionary mechanism for gene flow among populations (Levins 1964) which allows animals to exist in heterogeneous and changing environments (Southwood 1962).

Dispersal is a broad term, meaning the scattering of members of a population so that the mean distance between individuals is increased. It may include movements within as well as those away from a habitat. For flying insects, movement within a habitat is usually termed 'trivial' or 'appetitive', and is characterized by relatively short flights and a responsiveness to vegetative stimuli (Kennedy 1961, Southwood 1962, Johnson 1969). Dispersal away from a habitat is termed migration, and usually involves sustained, undistracted flight; often by pre-reproductives (Kennedy 1961, Southwood 1962, Johnson 1969).

Distinctions between migratory and non-migratory movement are not always clear. For example, differences may involve only levels of thresholds for responsiveness to stimuli (Kennedy 1961), or the scale of movement (Hughes 1979). The criterion that migration must involve a change of habitat is somewhat ambiguous, since what constitutes a habitat varies among species (Hassell & Southwood 1978, Whalon & Croft 1987). There is likely a continuum of dispersal between short-range appetitive movements and the long-range, persistent flight of migration (Johnson 1969), that might be termed medium-range dispersal. Little is known about this level of

movement. Most studies have focused on migration, perhaps because it is often spectacular, involving large numbers of individuals. However, medium-range dispersal may result in a change of breeding habitat, and therefore provide the same ecological and evolutionary functions as migration (Taylor & Taylor 1977).

The evolutionary significance of insect dispersal is that it allows a species to keep pace with changes in the locations of its habitat. Evidence for this theory comes from observations that dispersing insects tend to be occupants of temporary habitats (Southwood 1962). The nature and frequency of environmental patterns in these habitats, and the species involved determine what type of dispersal is utilized (Hughes 1979). Changes that occur regularly over time tend to produce obligate dispersal, meaning that it occurs independent of factors in the immediate environment (Southwood 1962). This situation may result, for example, due to seasonal changes in the environment, or in some cases because of management, as in agricultural systems.

Habitat changes that are irregular tend to produce facultative dispersal, where emigration is triggered by some factor in the immediate environment that indicates the advance of unfavorable conditions (Southwood 1962, Johnson 1969). This is proposed to be a highly evolved mechanism for movement rather than an immediate response to adversity, particularly when long-range, persistent flight is produced. In some instances a facultative response to crowding may produce increased trivial movements resulting in inadvertent dispersal of vagrants beyond the original breeding habitat (Southwood 1962).

Dispersing insects tend to be r-selected, in that they are rapid colonizers with a high potential for population increase (Begon & Mortimer 1981). That

insect pests as a group are apt to be r-selected (Stinner et al. 1983) is not surprising, since this is an effective strategy for coping with the impermanence of agricultural ecosystems. In commercial agricultural, damage by insect pests is often dependent on recolonization each year, because intensive use of insecticides prevents insects from overwintering within the system. Whalon & Croft (1987) demonstrated the effect surrounding habitat has on the numbers of pest insects caught in orchards. For Michigan, these include such major pests as apple maggot, *Rhagoletis pomonella*; codling moth, *Cydia pomonella*; and plum curculio, *Conotrachelus nenuphar*, all of which typically reside in unmanaged fruit trees or other habitats at variable distances from the potential target orchard.

Determining factors that regulate movement from source habitats is necessary for understanding the ecology of dispersing insects. From a practical standpoint, including source habitats in management considerations can provide new opportunities for management. These might include increased capabilities for scouting or warning providing lead time before economic levels are attained, the modification of source habitats, or management along invasion routes (Rabb 1985).

Apple Maggot Dispersal

The importance of apple maggot fly (AMF), *Rhagoletis pomonella* dispersal was recognized early in the history of commercial orcharding, because of observations that neglected, unmanaged apple trees were often sources of AMF infesting commercial orchards (Phipps & Dirks 1932, Bourne et al. 1934).

Apple maggot is usually described as a poor disperser (Whalon & Croft 1985), as in mark-recapture studies most flies are captured close to the release site (Reissig 1977, Neilson 1971, Maxwell 1968). These results probably reflect

the facultative nature of AMF dispersal and not a lack of ability, since AMF can travel over fairly large areas (e.g. up to 1 mile, Maxwell and Parsons 1968) when fruit is absent at the release site. Experiments on foraging behavior also indicate that AMF will not disperse when fruit is abundant (Roitberg & Prokopy 1982). The facultative nature of apple maggot dispersal is further suggested by the often episodic nature of infestations of commercial orchards (Leroux and Mukerji 1963, Hamilton and Gage in review), and by the variability in delay times from emergence in unmanaged apple sites until arrival in commercial orchards (Olsen 1982).

A number of authors have postulated that AMF dispersal is dependent on factors related to host fruit quality and/or density (Prokopy & Hauschild 1979, Olsen 1982, McNeil & Roitberg 1985). The density of host fruit and the level of oviposition deterring pheromone (ODP) both affect the giving up time (sensu Krebs et al. 1974) of an AMF within a host tree (Roitberg et al. 1982).

Host fruit density is highly variable in nature due to differences in the phenologies of different apple varieties, which causes fruit to mature and drop at different times. Apple variety also affects alternate bearing patterns, susceptibility to frost (determining fruit set) and pest damage, which may affect the rate of fruit drop (Keck 1934, Dean & Chapman 1973). Variability among unmanaged apple trees, and from year to year may explain variation in the frequency and timing of apple maggot infestation commercial orchards.

Quality of host fruit may also play a role in AMF dispersal. Prokopy (1972) suggested that the exodus of female flies from a tree harboring ripe fruit may be due at least in part to the buildup of ODP over time. In the laboratory, females tethered to flight mills and exposed to infested, ODP marked fruit displayed long distance flight (>1000m) more frequently and flew further than

those exposed to clean fruit (Roitberg et al. 1984). Dispersal in nature is proposed to result from the exhaustion of suitable fruit, due to partitioning of foraging and oviposition by females. This system appears to function for AMF in hawthorns (*Crataegus* spp.), based on observed uniformity in the distribution of eggs among fruit (Averill & Prokopy 1989). Uniformity in the distribution of eggs has been noted among apple tree quadrants (Leroux & Mukerji 1963, Stanley et al. 1987), and has been attributed to the role of ODP as an epideictic (dispersal) pheromone.

Most studies of the influence of ODP on apple maggot behavior have used *Crataegus* as the host, where usually only one apple maggot per fruit will develop to maturity (Prokopy 1981). ODP is likely to be less effective in deterring multiple ovipositions in apples for several reasons: greater size of apple fruits allow several maggots to develop to maturity, and is reflected in multiple ovipositions (Prokopy 1972); the longer a female is deprived of fruit the greater the tendency for her to accept fruit marked with ODP (Roitberg et al. 1983); and environmental parameters such as rainfall are known to alter the residual activity of ODP (Averill & Prokopy 1987). ODP may have little effect on oviposition in apples in nature, where weather conditions and the availability of fruit are highly variable.

In addition to factors relating to host fruit quality and density, residence time for an AMF within a tree is positively related to the distance to neighboring trees (Roitberg & Prokopy 1982). This would be predicted from foraging behavior theory where optimum residence time in a patch (tree) is positively related to the time spent traveling between patches (Parker & Stuart 1976). This result suggests movement away from a source habitat will occur when considerable time has elapsed since locating a suitable fruit. Moreover, it represents an efficient foraging strategy where the probability of

locating suitable hosts, after leaving the source habitat will be highly variable. The above led McNeil and Roitberg (1985) to postulate a model for apple maggot dispersal where frequencies of distance traveled have a bimodal distribution as most movement is short range but under certain conditions longer flights are initiated.

Lack of information on factors regulating facultative dispersal of the apple maggot results in inefficient and sometimes ineffective management of this pest. Area-wide control measures are often based on the timing of emergence in a particular site, which fails to account for variability in pest pressure for individual orchards. This variability was shown for Michigan orchards by the fact that no apple maggot flies were captured in ca. one-half of 388 commercial orchards sampled between 1981 and 1984 (Hamilton & Gage in review).

Variability in the timing of arrival of AMF in commercial orchards makes prediction difficult, and many growers follow a calendar spray regime. Because of the low market tolerance for apple maggot damage, this may result in 5 pesticide applications aimed at apple maggot. In at least some instances these result in unnecessary economic and ecological costs, because arrival of flies in the orchard may be significantly delayed in relation to activity in unmanaged sites. This delay is often greater than that attributable to reproductive maturation, and is therefore probably dependent on resources in the source habitat. Understanding how these factors affect emigration of AMF from source habitats may enable prediction of both timing and severity of apple maggot attack in commercial orchards (Hamilton & Gage in review).

The main objective of this study was to determine what factor(s) initiate facultative dispersal of AMF by examining 1) the composition of immigrating populations, and 2) the role of fruit density and ovipositon

deterring pheromone in the emigration of AMF from apple trees. A second objective was to examine the temporal dynamics of movement of AMF from unmanaged apple trees into an experimental orchard.

Apple Maggot Biology

The apple maggot is endemic to eastern and midwestern United States, breeding originally in the fruits of native hawthorns (*Crataegus* spp.). A host shift to cultivated apple first occurred in New England in the middle of the last century (Bush 1969). The species presently exists as both apple and hawthorn infesting races.

Apple maggots typically have one generation per year. Adults emerge from pupae that have overwintered in the soil underneath infested trees. Emergence in Michigan usually begins in mid to late June and lasts until mid August. Adult females are sexually immature upon emergence and are presumed to feed on primarily honeydew and leaf exudates for a period of 1 to 2 weeks. Mating takes place on the fruit, and may occur throughout adult life. Once eggs are mature, they are deposited just under the surface of the skin of susceptible fruits. Insertion of the ovipositor causes a characteristic puncture ("sting") which remains as a record of probing. The female then drags her ovipositor on the fruit surface laying down an oviposition deterring pheromone (ODP) which deters subsequent oviposition by herself and other females (Prokopy et al. 1976). Eggs hatch in 3-7 days and the small larva begins tunneling in the fruit leaving characteristic brown trails. This damage causes fruit to drop prematurely. Larvae pass through 3 instars within the fruit requiring 2-4 weeks for development. At the end of the third instar, the larva exits the fallen apple and passes a final instar in the soil before pupating.

Chapter 1.

Temporal Dynamics and Composition of Dispersing Populations
of Apple Maggot Flies

A study of dispersing populations of apple maggot flies (AMF) was conducted at the Michigan State University Kellog Biological Station (KBS) in Kalamazoo Co., MI. AMF were caught on traps set in the KBS orchard for the first time in the summer of 1986. Because this was the first season the orchard had produced fruit, no AMF could have overwintered in the orchard, and those captured were certain to have resulted from immigration. The nearest potential host trees outside the orchard were ca. 500 m away, a distance that would have required inter-habitat movement of AMF. This situation provided an opportunity to study medium-range dispersal of AMF through non-orchard environments, a subject about which little was known.

The short time (15 days) during which AMF were trapped in 1986 suggested two possible scenarios for the emigration of flies from unmanaged apple trees around the orchard: 1) environmental factors produced conditions favorable for dispersal so that flies emigrated from a number of sources at ca. the same time, or 2) a relatively large number of flies emigrated from one location in response to conditions particular to that site. An answer to this question would help determine factor(s) that initiate emigration of AMF.

Objectives of this study were: 1) to examine factors regulating facultative dispersal by determining a) which members of AMF populations dispersed (in relation to sex and age), and b) which host trees were sources of immigrant AMF in the KBS orchard; and 2) to study spatial and temporal dynamics of inter-habitat movement of AMF.

8

Materials and Methods

The KBS orchard was a 5 year old 1.5 hectare orchard of mixed disease-resistant apple varieties in which insecticides had never been used. In 1987, the study site also included unmanaged apple trees in the vicinity of the orchard, and non-orchard habitat between these trees and the orchard (Figure 1).

Activity in the KBS orchard was monitored for 3 consecutive years using two types of visual attractant traps: 2.5-inch diameter plastic red sticky spheres (fruit mimics) coated with Tanglefoot®, and yellow Pherocon AM® traps (foliage mimics) baited with an ammonium stearate feeding attractant. In addition to providing information for the timing of control strategies, these traps have been used to estimate seasonal trends in the abundance of flies (Prokopy 1968), and to monitor dynamics of adult activity for comparative studies (Reissig and Tette 1979, Olsen 1982, Aliniazee and Westcott 1987). One of each trap type was hung in trees throughout the orchard. Traps numbered 36, 51 and 72 in 1986, 1987 and 1988, respectively.

Six sites outside the orchard, comprising 41 unmanaged apple trees were identified as possible hosts for AMF. One red and one yellow trap was hung in each tree in foliage containing fruit clusters. Irregularity in the distribution of fruit in trees was common, but an attempt was made to position traps so as to maximize AMF attraction (Reissig 1975a, Drummond et. al 1984).

Monitoring in the non-orchard environment between unmanaged apple trees and the orchard consisted of the erection of T-shaped wooden "trees" (2m tall x 1m across) which were placed in holes drilled into the ground lined with a piece of 30 cm PVC pipe. These traps were similar to
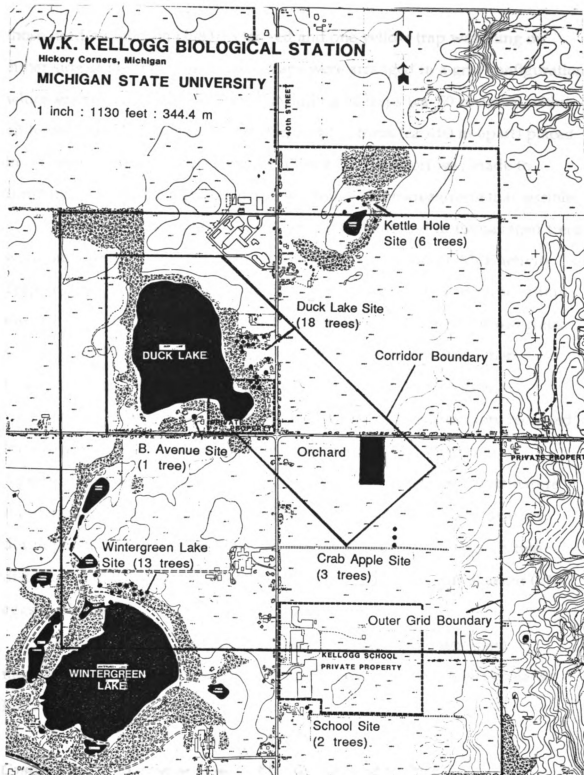
Figure 1. Map of Kellog Biological Station study site showing the orchard, unmanaged apple tree sites, and grid boundaries.

those used by Johnson (1983). One red and one yellow trap was hung on either side of the trap cross-piece. Traps were arranged in a grid configuration which encompassed a 6.2km^2 area, including 92 traps (ca. 50 m apart) within an hypothesized immigration corridor, and 121 traps (ca. 100 m apart) placed in the area surrounding the corridor (Figure 2). An effort was made to construct as complete a grid as possible, though some areas were inaccessible.

Traps hung in apple trees, both in the orchard and in unmanaged trees were sampled 2-3 times per week during the main period of AMF activity. Traps within the corridor were sampled 2 times per week, and those within the grid surrounding the corridor 1 time per week. All Pherocon AM traps were replaced every 2 weeks. Red sticky spheres were replaced when tackiness of the Tanglefoot was diminished due to rainfall or debris.

Date of capture, foraging intent, trap preference and sex were recorded for all AMF caught on traps. Females were dissected to determine reproductive stages, which were classed into 1 of 5 categories: 1) immature (no definite structure within the abdomen), 2) immature (slight ovarian development), 3) immature (obvious ovarian development, eggs in two discrete bundles), 4) gravid (abdomen full of mature eggs) and 5) spent (<10 eggs in abdomen).

Air temperature degree days (base 50 °F) were estimated from measurements of maximum and minimum temperatures (Baskerville & Emin 1969).

Results and Discussion

Composition of Immigrant Apple Maggot Fly Populations

The pattern of trap catch for apple maggot flies in the orchard was similar for all 3 years of the study (Figure 3a). The majority of flies was caught on red spheres rather than yellow traps, suggesting that AMF immigrating
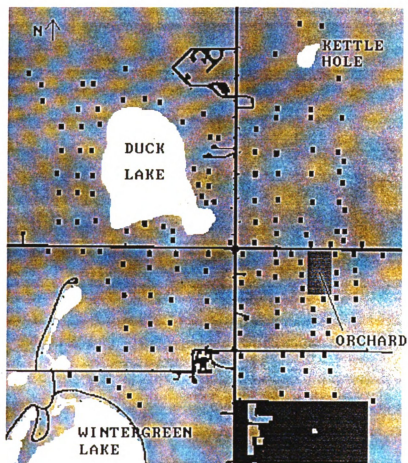
Figure 2. Map of the Kellog Biological Station showing layout of the grid of apple maggot traps.

into the orchard were in search of apples as sites for mating and oviposition, rather than food. This assumption is supported by data from the dissection of females, which showed that most females trapped in the orchard were reproductively mature (stages 4 &5, Figure 3b). Reproductive maturity of females on yellow traps was not evaluated in this study because of the small number of flies caught.

These results suggest that the majority of dispersing apple maggot females are capable of damaging fruit by the time they arrive in orchards. Management in commercial orchards includes removal of most fruit (by picking), and the use of insecticides for apple maggot control. Therefore, most AMF found in commercial orchards are thought to result almost exclusively from immigration, rather than from pupae overwintering in the orchard. This assumption is supported by most studies of trap preferences in commercial orchards. Monitoring by pest management scouts in Michigan from 1981-1984 showed red traps were more effective (caught flies when yellow traps did not) in 62.7% of orchards where both trap types were used, and in ca. 58% of these orchards no flies were caught on yellow traps (Hamilton & Gage in review). Similar results were obtained by Prokopy and Hauschild (1979), in that red spheres in commercial orchards consistently caught greater numbers of AMF than Pherocon AM traps.

Red spheres were also more effective in capturing gravid females in the KBS orchard (Figure 3b). Olsen (1982) found that in commercial orchards, yellow Zoecon® AM traps caught a greater proportion of gravid females than red spheres, but this result was apparently related to the greater proportion of males caught on red spheres in his study. Females and males in our study were caught in roughly equal proportions for all 3 years (Figure 3a), indicating

a.
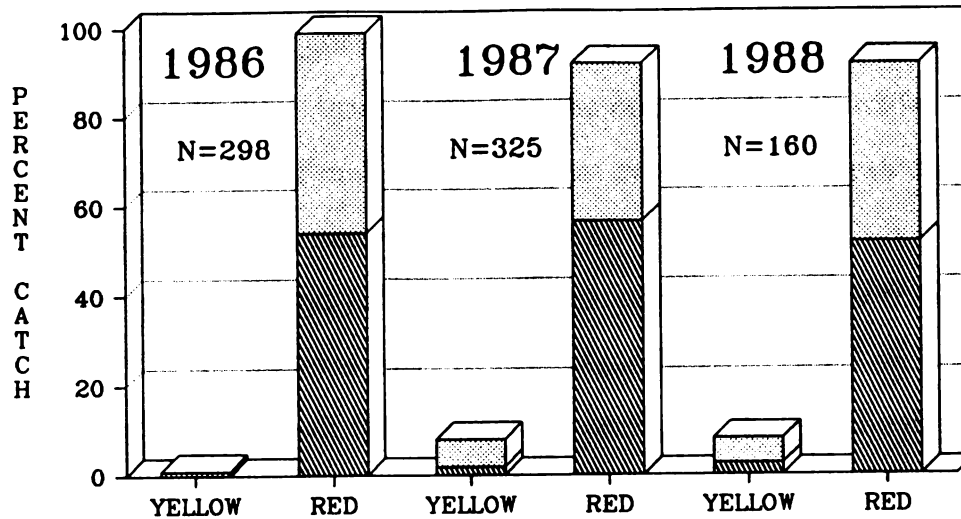
b.
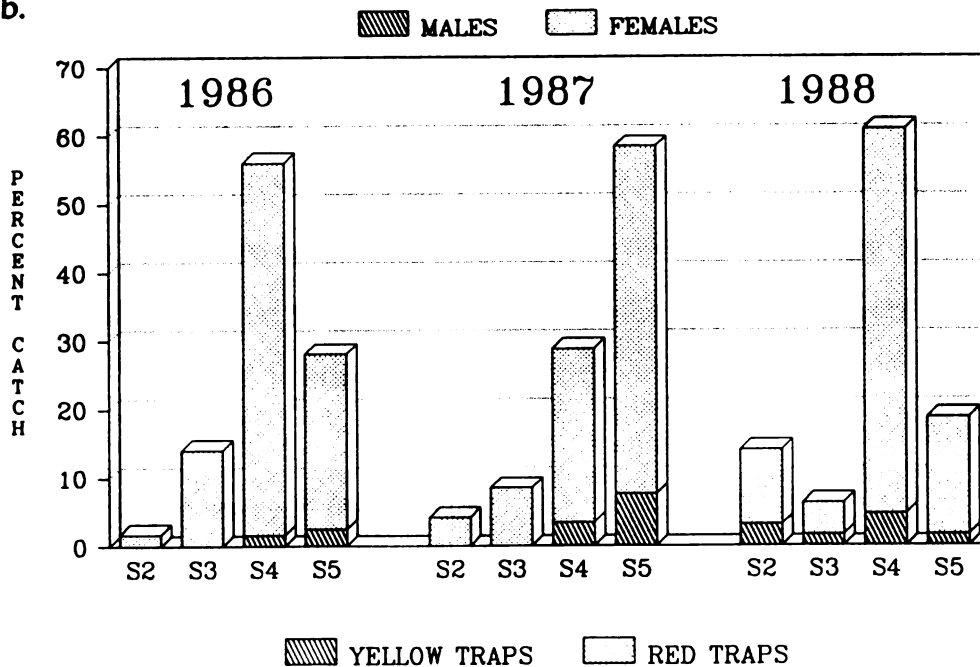
Figure 3. Apple maggot fly trap catch for each of 3 years at the Kellog Biological Station orchard. a. Proportion of female and male flies caught on red and yellow traps. b. Proportion of females captured on red and yellow traps according to stage of reproductive maturity (S=stage). S2-immature, slight ovarian development; S3-immature, eggs in 2 discrete bundles; S4-gravid, abdomen full of mature eggs; S5-spent, (<10 eggs in abdomen).

that males as well as females dispersed. Dispersal of both sexes may result in increased reproductive success, since multiple matings in the laboratory increased both fertility (egg hatch) and fecundity (egg-laying rate and longevity) of apple maggot females (Opp & Prokopy 1986). Assuming that flies responded to traps upon arrival in the orchard, the coincidence in timing of catch for females and males suggests that both sexes emigrated from unmanaged sites at the same time (Figure 4).

Reissig (1975b) and Johnson (1983) reported that yellow traps caught more flies than red spheres early in the season in abandoned orchards. Olsen (1982) reported this result for commercial orchards, though the difference was not significant. The assumption of yellow traps capturing AMF early in the season is often used by pest managers, who hang yellow traps to detect AMF before they are capable of damaging fruit. Our results raise a question as to the validity of this assumption, since first catch occurred earlier for red traps (July 4 and 8) vs. yellow traps (July 13 and 20) in 1987 and 1988, respectively (almost no flies were caught on yellow traps in 1986). Prokopy and Hauschild (1979) also found that first catch in commercial orchards occurred on red spheres in 14 out of 16 commercial orchards studied.

Timing of apple maggot fly activity

AMF activity plotted as a function of degree days (DD, base 50°F.) showed considerable variance in the pattern and timing of catch among the 3 years of this study (Figure 4). Activity began earlier in 1987 and 1988 (ca. DD 1100-1250) compared to 1986 (ca. DD 1500). Comparison of early activity in the orchard vs. unmanaged apple trees in 1987 showed little difference in the time of first catch (Figure 5). These observations raised the question of
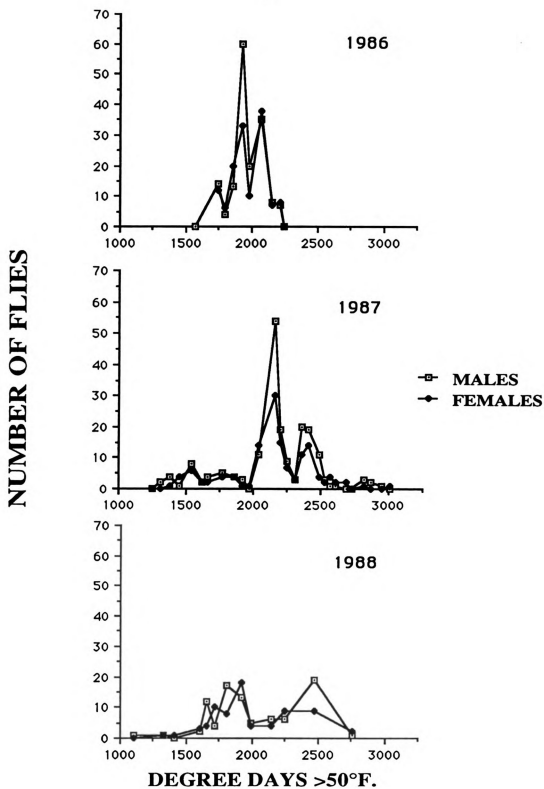
Figure 4. Numbers of female and male apple maggot flies caught on red and yellow traps, for 3 years in the Kellog Biological Station orchard.
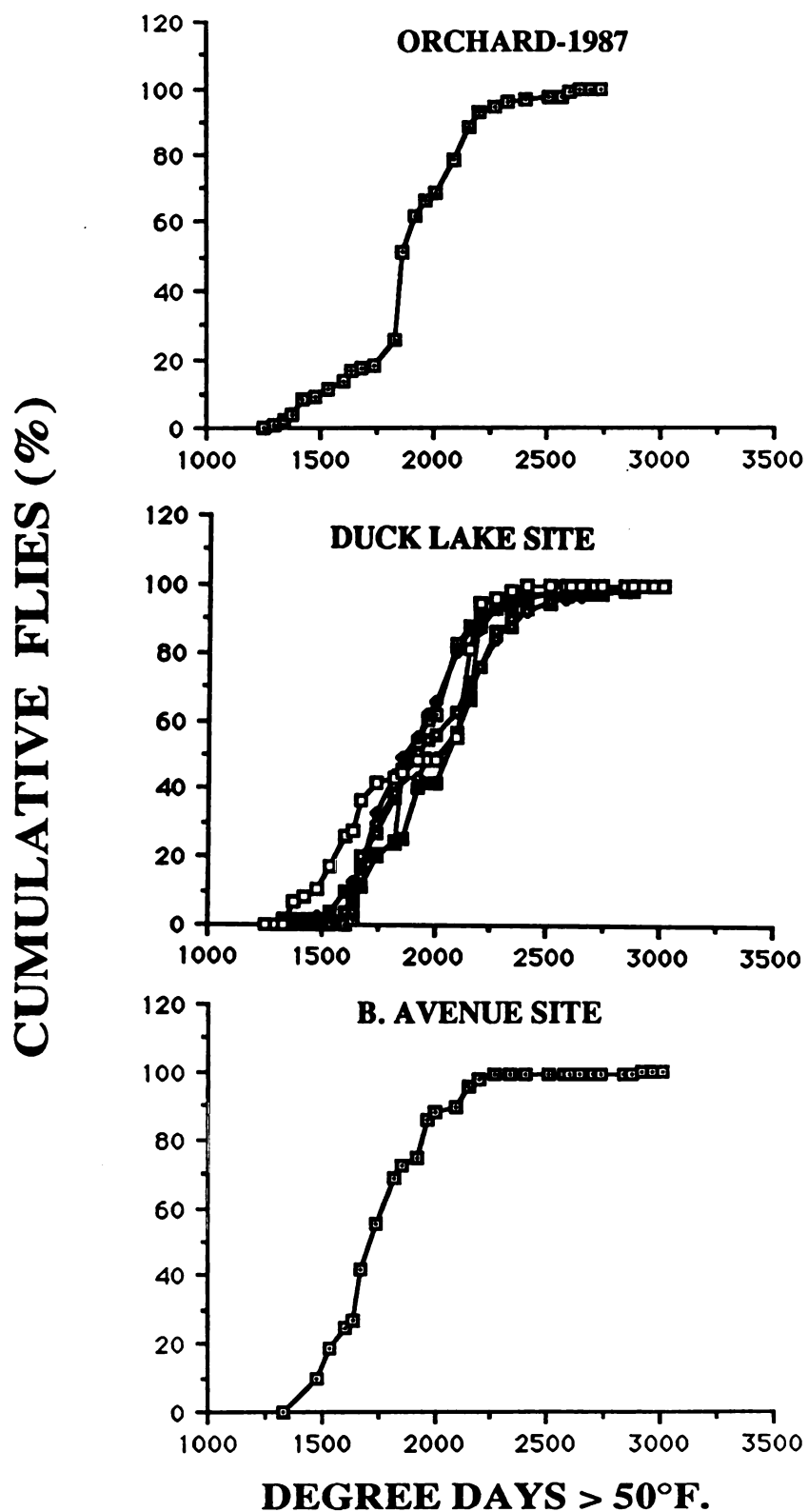
Figure 5. Cumulative number of apple maggot flies caught in 1987, on red and yellow traps in the Kellog Biological Station orchard, and for individual trees in unmanaged apple sites (B. Avenue and Duck Lake).

whether apple maggots had overwintered in the orchard. Examination of the timing of catch for apple maggot females showed that the first flies caught included mature as well as immature females (Figure 6), which suggested that at least some AMF caught early in the season could have been immigrants. Early emigration of AMF from unmanaged apple trees may have occurred because of biennial bearing patterns which were noted for a number of unmanaged apple trees in this study. Traps within trees having an "off" year failed to capture AMF, even though large numbers of flies were captured the previous year when fruit was abundant. The source of early AMF in the KBS orchard in 1987 and 1988 could not be positively determined from this study. However, resident flies, if any, should have been few in number, because the proportion of immature females did not change appreciably from that in 1986, when a resident AMF population was not possible. Proportions were 15.7, 12.7 and 19.3 for 1986, 1987 and 1988, respectively (Figure 3b).

Monitoring Inter-Habitat Movement of Apple Maggot Flies

The most likely sources of AMF immigrating to the KBS orchard were two sites to the NW of the orchard (Figure 1), where activity peaked earlier (B. Avenue, ca. DD 1700; Duck Lake, ca. DD 1850-2050) than in the orchard (ca. DD 2150, Table 1, Figure 6). This observation is speculative, since efforts to trap flies en route to the orchard failed. The grid of traps placed in the area between the orchard and unmanaged apple trees caught only 2 flies; a mature female and a male, ca. 200 m West of the orchard on 23 July (1858 DD, base 50°F.). It is not known whether trap density was a factor in traps not capturing flies. The fact that this trap design was successful in capturing flies within a non-orchard habitat (Johnson 1983) but not in this study suggests
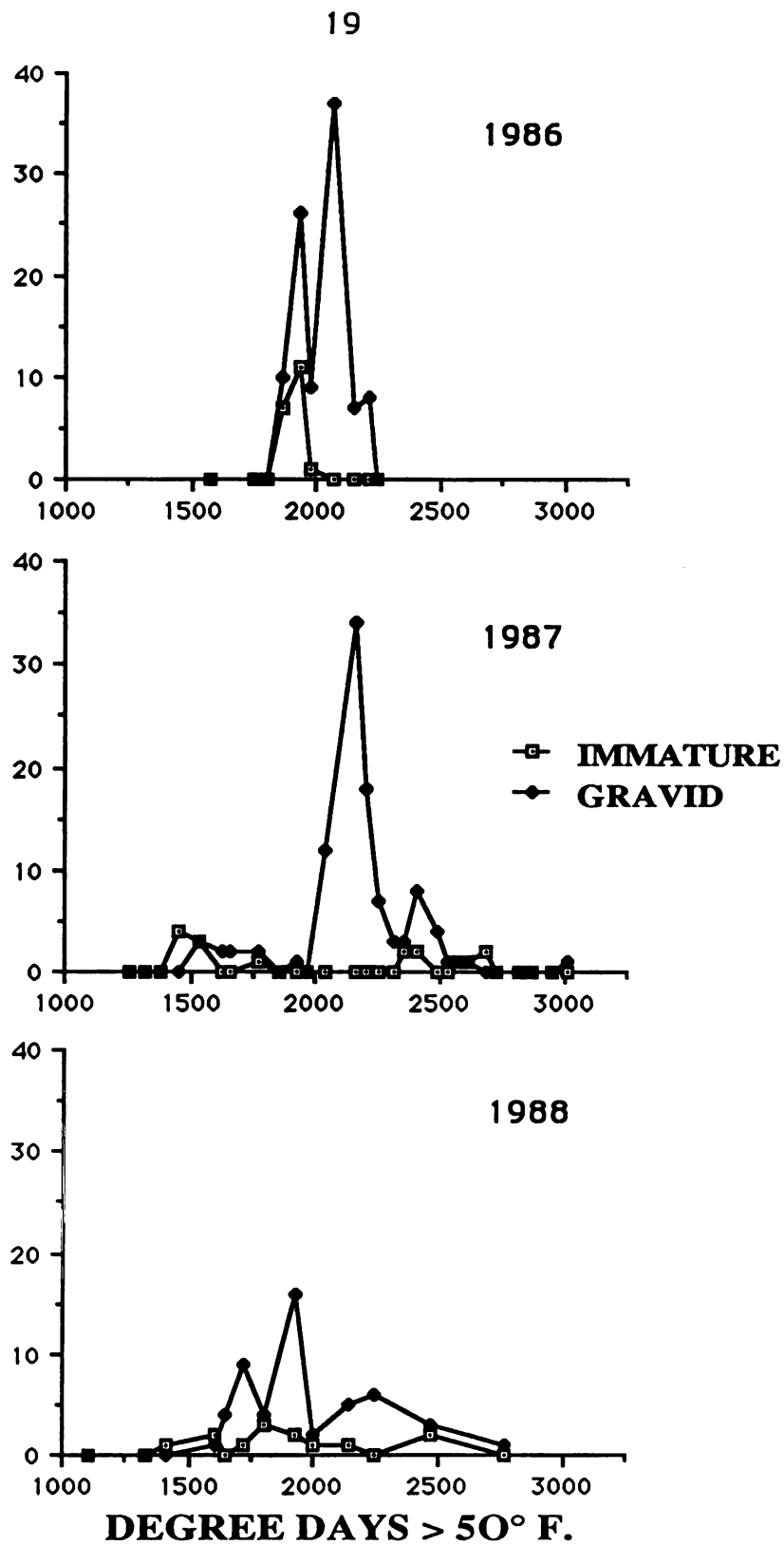
Figure 6. Numbers of gravid and immature female apple maggot flies caught on red and yellow traps for 3 years in the Kellog Biological Station orchard.

Table 1. Timing of peak apple maggot fly activity and total numbers of flies caught in the KBS orchard and unmanaged apple tree sites in 1987.

==

Location	No. of trees	Total Flies Caught	Peak Activity(DD)[2]
Orchard	51[1]	320	2150
Duck Lake	18	769	1850-2050
B. Avenue	1	93	1700
Kettle Hole	6	305	2250-2300
School	2	64	2170
Wintergreen L.	13	44	*

----

1 51 out of the total 373 trees contained traps.

2 Peak activity = 50% cumulative catch in degree days (DD) base 50 °F.

* Peak activity not determined because of the small number of flies caught/tree.

that stimuli eliciting attraction of AMF might differ for intra-habitat vs. inter-habitat movement. This study suggests that AMF do not engage in the persistant, undistracted flight of true migrants, since this is usually accomplished by immature females (Johnson 1969), and most females caught in the orchard were gravid. Though little is known about longer-range movement of AMF, there is some indication that flight may occur at heights greater than the typical height (<2 m) for shorter-range movement. Moericke et al. (1975) found that the flight of AMF, as measured by response to 2-dimensional vertical rectangles, tended to be higher further from the nearest host trees. It is possible then, that the 2m height of traps used in this study was too low to capture AMF.

Visual stimuli provided by real trees have been shown to be important in the attraction of AMF (Moericke et al. 1975). Such stimuli were not essential for attracting AMF moving within a habitat in Johnson's (1983) study, but may be necessary for the attraction of AMF moving longer distances between habitats.

This study supports the idea that AMF immigrating to commercial orchards are reproductively mature and in search of sites for mating and oviposition rather than food. It also suggests that initiation of emigration from unmanaged apple habitats is related to the lack of of suitable host fruit in these sites.

Chapter 2.

Factors Initiating Dispersal of Apple Maggot Flies

In the summer of 1987, differences in late season apple maggot fly (AMF) activity, as measured by trap catch, were noted in the Upjohn® Co. orchard in Kalamazoo Co., MI. Activity declined first in early apple varieties, suggesting that flies were dispersing from these trees. The decline in trap catch also suggested that dispersal was related to abundance or quality of fruit as an ovipositional resource, since these factors differ between early and late varieties.

Differences in the rate of mortality of AMF among apple varieties might also account for differences in late season activity. This was not thought to be the case in the Upjohn orchard, since the timing of emergence of AMF from different apple varieties in the orchard was not significantly different (Hamilton et al. in review). To further explore this possibility, however, the temporal dynamics of AMF activity among apple varieties was compared.

Because AMF dispersal occurs during late summer when seasonal weather changes are taking place, the possible influence of certain weather parameters on fly activity could not be discounted. Rainfall, temperature and windspeed were examined because they have been shown to affect trap catch of other Dipterans (Burnett & Hays 1974, Dale & Axtell 1975, Whitfield 1981). Barometric pressure was thought to be a potentially important variable based on its effect on the trap catch of Tabanids (Burnett & Hays 1974), its influence on apple maggot fly behavior (Averill & Prokopy 1987), and on unsubstantiated claims that fly catch in commercial orchards is related to rain storms (Hamilton & Gage in review). Data on barometric pressure was not

available for this study. Relative humidity was instead correlated with fly activity, because of its expected relationship to storm activity.

The objectives of this study were to 1) monitor apple maggot adult activity to examine seasonal dynamics in relation to apple variety, and to determine the timing of fly dispersal; 2) examine the effect of host fruit density over time on the dispersal of apple maggot flies, and 3) use the distribution of apple maggot eggs among apples as an index for ODP activity, to determine if egg distribution was uniform at the time of apple maggot fly dispersal.

Part 1. Monitoring Apple Maggot Fly Activity

Materials and Methods

The Upjohn orchard comprised ca. 5 ha. of 30-40 year old standard, unpruned apple trees, representing 5 varieties. Three varieties were used in this study: Wealthy, McIntosh and Northern Spy, all of which had substantial fruit loads. No insecticides had been used in the orchard for 8 years and the orchard supported a large apple maggot population. Orchard boundaries included woods and pasture to the West, and open fields to the North, East and South.

Timing apple maggot fly dispersal

The timing of AMF dispersal was determined by monitoring adult activity with Pherocon® AM traps and plastic red 2.5-inch diameter spheres coated with Tanglefoot® (*The Tanglefoot Co., Grand Rapids, MI.*) One of both trap types was hung in each of three trees for Wealthy and Northern Spy varieties (Figure 7). Six trap pairs were hung in McIntosh trees since this variety had two locations in the orchard (3 trees x 2 locations). McIntosh trees were designated McIntosh 1 and McIntosh 2 to account for possible differences in activity that might have occurred due to differences in location and adjacent apple varieties. Traps were hung ca. 1 m apart at eye level, near the periphery of the tree canopy and were located in the directional quadrant where fruit was most abundant. This criteria was thought to be more important than directional position of the tree quadrant (Reissig 1975a) since fruit were sometimes absent or sparse in parts of a tree.

UPJOHN ORCHARD

O O O O O O O O O O O O O
O ● O O O O O O ● O O ●
● O O O O O O O O O O O
O O O O O O O O O O O O
O O O O O O O O O O O O
O O O O O O O O O O O O
O O O O O O O O O O O O
● O O O O O O O O O O O
O O O O O O O O O O O O
O O O O O O O O O ● O O
O O O O O O O O O O ●
● O O O O O O O O O O O
O O O O O O O O O O O O
O O O O O O O O O O O O
O O O O O O O O O O O O
O O ● O O O O O ● O O O
O O O O O O O O O O O O
O O O O O O O O O O O O
O O O O O O O O O O ●
O ● O O O O O O O O O
W M M J J S N N N N M M

237.5 m

↑
N

200 m

W=Wealthy   O apple trees
M=McIntosh   ● apple trees containing traps
J =Jonathon ⎤
            ⎥ non-fruiting
S =Snow   ⎦
N=Northern Spy

Figure 7. Diagram of Upjohn Co. orchard showing apple trees containing apple maggot traps.

Apple maggot flies were counted and then removed from traps every 2-3 days beginning 8 July until 9 September, 1988. Traps were also sampled on 13, 17 and 27 September. Pherocon traps were replaced at least every 2 weeks; more often during periods of rain. Red spheres were replaced when tackiness of the Tanglefoot decreased due to rain or when the trap became cluttered with debris.

Statistics were performed on combined catches for red and yellow traps. This total was thought to be less biased than catch on either trap alone, since effectiveness of the two traps in unmanaged apple trees differs depending on the time of season (Reissig 1975b, Johnson 1983). The mean number of AMF caught per day was subjected to an ANOVA for each day that traps were sampled to compare activity between apple varieties. Air temperature degree days (base 50 °C) were estimated from measurements of maximum and minimum temperatures (Baskerville & Emin 1969).

Results and Discussion

Comparison of trap catch among apple varieties for each sample date showed an initial difference on 8 July (672 DD, Table 2, Figure 8). After this date, no significant difference was found until fairly late in the season on 10 August (1131 DD). Differences between early (Wealthy and McIntosh) vs. late (N. Spy) varieties were consistent through late season activity until 2 September (1371 DD).

These results suggest that prior to late season, all three apple varieties were similarly attractive to apple maggot flies. This is somewhat surprising since apple maggot flies are reported to attack earlier varieties first (Dean & Chapman 1973, Neilson et al. 1981). However, the high level of attractiveness of Northern Spy early in the season was shown in this study both by the

Table 2. Sample dates showing significant differences among apple varieties, and mean comparisons for the number of apple maggot flies caught day^{-1} on sticky traps in the Upjohn orchard.

Date	DD[2]	F value[1]	Apple Varieties[3]			
			Wealthy	Mc-1	N.Spy	Mc-2
7/8	672	4.17*	2.5a	0.5a	0.2a	0.6a
8/10	1131	4.24*	36.3a	13.0a	29.0a	4.8a
8/15	1210	8.09**	27.5ab	12.5a	34.2b	8.8a
8/20	1271	13.1**	6.7a	4.2a	24.4b	3.7a
8/22	1287	8.39**	7.3a	2.2a	24.7b	2.5a
8/25	1313	9.81**	1.2a	5.0a	28.4b	3.7a
9/2	1371	31.2**	6.2a	3.3a	26.3b	1.3a

1 from ANOVA *(P>0.05), **(P>0.01).

2 Degree Days >10°C.

3 Means in a row (not column) followed by the same letter are not significantly different from each other (Tukey's HSD). Mc-1 and Mc-2 = McIntosh variety.
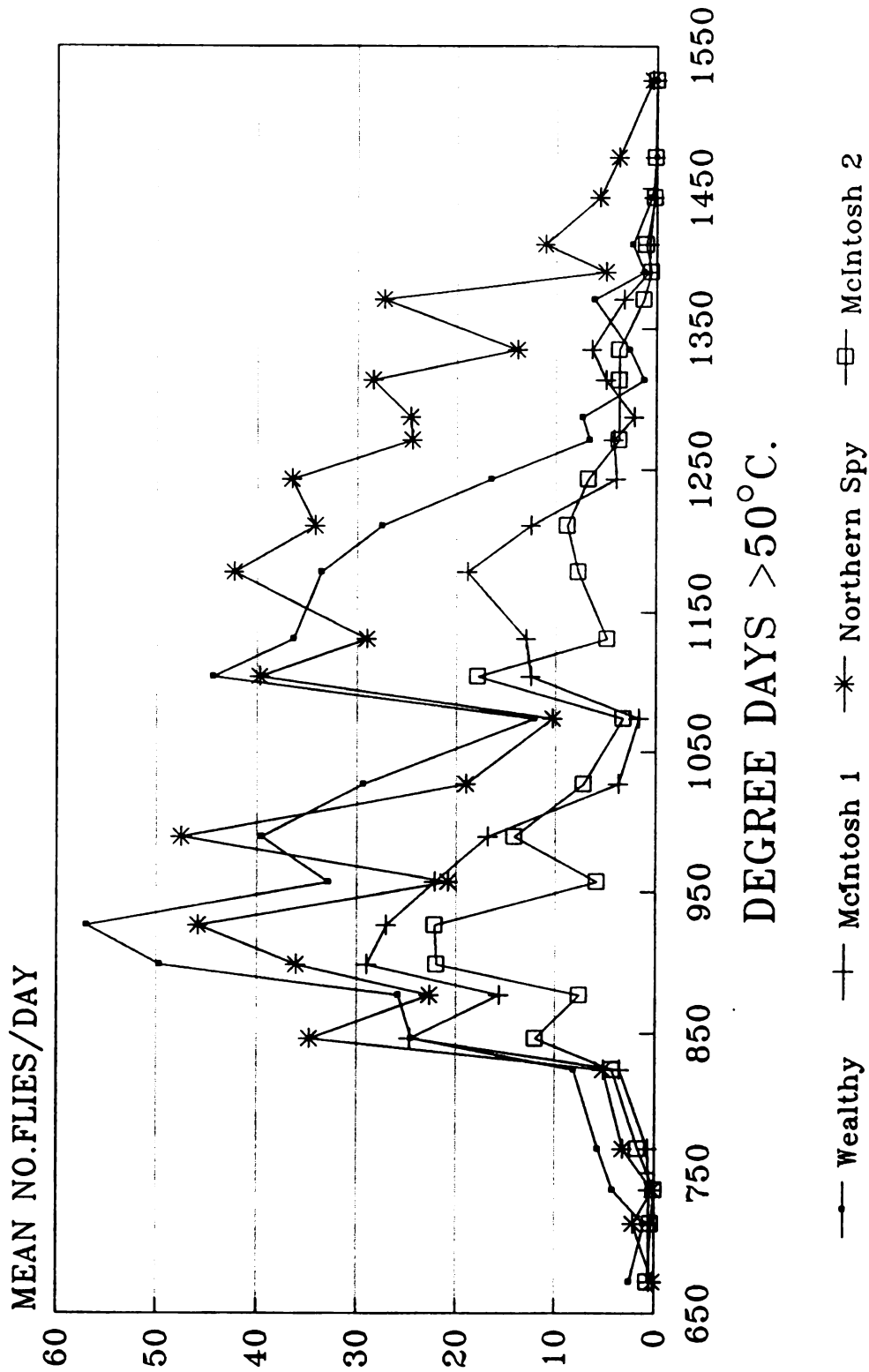
Figure 8. Mean number of apple maggot flies caught day^{-1} on red and yellow sticky traps, for different apple varieties in the UpJohn orchard.

numbers of flies caught and by apple maggot damage. Mean numbers of oviposition punctures per apple counted for apple collections made on 28-29 July were 3.02, 3.44, and 6.96 for Wealthy, McIntosh and Northern Spy, respectively.

Differences in late season activity between early and late varieties were likely the result of AMF dispersal from early varieties for a number of reasons. Temporal synchrony for early to mid season activity among apple varieties suggests that a significant difference in the rate of fly mortality among varieties was unlikely. Similarity in temporal dynamics would be expected based on studies of emergence, where no differences were found in time of emergence between apple varieties in the Upjohn orchard (Hamilton et al. in review). This result has been noted in other orchards as well (Dean & Chapman 1973). Also, because of the close proximity of different varieties in the orchard, it is unlikely that flies emerging from under a tree of a particular variety were limited to that variety in their activity.

Distributions of AMF for all apple varieties were apparently bi-modal (Figure 8). This raised a question of whether a second emergence of AMF, perhaps in relation to rainfall, might have occurred that would have accounted for the second peak. Examination of plots separating catch on red and yellow traps (Figure 9) showed that second peaks were due mainly to increased catch on red traps, indicating that bi-modal distributions were not likely due to emergence. A sudden increase in emergence of flies should have been reflected in an increase in the number of flies caught on yellow traps, since immature AMF are more likely to respond to the feeding stimulus provided by yellow Pherocon AM traps (Prokopy & Hauschild 1979).
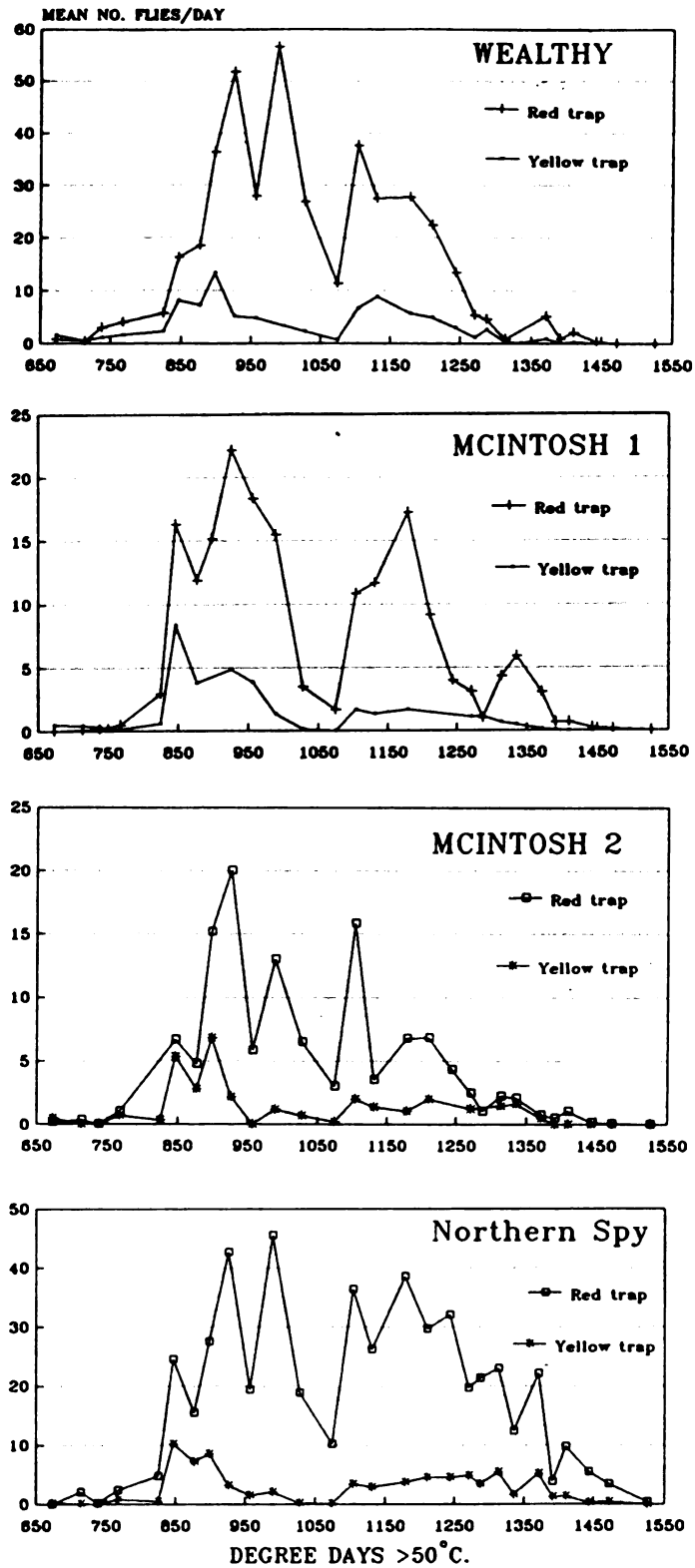
Figure 9. Mean number of apple maggot flies caught day^{-1} by trap type (red or yellow) for apple varieties in the Upjohn orchard.

Weather related factors are a possible explanation for patterns of trap catch in this study, though little is known about their influence on trap catch of AMF. Understanding the influence of weather on the dynamics of activity was not thought to be crucial in this study, since a comparison between apple varieties was the primary objective. This study assumed that weather influences on trap catch should not have differed greatly among varieties.

The results of this study support the theory that declines in trap catch for early apple varieties was due to dispersal of flies. Continued AMF activity in the (late) Northern Spy variety may have represented either a movement of flies from early to a late variety, or the lack of dispersal of flies present in Northern Spy trees. Regardless, it indicates a difference in "attractiveness" between early and late apple varieties that is important in terms of the quality and or density of host fruit.

Part 2. Effect of Host Fruit Density on Dispersal

Materials and Methods

Fruit drop in the Upjohn orchard was monitored for a total of 9 trees of Wealthy and McIntosh varieties (Figure 7). Northern Spy trees were not included because the late timing of apple drop prevented total numbers from being counted. Also, factors other than apple drop were thought to influence declines in AMF activity for this variety because declines occurred before any substantial number of fruit had dropped.

On each day that traps were monitored for AMF, all apples falling into a 2m X 2m area under the tree were counted and then removed. The area of fruit collection was located in the same directional quadrant of the tree in which traps were placed. Apple collection continued until all of the fruit within a tree had dropped.

Stepwise linear regression analysis was used to examine effects of apple density, maximum temperature, windspeed and relative humidity on the number of apple maggot flies caught per day. Rainfall was considered separately because its influence on trap catch was not thought to be linear (see Appendix I). Other variables were omitted one at a time by selecting the variable with the largest (non-significant, $P>0.05$) value of P and re-computing the regression. A separate analysis was conducted for Wealthy, McIntosh 1 and McIntosh 2 varieties. Apple density within a tree was calculated for each date by taking the total number of drops for a tree minus cumulative drops to that date. All data points $\geq$ 1104 DD were included in the regression, as this point was estimated to be the beginning of dispersal from Wealthy trees (Figure 8) and therefore the earliest that dispersal should have occurred in the orchard.

Results and Discussion

The pattern of apple drop was similar among Wealthy trees, with peak drop (50 % cumulative drop) occurring at ca. 1075 DD (Figure 10). The pattern of apple drop for McIntosh trees was somewhat less synchronous, but all replicates peaked later than Wealthy trees, between 1125-1225 DD. No consistent difference in time of peak drop was apparent between McIntosh 1 and McIntosh 2.

Examination of number of apples in trees vs. number of flies caught showed similarities in the overall magnitude of these two factors within varieties (Figure 11). This suggests that the number of flies foraging within a tree was proportional to fruit density, though possible differences in the effectiveness of traps based on fruit density was not assessed.

Stepwise linear regression analysis eliminated the weather variables maximum temperature, wind speed and relative humidity from the model. Apple density, however, was found to be a good determinant of the decline in AMF activity ($P>0.001$, $R=.95$, $.84$, and $.85$ for Wealthy, McIntosh 1 and McIntosh 2, respectively, Figure 12). Solar radiation contributed significantly ($P=0.05$) to the model for McIntosh 2, accounting for 7% of the variation ($R=.91$, $P>0.001$) in the model containing variables for apple density and solar radiation.

Because apple density is based on cumulative drop, this study suggested that a threshold of apple density may have been important for the initiation of dispersal. This is somewhat difficult to ascertain from this study, since fluctuations in fly activity make the precise time of dispersal ambiguous. However, inspection of plots of apple maggot fly activity suggested that dispersal probably began later than 1104 DD for the McIntosh trees, possibly at ca. 1179 and 1211 DD for McIntosh 1 and McIntosh 2,
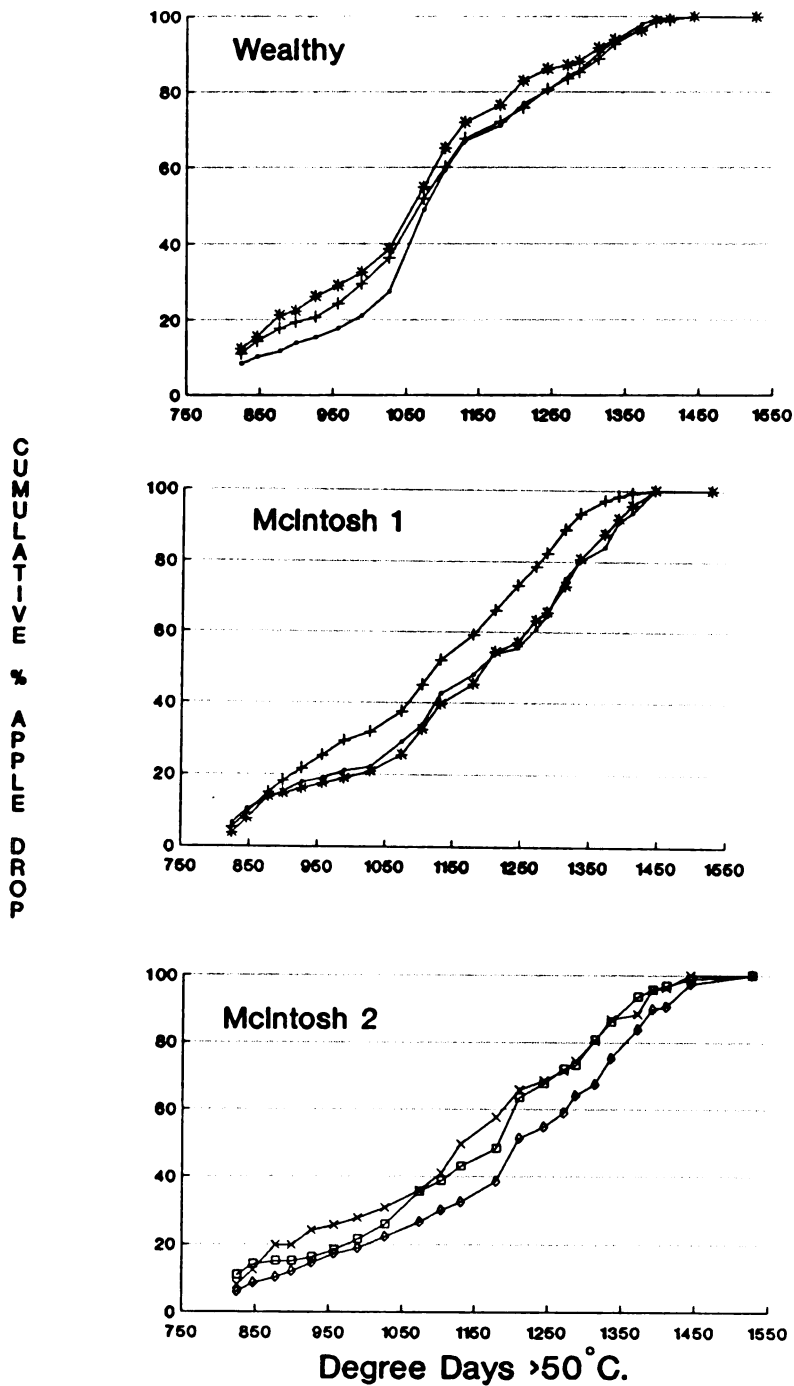
Figure 10. Cumulative percent apple drop for individual trees of different apple varieties in the Upjohn orchard.
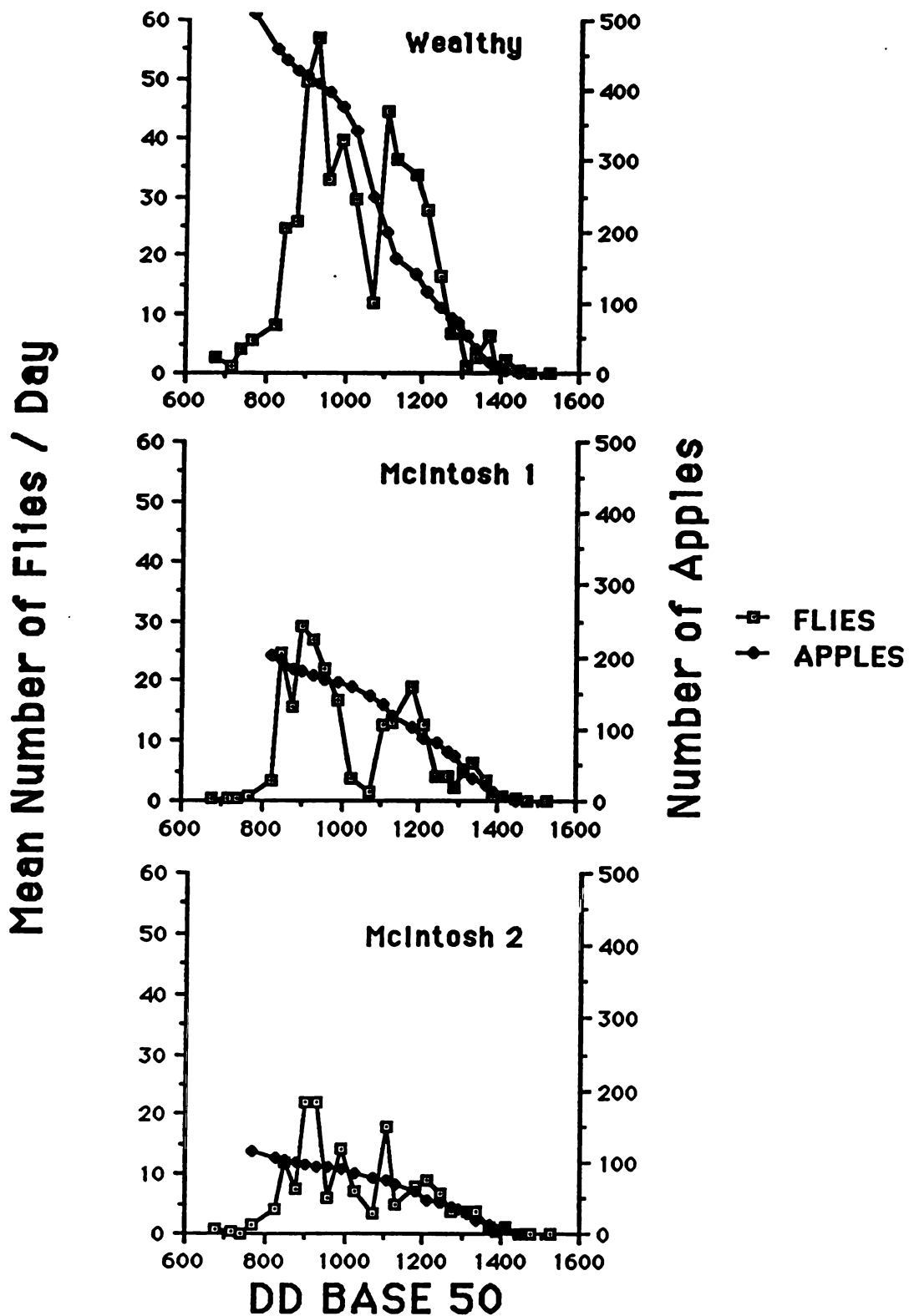
Figure 11. Relationship between trap catch and apple density for early apple varieties in the Upjohn orchard. Apple density within a tree was calculated for each date by taking the total number of drops for a tree minus cumulative drops to that date.
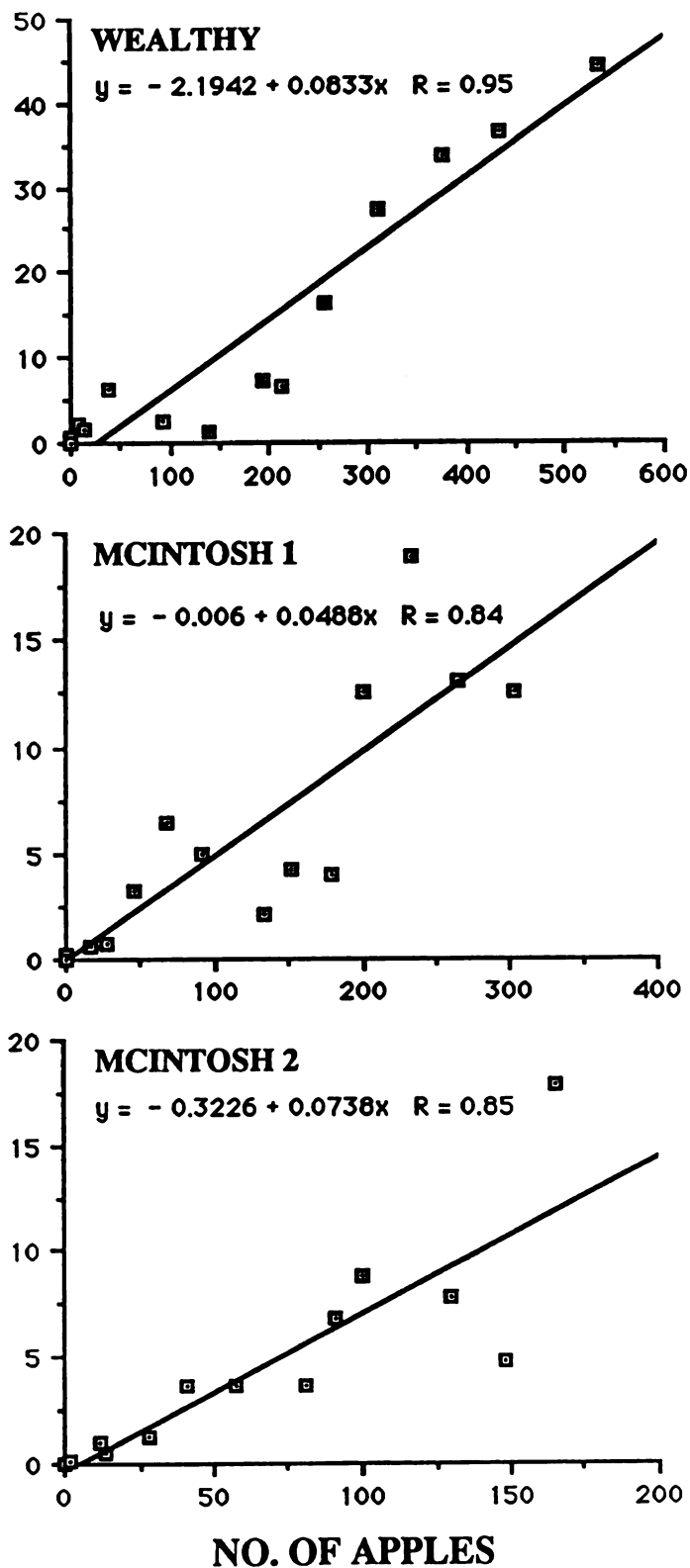
Figure 12. Relationship between trap catch and apple density for apple varieties in the Upjohn orchard. Apple density within a tree was calculated for each date by taking the total number of drops for a tree minus cumulative drops to that date.

respectively (see arrows, Figure 13). If these times are accurate, then a threshold effect was evident since dispersal would have begun at ca. 50-60% apple drop for both varieties.

This study shows the importance of apple phenology for the timing of AMF dispersal. Apple density is apparently the predominant factor regulating the timing of dispersal, given the amount of variation explained by regression, and the lack of significance of all but one weather variable. The significant effect of solar radiation for the McIntosh 2 variety indicates the need for a better understanding of the influence of weather on AMF trap catch.
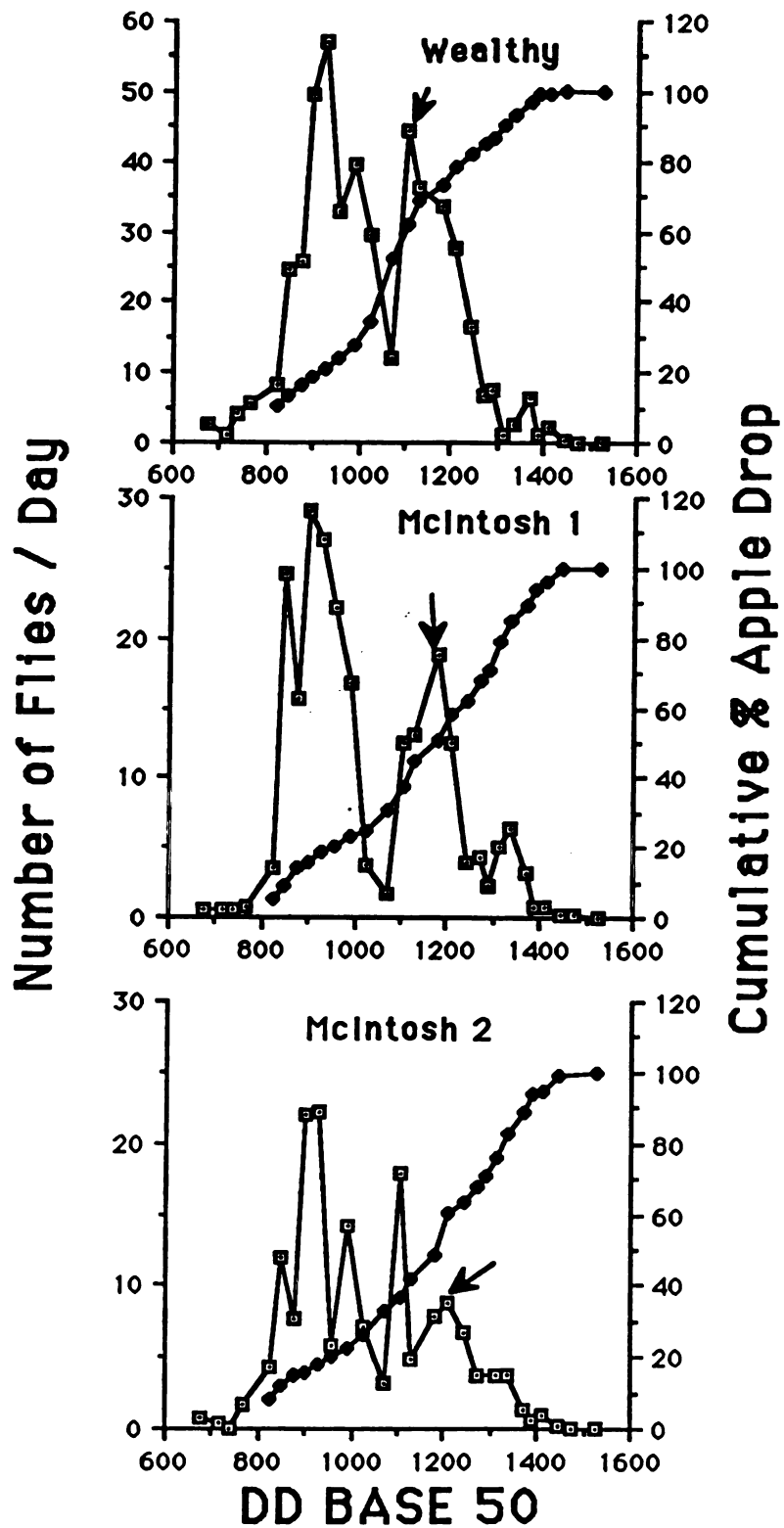
Figure 13. Relationship between mean trap catch of apple maggot flies and cumulative percent apple drop for apple varieties in the Upjohn orchard. Arrows indicate hypothesized beginning of fly dispersal.

Part 3. Distribution of Eggs Among Apples as an Index of Oviposition Deterring Pheromone Activity

Materials and Methods

Three collections of apples were made corresponding to "early", "peak" and "declining" apple maggot fly activity. These periods were estimated from the number of flies caught in traps. The first (early season) samples of apples for dissection were collected on 27 July for Wealthy and 28 July for McIntosh and Northern Spy, the second (peak activity) on 8 August for all three varieties, and a third (declining activity) on 22 and 26 August for Wealthy and McIntosh, respectively. A third (declining) sample was not collected for Northern Spy since most fruit remained on these trees when sampling was concluded in late September. Because of the late date, decline in fly activity was thought to reflect seasonal mortality rather than dispersal related to fruit quality or density. Five fruit were randomly selected from both a lower (0-2 m) and upper (2-4 m) strata, from each of 10 trees (early and peak samples) or 8 trees (declining sample), for each apple variety. Fruit was refrigerated at 5° C. until dissection.

Circumference of each fruit was recorded as a measure of relative fruit size. Apples were examined with a binocular microscope for oviposition punctures, and the number of unhatched eggs (or newly eclosed first instars) was recorded. These eggs and larvae represented a limited period of female egg laying activity since eggs usually hatch within a week (Dean and Chapman 1973).

Apples were grouped into units of 5 to meet requirements for ANOVA and LSD mean comparisons. The number of eggs per cm^2 surface of apple was compared for different activity periods, varieties, and tree strata, to

take into account increases in apple size as the season progressed. Distribution of eggs among apples was assessed by calculation of b from Taylor's Power Law (Elliot 1977).

Results and Discussion

Comparison of parasitism by R. pomonella between activity periods, apple varieties and tree strata

Overall trends in the number of eggs per apple and per cm^2 apple surface suggested that designation of fly activity periods was meaningful in that the largest numbers of eggs generally occured during the peak activity period (Table 3). LSD comparisons of means, however, showed differences between activity periods were significant only for Wealthy trees (4 out of 6 contrasts, Table 4).

Comparisons of the mean number of eggs per cm^2 apple surface showed no significant differences between upper and lower tree strata, with the exception of one sample (N. Spy, peak season). Sampling constraints in this study prevented the collection of apples from the very tops of trees. It is not likely that this influenced results, since previous studies have indicated that representative samples for apple maggot damage can be taken from any part of the tree (Stanley et al. 1987, Leroux & Mukerji 1963).

Differences in numbers of eggs between apple varieties were significant during peak activity in 4 out of 6 contrasts which suggested that apples differed in "attractiveness", in terms of suitability for oviposition during this time. In order to compare numbers of eggs between apple varieties, it must be assumed that rates of oviposition were not affected by differences in the number of apples present in trees. This assumption is based on the fact that flies could move easily between varieties, and on the indication that the number of flies

Table 3. No. of apple maggot eggs in relation to activity period, apple variety and tree strata.

Sample	Variety	Stratum	Tmt.	N	Eggs/apple (mean±SE)	N	Eggs[1]/cm^2 (X 10E-3) (mean+SE)
Early	Wealthy	1	1	49	.37 ± .53	10	1.7 ± .91
		2	2	49	.27 ± .32	10	1.0 ± .33`
	McIntosh	1	3	50	.38 ± .44	10	1.1 ± .29
		2	4	48	.46 ± .51	10	1.2 ± .24
	N. Spy	1	5	46	.78 ± .93	9	2.5 ± .52
		2	6	47	.58 ± .95	10	1.7 ± .53
Peak	Wealthy	1	7	41	1.50 ± .28	8	4.3 ±1.00
		2	8	42	1.50 ± .19	9	5.2 ± .12
	McIntosh	1	9	50	1.00 ± .09	10	2.3 ± .15
		2	10	48	.17 ± .18	10	4.0 ± .71
	N. Spy	1	11	48	1.00 ± .20	10	3.2 ± .22
		2	12	49	.53 ± .42	10	1.5 ± .22
Declining	Wealthy	1	13	38	.13 ± .12	8	3.2 ± .13
		2	14	34	.24 ± .25	7	5.6 ± .18
	McIntosh	1	15	40	.18 ± .25	8	3.0 ± .12
		2	16	38	.21 ± .33	8	4.0 ± .19

1 No. eggs/cm^2 apple surface

Table 4. Differences between means for the no. of apple maggot eggs per cm^2 apple surface.

==

Comparisons between:

Fly Activity Periods

<u>Variety</u>	<u>Tmt.[1] Contrast</u>	<u>Mean Difference[2]</u>
Wealthy	1- 7	.0260 *
	7-13	.0040 *
	1-13	.0014 NS
	2- 8	.0042 *
	2-14	.0005 NS
McIntosh	3- 9	.0008 NS
	9-15	.0001 NS
	3-15	.0008 NS
	4-10	.0008 NS
	10-16	.0000 NS
	4-16	.0008 NS
N. Spy	5-11	.0007 NS
	6-12	.0002 NS

----

1   Upper and lower strata were examined separately.
    (see Table 3 for treatment descriptions)

2   * Significant (P>0.05, LSD test for mean comparisons)

Table 4. (continued)

===

Comparisons between:

	Apple Varieties		**Tree Strata**	
	Tmt. Contrast	Mean Difference	Tmt. Contrast	Mean Difference
Early	1 -3	.0006 NS	1- 2	.0007 NS
	3- 5	.0014 *	3 -4	.0008 NS
	1 -5	.0007 NS	5 -6	.0007 NS
	2 -4	.0001 NS		
	4 -6	.0006 NS		
	2 -6	.0007 NS		
Peak	7 -9	.0041 *	7 -8	.0009 NS
	9-11	.0030 *	9-10	.0002 NS
	7-11	.0011 NS	11-12	.0017 *
	8-10	.0048 *		
	10-12	.0011 NS		
	8-12	.0035 *		
Declining	13-15	.0000 NS	13-14	.0002 NS
	14-16	.0002 NS	15-16	.0000 NS

----

present in trees (based on trap catch), appears to be a function of the number of apples (Figure 11) varieties, and the number of flies present in trees (based on trap catch) appears to be a function of the number of apples (Figure 11).

Distribution of eggs among apples

Distribution of eggs among apples was random for all three sample periods: early, $b=1.05 \pm .197$; peak, $b=.79 \pm .294$; and declining, $b=1.49 \pm .660$ (Figure 14). No uniformity in egg distribution was found. This suggests that ODP was not a factor in the dispersal of flies from trees, or in regulating oviposition during the other times that apples were collected.

This result does not agree with a study conducted by Cameron and Mukerji (1974) which examined egg distribution among apples that were non-uniformly distributed within trees. Though the authors claimed that egg distributions were uniform, b values they provided indicated that distributions were clumped (Taylor 1961). Visual observations indicated that apple distribution among trees in our study was also not uniform. However, differences in egg distribution between Cameron and Mukerji's study and ours may have been the result of differences in the distributions of apples.

The conclusion that ODP was not at work in the Upjohn orchard during the time periods examined is supported by the high levels of apple maggot damage present. Total numbers of oviposition punctures were counted only for the first collection of apples, and therefore underestimate seasonal damage. Mean numbers of punctures per fruit were 3.02 (Wealthy), 3.44 (McIntosh), and 6.96 (N. Spy). It is possible that ODP was not present long enough to deter oviposition, since significant rains occurred prior to apple collections on 23 July (46mm); and on 5 (46mm), 15 (34mm), and 23 (10mm) of August. It is also possible that ODP is ineffective in an orchard situation
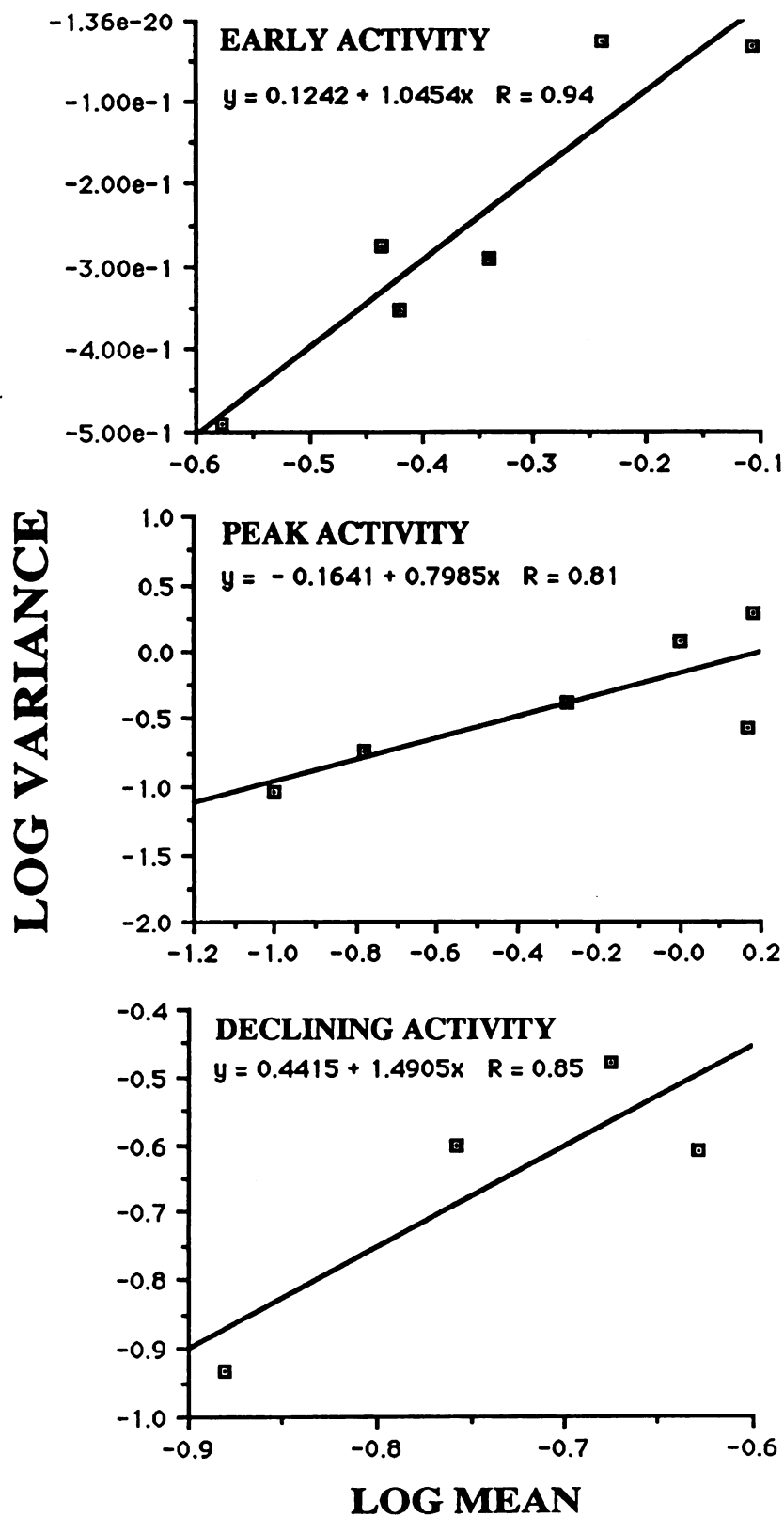
Figure 14. Relationship between mean and variance of the number of apple maggot eggs apple^{-1} for 3 periods of apple maggot fly activity in the Upjohn orchard.

where large apple maggot populations may foster strong "drives" to oviposit among females.

Chapter 3.

Directional Movement of Apple Maggot Flies

A number of experimental releases of apple maggot flies (AMF) was conducted at the Kellog Biological Station in the summer of 1988. Flies were released into an arena containing 24 potted apple trees arranged in 3 concentric circles. The objective was to determine if there was a directedness to AMF dispersal, and if so, whether direction was related to wind. Information on the directional movement of AMF would be helpful in predicting the pest threat potential of unmanaged apple trees, and might also provide insight into behavioral aspects of apple maggot dispersal.

Materials and Methods

Apple maggots for release were obtained from infested Wealthy and McIntosh apples collected from the Upjohn Company orchard in the Fall of 1987. Apples were placed on one-half inch mesh hardware cloth set over plastic trays containing moist vermiculite. Vermiculite was sifted once a week to collect and count apple maggot pupae, which were then stored at 3° C. in plastic containers until the following Summer. Pupae were removed from cold storage and held at ca. 25 °C. until adult emergence. When the first flies emerged, vermiculite containing pupae was transfered to a pan of water where floating pupae were collected by skimming the surface. These were allowed to air dry on paper towels. Once dry, pupae were transfered to a paper bag containing a small amount of Dayglo® fluorescent powder and were gently shaken to distribute the dye. Dye-coated pupae were placed ca. 200 each in plastic petrie dishes filled with vermiculite kept moist by periodic additions of water. These were set inside emergence cages.

47

Apple maggot adults were held at 22 °C. on a 16:8 light: dark regime. Flies fed ad lib on filter paper that had been dipped in a liquid mixture of brown sugar and yeast hydrolysate. At least twenty four hours before release, cages containing flies were moved to an outside shelter, to allow some time for acclimatization.

The release site was a 200 X 225 m alfalfa field bordered on the North by a tree-lined road, on the South by an open grass pasture, and by woods to the West and East (woods to the east began at ca. 90 ° and ran south along the east edge of the field, Figure 18). Apple trees were arranged in 3 concentric circles at distances of 33, 66 and 100 m from the center. Each circle contained 8 non-fruiting, 7-8 year old crab apple trees (*Malus sargenti* sp.) ranging from 1.5 to 2 m in height. One 2.5-inch red sticky sphere and 1 yellow Pherocon® AM trap (cut in half) were placed in each tree. Each tree also contained a vial of synthetic apple volatile. The release point consisted of 5 crab apple trees without apple maggot traps, in the center of the arena.

Statistical Analysis

Data in the form of measurements of angles are considered circular variables and require methods in circular statistics for analyses. Rao's spacing test was used to determine if AMF catch distributions indicated a directedness to movement. This test is suitable for multimodal as well as unimodal distributions (Batschelet 1981). Mean angle of capture (based on tree location) and mean wind direction were calculated for each date that distribution differed from randomness (Batschelet 1981). Data for wind came from weather stations at the Kellog Biological Station. Wind direction for a given date represented the mean of hourly wind vectors for that date from 0800-2000 hours.

tree-lined road

225 m

woods

200 m

alfalfa

33 m

chain-link fence

open grass pasture

woods

N

● potted apple trees
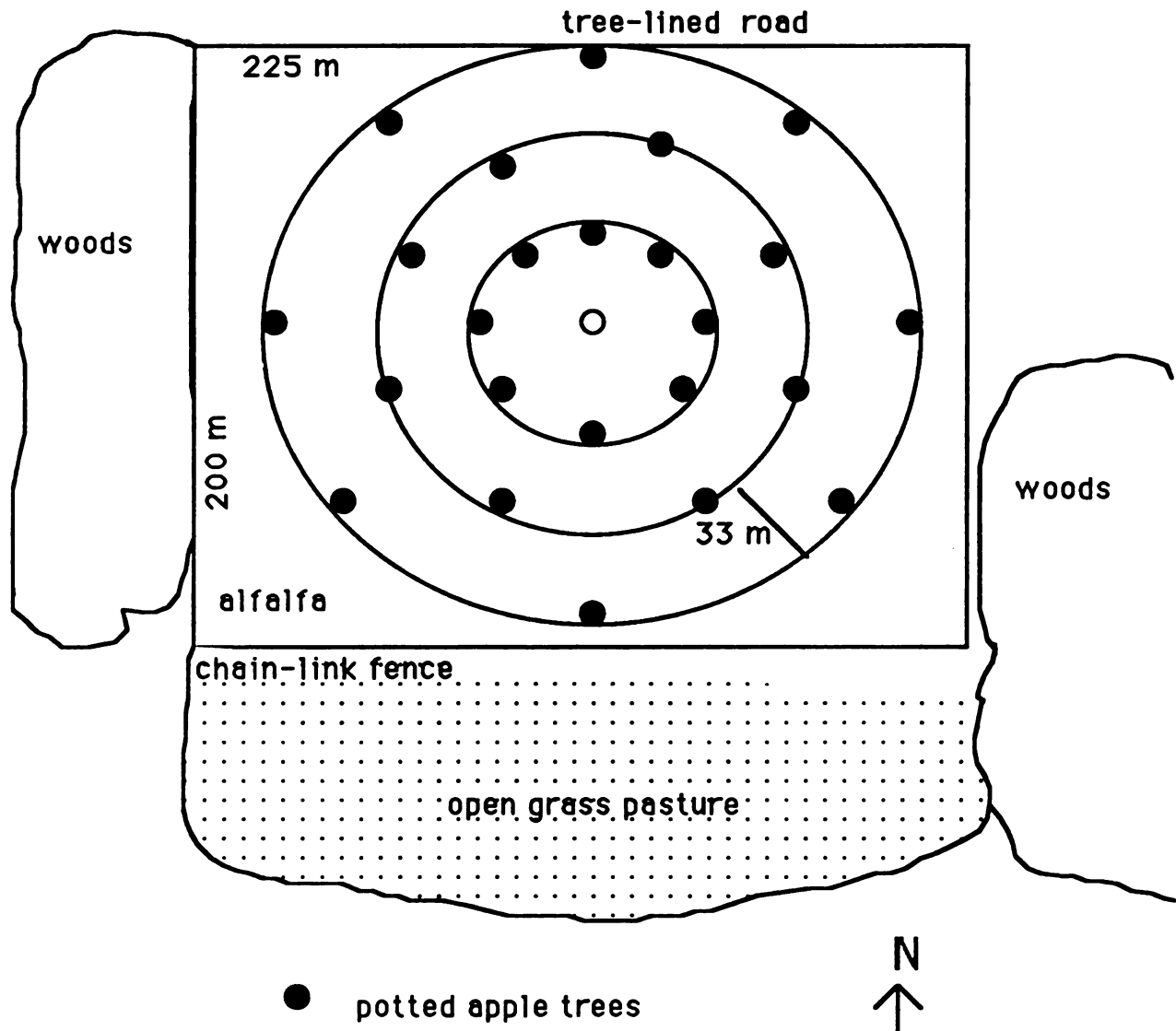
Figure 15. Diagram of release site for apple maggot flies at the Kellog Biological Station.

Results and Discussion

A total of 154 AMF were recaptured from the 5 releases. Percentage of recapture within a release ranged from 2.6 to 7.0 % (Table 5). All of the 24 potted apple trees caught AMF at some point in the study, though catch for individual trees varied among releases (Figure 16). More flies were caught in the innermost (33m) circle of traps, but this result was not surprising because these traps were more dense in relation to area than those further from the release point.

Distributions of AMF capture were examined for 10 different dates and for all releases combined to determine whether there was deviation from randomness. Significance was found for 4 dates on 1, 8, 14, and 15 September, and for the overall distribution of AMF for the combined releases (Table 6). Examination of individual dates to determine if directedness was related to wind direction showed no apparent relationship between mean angle of capture and mean wind direction (Table 7). Orientation into the wind (anemotaxis) might be expected to show a small angular deviation between angles of capture and wind direction. On the other hand, displacement due to wind acting as a medium for movement should show an ca. 180° difference in angular deviation. Neither of these situations was indicated by these data, though some caution must be exercised because of the small number of samples. It is also possible that anemotaxis operated only within a short distance, after considerable displacement had already occurred, in which case it would not have been shown by this study.

The proportion of AMF moving in a given direction was determined by dividing the arena into 8 22.5° sectors, each containing 3 trees (Figure 17). For dates where directedness was significant, most flies were captured in

Table 5. Statistics for 5 releases of apple maggot flies at the Kellog Biological Station by release, including total numbers released, numbers of immature and mature flies, and percent recaptured.

release date	females/ males [1]	immature/ mature[2]	total released	number recaptured	%
Aug. 21	196/102	0/196	298	21	7.0
Aug. 26	---	254/211	465	12	2.6
Sept. 1	---	251/186	437	25	5.7
Sept. 8	---	527/517	1044	57	5.2
Sept. 14	---	322/540	862	39	4.5

1   sex ratios determined for the first release only

2   immature flies 1-7 days old

  mature flies >7 days old

No. 1 (21 flies)

No. 2 (12 flies)

No. 3 (25 flies)

No. 4 (57 flies)

No. 5 (39 flies)
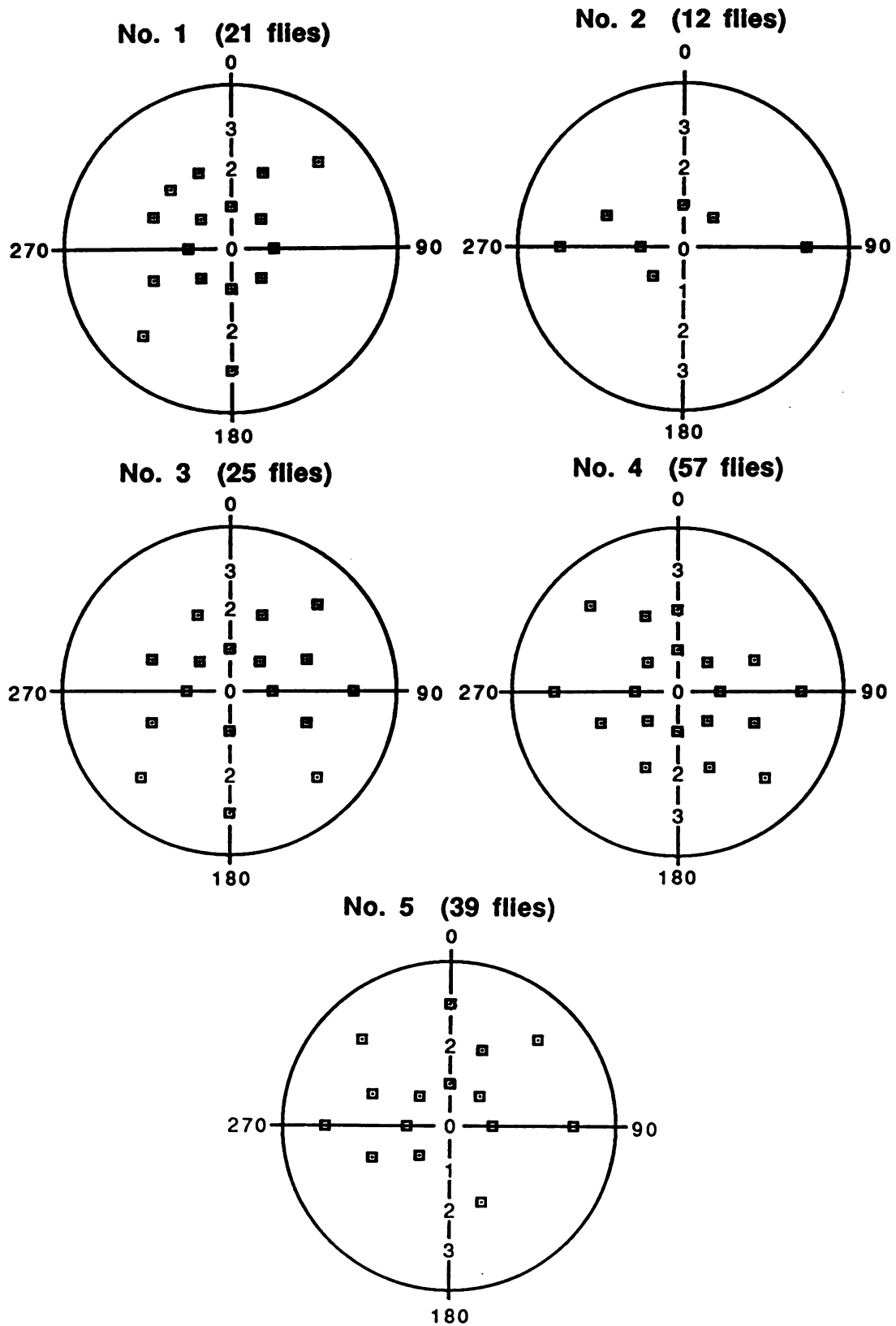
Figure 16. Locations of potted apple trees that caught apple maggot flies, and the number of flies caught for each of 5 releases.

Table 6. Actual and critical values of U for determining significance in the directedness of apple maggot fly dispersal using Rao's spacing test.

===

Date	No. of flies	U^1	U(alpha=.05)
8/21	11	84.0	170.3
8/22	7	77.0	177.8
8/26	6	173.0	180.7
9/1	12	172.5*	169.2
9/2	9	115.0	173.5
9/8	27	240.0*	158.9
9/9	12	120.0	169.2
9/10	8	112.5	112.5
9/14	25	230.4*	158.9
9/15	13	193.8*	167.8
All Releases	150	321.6*	144.7

- -

1   * indicates significant difference from randomness, U > U (alpha).

Table 7. Angular deviation of mean angle of apple maggot fly capture from the mean wind vector.

===

Date	Mean angle of capture°	Mean wind direction°	Angular deviation°[1]
9/1	289.2 ± 21.2	171.8 ± 4.4	117.4
9/8	51.5 ± 10.1	174.1 ± 3.8	122.6
9/14	290.4 ± 12.0	284.1 ± 14.8	6.0
9/15	44.2 ± 17.1	84.7 ± 3.5	40.5

----

1   Based on the smallest angular distance given that 0°= North and angles are numbered clockwise.

Figure 17. a. Diagram showing division of release site into 8 directional sectors. b. Proportion of apple maggot flies caught in each of 8 sectors for dates where distribution was significantly different from randomness, and for all releases combined.

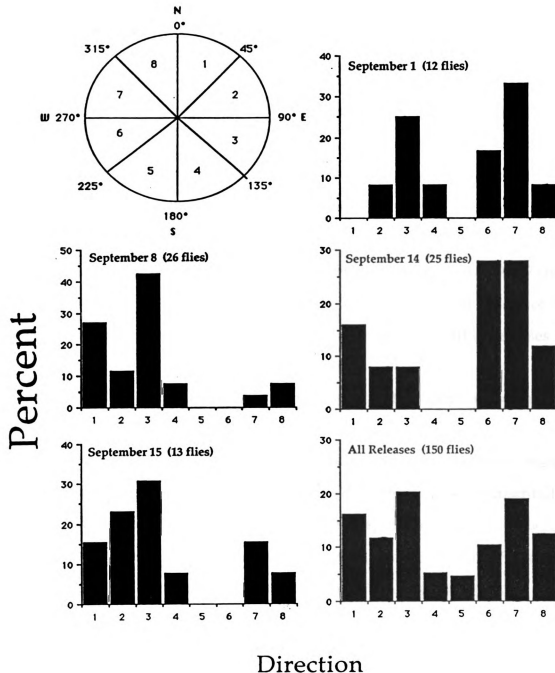sectors 3 and 7, while the fewest were caught in sectors 4 and 5. This was also the pattern for all releases combined. The reason for this is not known, but may have been related to visual cues provided by large trees, which were present on all field borders except the south. There is also the possibility that AMF left the field, perhaps to feed in adjacent areas, and then returned, which might bias the direction of capture. The possibility that AMF entered the release arena from outside areas can not be excluded because fluorescent marks on flies were not always discernable. This is likely a remote possibility, however, because traps hung in apple trees near the release site were no longer catching AMF at the time of releases. It is possible that AMF could have come from the adjacent woods, but the coincidence in timing of capture with releases indicates that most flies were likely the result of releases (Figure 18).

Studies using distributions resulting from trap catch are always limited by the fact that trap catch is an end result that does not track actual insect movement. This study therefore assumes a relationship between angle of capture and direction of orientation. Based on the number of distributions that did not differ from randomness and the apparent lack of correlation between angles of capture and wind direction, direction of AMF dispersal appears to be independent of wind direction. The degree to which directedness in AMF dispersal occurs is not clear from this study since randomness was indicated for ca. one-half of the distributions examined. Results may have been limited by the number of flies released. Releases of larger numbers of flies in an arena similar to the one in this study might provide an answer to this question. In addition, the success in captures of flies at all distances in this study indicates that this experimental set-up may be useful in studying possible long range cues in the attraction of AMF.
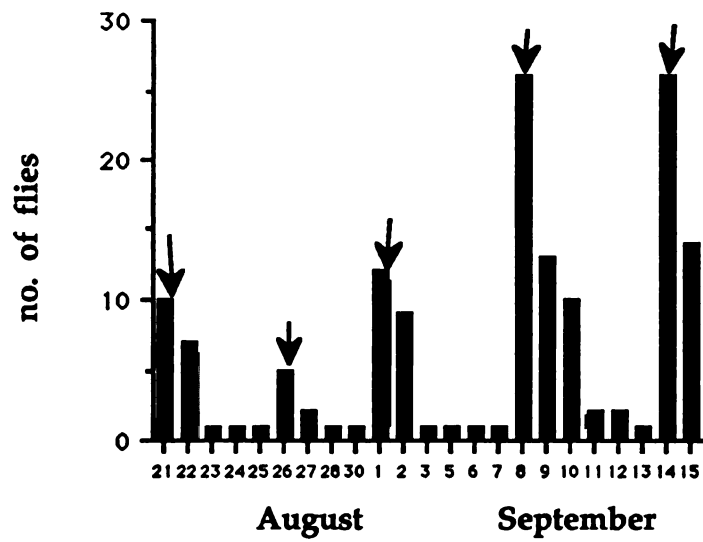
Figure 18. Number of apple maggot flies caught day^{-1} in release arena at the Kellog Biological Station. Arrow indicate days on which flies were released.

APPENDICES

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: _____1990-02_____

Title of thesis or dissertation (or other research projects):

Facultative Dispersal of the Apple Maggot, <u>Rhagoletis</u>

<u>Pomonella</u> (Walsh)(Diptera: Tephritidae).

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)
__Janyce Marie Ryan_____

_____

_____

Date _May 12, 1990_

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Included as Appendix 1 in copies of thesis or dissertation. Museum(s) files. Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

Voucher Specimen Data

Page __1__ of __1__ Pages

		Museum where deposited	M.S.U.	
Number of:		Other		
		Adults ♂	9	
		Adults ♀	10	
		Pupae		
		Nymphs		
		Larvae		
		Eggs		

Species or other taxon	Label data for specimens collected or used and deposited
DIPTERA: TEPHRITIDAE Rhagoletis pomonella	Kalamazoo Co., MI September, 1987

(Use additional sheets if necessary)

Investigator's Name(s) (typed)
Janyce Marie Ryan

Date May 17, 1990

Voucher No. __1990-02__
Received the above listed specimens for
deposit in the Michigan State University
Entomology Museum.

Roland L. Fischer 17 May 1990
Curator   Date

Appendix 2

Effects of Rainfall on Apple Maggot Fly Activity

Inspection of plots of apple maggot fly (AMF) activity showed frequent, rapid declines in trap catch that occurred at ca. the same time for most trees (Figure 19). Since declines corresponded with sample dates preceeded by rainfall, this relationship was examined by conducting paired T-tests of trap catch following rain vs. that not following rain. Five days following rainfall were selected within the main period of apple maggot fly activity; ca. 850-1200 DD (Figure 20), and these were paired with the day closest in DD that was not preceeded by rainfall (Table 8). Each pair served as a replicate within blocks (apple varieties) . Dates within a pair differed by <50 DD accumulations so that fly density, excluding the influence of environmental parameters, was assumed to be similar.

Results of paired T-tests were significant (P>0.05) for all varieties, indicating that apple maggot fly activity was significantly reduced on days immediately following rainfall (Table 9). Omission of data points for all "rain" days (11 sample dates were preceeded by rain and therefore omitted) had the effect of "smoothing out " curves, (Figure 21).

Rainfall appears to decrease AMF activity. This result seems reasonable, since flies might be expected to take cover during rains. It should be considered with some caution, however, since other weather parameters (e.g. windspeed and solar radiation) are likely to be correlated with rainfall. In addition, the relationship between rainfall and trap catch is probably more complex, and depends on intensity and duration of rainfall as well as accumulation. A light rainfall in some instances may increase trap catch (Looses 1976). This study indicates that there is a need for more information
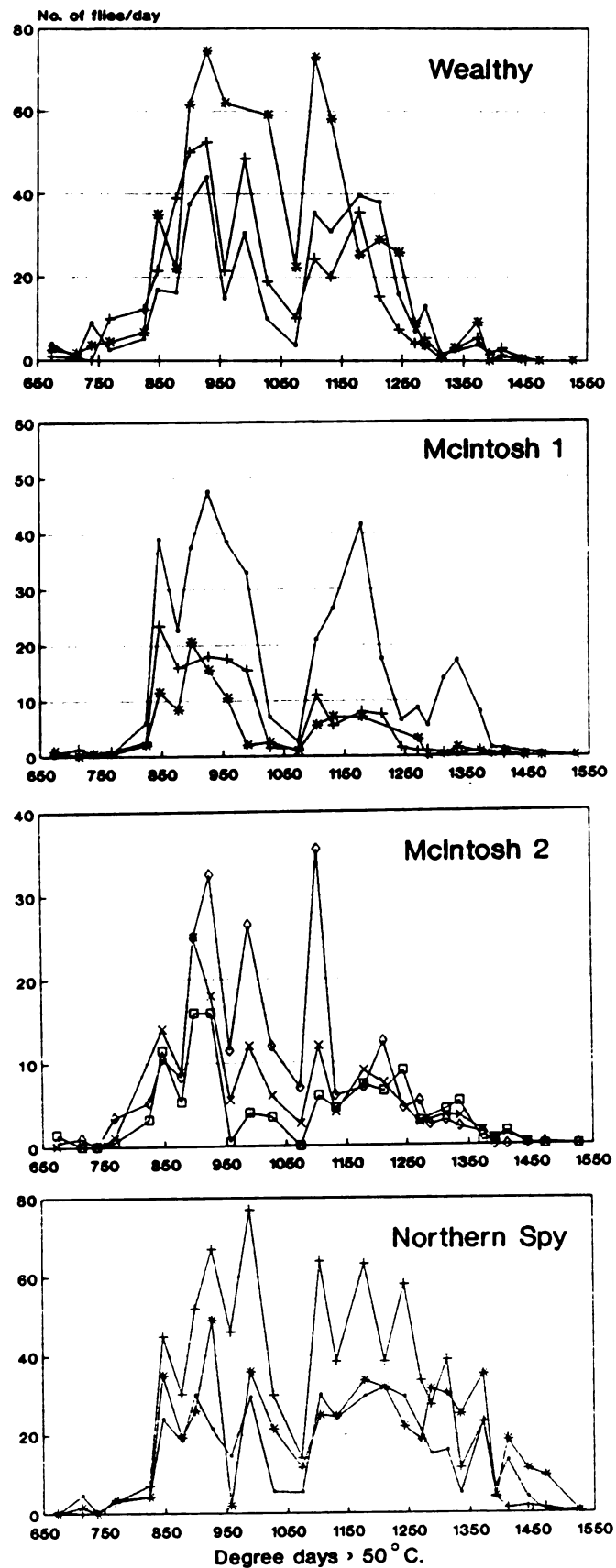
Figure 19. Combined red and yellow trap catch of apple maggot flies for indivual trees of different apple varieties in the Upjohn orchard.

Figure 20. Mean (combined red and yellow) trap catch of apple maggot flies for 3 replicates of each apple variety. Arrows indicate selected sample dates that were preceeded by rainfall ("rain" dates).

Table 8. Dates and degree day accumulations for days following rainfall vs. those not following rainfall.

Rep	"No rain" day	DD	"Rain" day	DD	Actual date of rain	Amount
1	7-26	899	7-24	877	7-23	46 mm
2	7-28	926	7-30	957	7-30	2 mm^2
3	8-1	989	8-3	1027	8-3	0.5 mm
4	8-8	1104	8-6	1074	8-5	46 mm
5	8-13	1179	8-10	1131	8-9	27 mm

1 Degree Days > 50 F°

2 Rain accompanied by avg. daily winds of 2.3 m/s

Table 9. Differences in activity and values of T for "rain" vs. "no-rain" days.

===

Block	Variety	DF	Differences in Activity [1](X+SE)	T
1	Wealthy	4	17.53 ± 6.19	2.83*
2	McIntosh 1	4	9.61 ± 1.80	5.34*
3	McIntosh 2	4	11.07 ± 2.59	4.27*
4	N. Spy	4	21.88 ± 3.59	6.10*

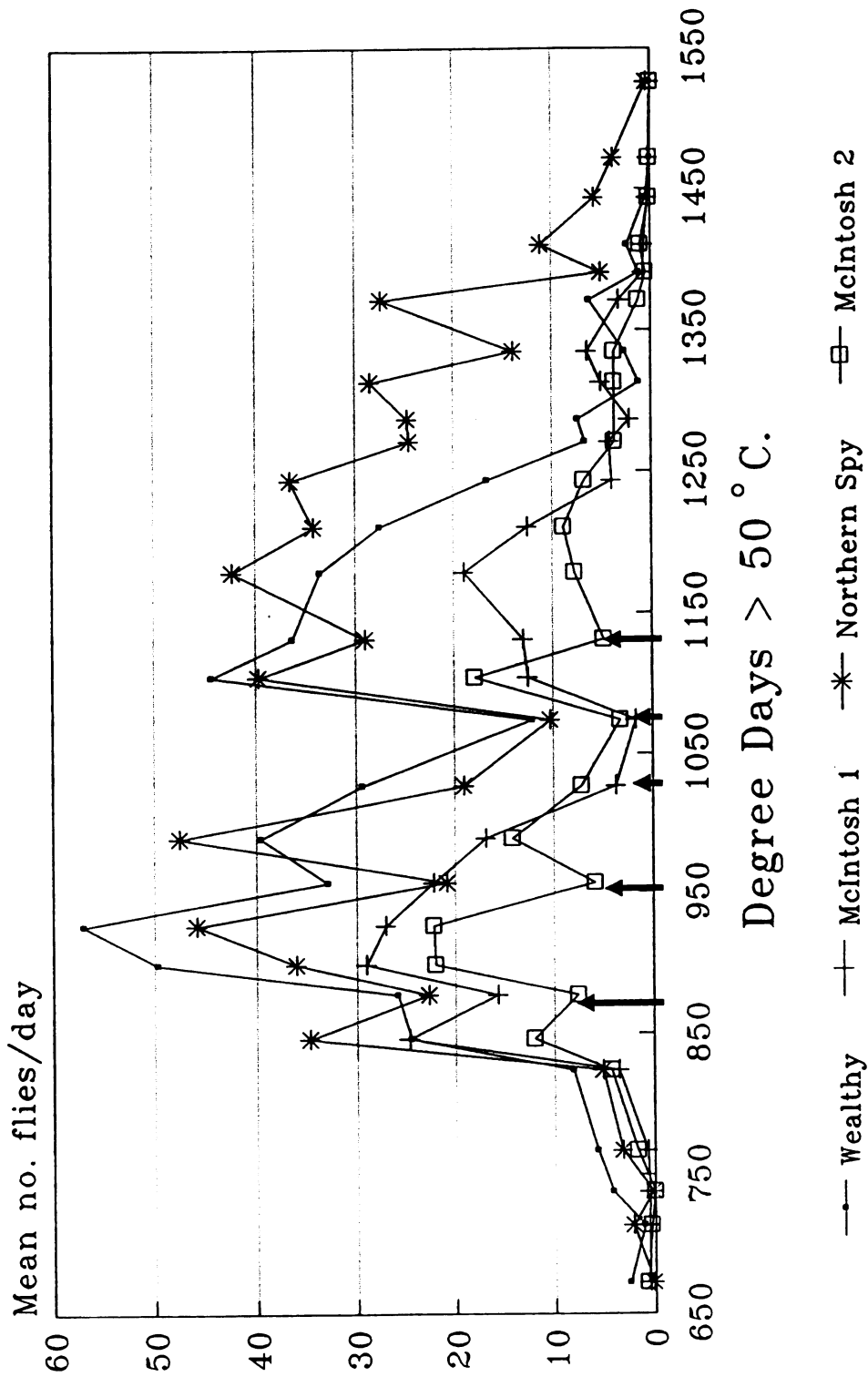1 measured as mean no. flies caught/day (N=3)
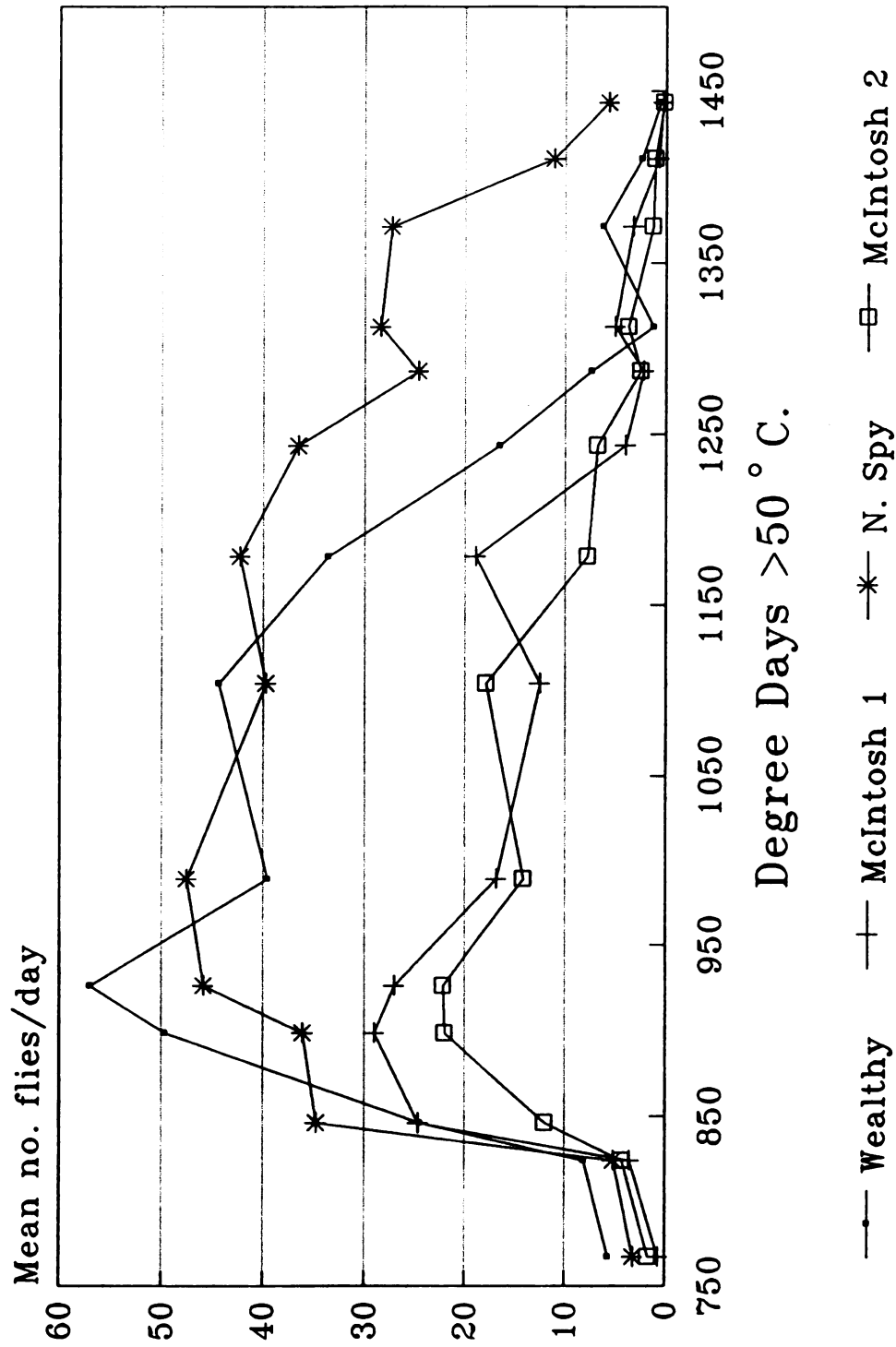* significant (P>0.05) Paired T-test

Figure 21. Mean (combined red and yellow) trap catch of apple maggot flies for 3 replicates of each apple variety, with "rain" dates omitted.

on the effects of weather on apple maggot behavior. A better understanding of these influences will allow more accurate interpretation of trap catch data.

LITERATURE CITED

LITERATURE CITED

Aliniazee, M.T. & R.L. Westcott. 1987. Flight period and seasonal development of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae), in Oregon. Ann. Entomol. Soc. Am. 80(6): 823-28.

Averill, A.L. & R.J. Prokopy. 1989. Distribution patterns of *Rhagoletis pomonella* (Diptera: Tephritidae) eggs in hawthorn. Ann. Entomol. Soc. Am. 82(1): 38-44.

Baskerville, G.L. & P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 514-17.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, Inc. New York.

Begon, M. & M. Mortimer. 1981. Population Ecology: A Unified Study of Animals and Plants. Blackwell Scientific Publications. Oxford.

Bourne, A.I., W.H. Thies & F.R. Shaw. 1923. Some observations on long distance dispersal of apple maggot flies. J. Econ. Ent. 27: 352-55

Burnett, A.M. & K.L. Hays. 1974. Some influences of meteorological factors on flight activity of female horse flies (Diptera: Tabanidae). Environ. Entomol. 3: 515-21.

Bush, G.L. 1969. Sympatric host race formation and specialization in frugivorous flies of genus *Rhagoletis* (Diptera: Tephritidae) Evolution 23: 237-51.

Cameron, P.J. & F.O. Morrison. 1974. Sampling methods for estimating the abundance and distribution of all life stages of the apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae). Can. Ent. 106: 1025-34.

Dale, W.E. & R.C. Axtell. 1975. Flight of the salt marsh Tabanidae (Diptera), *Tabanus nigrovittatus, Chrysops atlanticus* and *C. fugliginosus*: correlation with temperature, light, moisture and wind velocity. J. Med Ent. 12, 5: 551-57.

Dean, R.W. & P.J. Chapman. 1973. Bionomics of the apple maggot in eastern New York. NY St. Ag. Exp. Sta. Search 7. 63 pp.

Dingle, H. 1972. Migration strategies of insects. Science 175: 1327-35.

Drummond, F., E. Groden & R.J. Prokopy. 1984. Comparative efficacy and optimal positioning of traps for monitoring apple maggot flies (Diptera: Tephritidae). Environ. Entomol. 13: 232-35.

Elliot, J.M. 1977. Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates. Freshwater Biological Association Scientific Publication No. 25.

Hamilton, J.G. & S.H. Gage. Apple maggot, Rhagoletis pomonella (Walsh) occurrence and damage in Michigan apple orchards: a case study in analysis of the CCMS regional crop monitoring data base. In review.

Hamilton, J.G., S.H. Gage, & M.E. Whalon. Effect of soil moisture on adult emergence of apple maggot Rhagoletis pomonella (Walsh) (Diptera: Tephritidae). In review.

Hassell, M.P. & T.R.E. Southwood. 1978. Foraging strategies of insects. Ann. Rev. Ecol. Syst. 9:75-98.

Hughes, R.D. 1979. Movement in population dynamics. Pp. 14-34 In R.L. Rabb & G.G. Kennedy eds. Movement of Highly Mobile Insects: Concepts and Methodology in Research.

Johnson, C.G. 1969. Migration and Dispersal of Insects by Flight. Methuen, London.

Johnson, P.C. 1983. Response of adult apple maggot (Diptera: Tephritidae) to Pherocon AM traps and red spheres in a non-orchard habitat. J. Econ. Entomol. 76: 1279-84.

Keck, C.B. 1934. Relation of oviposition punctures of the mediterranean fruit fly to the premature dropping of citrus fruits. J. Econ. Ent. 28: 908-914.

Kennedy, J.S. 1961. A turning point in the study of insect migration. Nature 189: 785-91.

Krebs, J.R. J.C. Ryan, & E.L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 27: 953-64.

Leroux, E.J. & M.K. Mukerji. 1963. Notes on the distribution of immature stages of the apple maggot Rhagoletis pomonella (Walsh) (Diptera: Tephritidae), on apple in Quebec. Ann. Entomol. Soc. Quebec 8: 60-70.

Levins, R. 1964. The theory of fitness in a heterogeneous environment. IV. The adaptive significance of gene flow. Evolution 18: 635-38.

Maxwell, C.W. & E.C. Parsons. 1968. The recapture of marked apple maggot adults in several orchards from one release point. J. Econ. Ent. 61: 1157-59.

Moericke, V., R.J. Prokopy, S. Berlocher & G.L. Bush. 1975. Visual stimuli eliciting attraction of Rhagoletis pomonella (Diptera: Tephritidae) flies to trees. Ent. Exp. & Appl. 18: 497-507.

NcNeil, J.N. & B.D. Roitberg. 1985. Experimental analysis of individual behavior as a means to understanding population dispersal. In Makenzie, D.R. et al. eds. The Movement and Dispersal of Agriculturally Important Biotic Agents. Claitor's Baton Rouge, LA.

Neilson, W.T.A., I. Rivard, R. Trottier, & R.J. Whitman. 1976. Pherocon AM standard traps and their use to determine spray dates for control of the apple maggot. J. Econ. Entomol. 69 (4): 527-32.

Olsen, L.G. 1982. Parameters affecting emergence and management strategies of the apple maggot fly, Rhagoletis pomonella (Walsh) Diptera: Tephritidae. Ph.D. dissertation, Michigan State University.

Opp, S.B. & R.J. Prokopy. 1984. Comparative efficacy and optimal positioning of traps for monitoring apple maggot flies (Diptera: Tephritidae). Environ. Entomol. 13: 232-35.

Opp, S.B. & R.J. Prokopy. 1986. Variation in laboratory oviposition by Rhagoletis pomonella (Diptera: Tephritidae) in relation to mating status. Ann. Entomol. Soc. Am. 79: 705-10.

Parker, G.A. & R.A. Stuart. 1976. Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. Am. Nat. 110: 1055-76.

Phipps, C.R. & C.O. Dirks. 1932. Dispersal of the apple maggot. J. Econ. Ent. 26: 576-82.

Prokopy, R.J. & K.I. Hauschild. 1979. Comparative effectiveness of sticky red spheres and Pherocon AM standard traps for monitoring apple maggot flies in commercial orchards. Environ. Entomol. 8: 696-700.

Leroux, E.J. & M.K. Mukerji. 1963. Notes on the distribution of immature stages of the apple maggot Rhagoletis pomonella (Walsh) (Diptera: Tephritidae), on apple in Quebec. Ann. Entomol. Soc. Quebec 8: 60-70.

Levins, R. 1964. The theory of fitness in a heterogeneous environment. IV. The adaptive significance of gene flow. Evolution 18: 635-38.

Maxwell, C.W. & E.C. Parsons. 1968. The recapture of marked apple maggot adults in several orchards from one release point. J. Econ. Ent. 61: 1157-59.

Moericke, V., R.J. Prokopy, S. Berlocher & G.L. Bush. 1975. Visual stimuli eliciting attraction of Rhagoletis pomonella (Diptera: Tephritidae) flies to trees. Ent. Exp. & Appl. 18: 497-507.

NcNeil, J.N. & B.D. Roitberg. 1985. Experimental analysis of individual behavior as a means to understanding population dispersal. In Makenzie, D.R. et al. eds. The Movement and Dispersal of Agriculturally Important Biotic Agents. Claitor's Baton Rouge, LA.

Neilson, W.T.A., I. Rivard, R. Trottier, & R.J. Whitman. 1976. Pherocon AM standard traps and their use to determine spray dates for control of the apple maggot. J. Econ. Entomol. 69 (4): 527-32.

Olsen, L.G. 1982. Parameters affecting emergence and management strategies of the apple maggot fly, Rhagoletis pomonella (Walsh) Diptera: Tephritidae. Ph.D. dissertation, Michigan State University.

Opp, S.B. & R.J. Prokopy. 1984. Comparative efficacy and optimal positioning of traps for monitoring apple maggot flies (Diptera: Tephritidae). Environ. Entomol. 13: 232-35.

Opp, S.B. & R.J. Prokopy. 1986. Variation in laboratory oviposition by Rhagoletis pomonella (Diptera: Tephritidae) in relation to mating status. Ann. Entomol. Soc. Am. 79: 705-10.

Parker, G.A. & R.A. Stuart. 1976. Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. Am. Nat. 110: 1055-76.

Phipps, C.R. & C.O. Dirks. 1932. Dispersal of the apple maggot. J. Econ. Ent. 26: 576-82.

Prokopy, R.J. & K.I. Hauschild. 1979. Comparative effectiveness of sticky red spheres and Pherocon AM standard traps for monitoring apple maggot flies in commercial orchards. Environ. Entomol. 8: 696-700.

Prokopy, R.J. 1968. Sticky spheres for estimating apple maggot adult abundance. J. Econ. Entomol. 61(4): 1082-85.

Prokopy, R.J. 1972. Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. Environ. Entomol. 1:326-32.

Prokopy, R.J. 1981. Epideictic pheromones that influence spacing patterns of phytophagous insects. P. 181-212 In Nordlund, D.A., Jones, R.L. and W. Joe Lewis eds. Semiochemicals: Their Role in Pest Control.

Prokopy, R.J., W.H. Reissig and V. Moericke. 1976. Marking pheromones deterring repeated oviposition in Rhagoletis flies. Ent. Exp. Appl. 20: 170-78.

Rabb, R.L. 1985. Conceptual bases to develop and use information on the movement and dispersal of biotic agents in agriculture. Pp. 5-34 In Makenzie, D.R. et al. eds. The Movement and Dispersal of Agriculturally Important Biotic Agents. Claitor's Baton Rouge, LA.

Reissig, W.H. & J.P. Tette. 1979. Apple maggot (Diptera: Tephritidae) monitoring in an apple pest management program. Can. Entomol. 111: 621-25.

Reissig, W.H. 1975a. Performance of apple maggot traps in various apple tree canopy positions. Ibid. 68: 534-8.

Reissig, W.H. 1975b. Evaluation of traps for apple maggot in unsprayed and commercial orchards. J. Econ. Entomol. 68:445-8.

Roitberg, B.D. & R.J. Prokopy. 1982. Influence of intertree distance on foraging behavior of Rhagoletis pomonella in the field. Ecol. Entomol. 7:437-42.

Roitberg, B.D., J.C. Van Lenteren, J.J.M. Van Alphen, F. Galis, & R.J. Prokopy. 1982. Foraging behavior of Rhagoletis pomonella, a parasite of hawthorn (Crataegus viridis), in nature. J. Anim. Ecol. 51: 307-25.

Roitberg, B.D., R.S. Caire & R.J. Prokopy. 1984. Oviposition deterring pheromone influences dispersal distance in tephritid fruit flies. Ent. Exp. Appl. 35: 217-220.

Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. Biol. Rev. 37: 171-214.

Stanley, B.H., W.H. Reissig, W.L. Roelofs, M. R. Schwarz, & C.A. Shoemaker. 1987. Timing treatments for apple maggot (Diptera: Tephritidae) control using sticky sphere traps baited with synthetic apple volatiles. J. Econ. Entomol. 80(5) 1057-63.

Stinner, R.E., C.S. Barfield, J.L. Stimac & L. Dohse. 1983. Dispersal and movement of insect pests. Ann. Rev. Entomol. 28: 319-35.

Taylor, L.R. & R.A.J. Taylor. 1977. Aggregation, migration and population mechanics. Nature 265: 415-23.

Taylor, L.R. 1961. Aggregation, variance and the mean. Nature, Lond. 189: 732-35.

Trottier, R., I. Rivard, & W.T.A. Neilson. 1975. Bait traps for monitoring apple maggot activity and their use for timing control sprays. J. Econ. Entomol. 68(2): 211-13.

Whalon, M.E. & B.A. Croft, 1981. Dispersal of apple pests and natural enemies in Michigan. M.S.U. Ag. Exp. St. Res. Rep. 467, 23 pp.

Whalon, M.E. & B.A. Croft. 1987. Managing arthropod immigration and colonization: a community ecology approach. Pp. 511-26 In Makenzie, D.R. et al. eds. The Movement and Dispersal of Agriculturally Important Biotic Agents. Claitor's Baton Rouge, LA.

Whitfield, G.H. 1981. Spatial and temporal population analysis of the onion maggot (Hylemya antiqua (Meigen)), in Michigan. Ph.D. dissertation, Michigan State University.